A giant limulid trackway (*Kouphichnium lithographicum*) from the lithographic limestones of Cerin (Late Kimmeridgian, France): ethological and environmental implications

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Abstract A well-preserved large limulid trackway related to *Kouphichnium lithographicum* is described from the Upper Kimmeridgian Lithographic Limestones of Cerin (Ain, France). It is three meters long and exhibits ten successive sets of imprints characterized by a pair of well-preserved tetradactyl external imprints of legs VI (named pushers) and a variable number (mostly three pairs) of straight thin intermediate imprints (legs III–V). The trackway is unusually wide and was probably made by a very large adult approximately 38 cm wide and 80 cm long when related to the proportions of the modern *Limulus polyphemus*. The straightness of the trackway, the great repeat distance (stride), the length of series of leg imprints, their slight angle to the mid-line, the well-marked pusher (= leg VI) imprints and the absence of groove made by the telson all indicate fast progression of a vigorous animal on the sea-floor. This walking trackway can be easily differentiated from other limulid crawling, ploughing, and dying trackways usually found in lithographic limestones or other deposits of the geological record. Main characteristics of these different limulid trackways are evidenced. The occurrence of a living adult in the Cerin restricted lagoon is probably related to a brief period of connection with the open sea. This occurrence indicates either a passive introduction of the animal into the lagoon or a spawning behaviour.

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Introduction

Limulids (class: Merostomata; subclass: Xiphosura), commonly called "horseshoe crabs", are very distinctive and interesting arthropods. Merostomata are known from the Early Cambrian, and fossil limulids which are very similar to their modern relatives (suborder Limulina, Richter and Richter 1929) are known from the Devonian, perhaps Ordovician (Rudkin et al. 2008), and they show a maximum diversity during Triassic time (Moore et al. 2007). For these reasons, horseshoe crabs are classically considered as "living fossils" (Barthel 1974; Fischer 1984) and benefit from the special attention of palaeontologists. Living animals are well known and correspond to a North American species (*Limulus polyphemus*) and three Indo-pacific species (*Carcinoscorpius rotundicaudata, Tachypleus gigas* and *Tachypleus tridentatus*). A great amount of biological and ecological data is available, mainly for *Limulus polyphemus* (Eldredge 1970; Vosatka 1970; Rudloe 1981; Shuster and 1982; Botton 1984; Botton and Ropes 1987; Sekiguri 1988; Brockmann 1990; Shuster et al. 2003; Martin and Rindsberg 2007). Because of the special status of these animals, new data from the fossil record are of considerable paleontological and paleoecological interest.

Limulid trackways yield very informative data but they were first misinterpreted and attributed to diverse vertebrates such as dinosaurs, pterosaurs or primitive birds (Walther 1904; Jaekel 1929; Abel 1935; Caster 1938, 1939; Malz 1964). The name of the ichnospecies *Ornichnites*

caudatus proposed by Jaekel (1929), which is a clear synonym of *Kouphichnium lithographicum*, illustrates this misinterpretation. Today, these traces are well known, are mainly related to the ichnogenus *Kouphichnium* and lead to interesting behavioural conclusions. They are mainly known from Upper Palaeozoic (Willard 1935; Hardy 1970; Miller 1982; Chisholm 1983; Eagar et al. 1985; Conti et al. 199I), Triassic (Caster 1939, 1944; Linck 1943; Nielsen 1949; Wang 1993), and Jurassic (Oppel 1862; Caster 1940; Kolb 1963; Barthel 1974; Groiss 1975; Romano and Whyte 1987; Barthel et al. 1990; Schweigert 1998; Viohl 1998; Schweigert and Dietl 2002; Harris and Lacovara 2004) rocks. However, an impressive Oligocene trackway was also reported from Japan (Oishi et al. 1993; Lockley and Matsukawa 2009). Among the best traces are the trackways from the Upper Jurassic Lagerstätte of Solnhofen (Bavaria, Germany). Some of them are very famous because they include the dying animal at their end and are thus classified as mortichnia (Barthel 1978; Seilacher 2007). Traces illustrating the normal locomotion of living animals provide more information about the behaviour of limulids (Caster 1944; Goldring and Seilacher 1971). Such traces are often reported but generally without precise description. The Upper Jurassic lagerstätte of Cerin (lithographic limestones, Late Kimmeridgian) has yielded a remarkable limulid trackway whose detailed description is justified because of both an excellent preservation and a very large size. The trackway is exceptionally long and documents a relatively long period of locomotion. It is also very wide and implies a giant trackmaker.

Materials and methods

The Cerin Lagerstätte is situated 80 km East of Lyon in the Southern Jura Mountains (Fig. 1). A scientific excavation was organized in an abandoned quarry (Bernier et al. 1991a) where the lithographic limestone had been quarried during the nineteenth century (Bourseau et al. 1984). A bed-by-bed study including the systematic investigation of upper bedding surfaces measuring 70–150 m^2 was carried out. Many new observations have been published concerning trace fossils (Bernier et al. 1982, 1984; Gaillard et al. 1994b, 2003), algae (Bernier et al. 1991a, b), jellyfish (Gaillard et al. 2006), ammonites (Enay et al. 1994), asteroids (Breton et al. 1994), ophiuroids (Bourseau et al. 1991), echinoids (Bourseau et al. 1994), fish (Wenz et al. 1994), and pterosaurs (Buffetaut et al. 1990). Two specimens of limulids were also discovered (Gall et al. 1996) but limulid trackways had never been recorded before this study.

The Cerin Lithographic Limestone Formation was formed during the Late Kimmeridgian/Early Tithonian
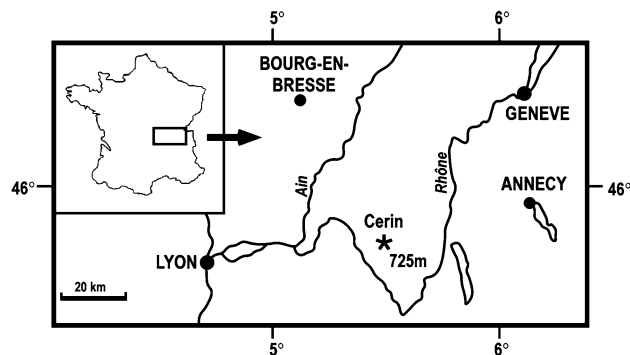

Fig. 1 Location of the Cerin Lagerstätte (Ain, France; 45° 46′ 44″ N–5° 33′ 15″ E)

(Enay et al. 1994). It consists of laminites at the base including rare flints overlain by the Lithographic Limestone sensu stricto where laminites alternate with thicker beds. Schematically, the thickness of micritic beds gradually increases from a few millimetres at the base to 5–25 cm at the top of the sequence. The rock is a typical lithographic limestone composed of a very pure, fine micrite (Bernier 1994). The grain size is generally 2–4 μm. Like the Solnhofen Lithographic Limestone, the Cerin Lithographic Limestone may be considered as an obrutionary stagnation deposit (Seilacher et al. 1985). Sedimentary structures and trace fossils indicate frequent emersions (Bernier et al. 1982, 1991c; Gaillard et al. 1994; Gall et al. 1985). The precise palaeoenvironment corresponds to the margin of a shallow tropical lagoon located on an extinct coral reef complex (Bernier 1984; Bernier et al. 1994; Gaillard et al. 1994). This dead coral reef complex belonged to a wide shallow carbonate platform bordering the deep Tethys Ocean (Fig. 2).

The giant limulid trackway was found in the lower Lithographic Limestones. It was uncovered at the end of the scientific work at the extreme base of the studied section where it is preserved on the top surface of an unnumbered bed. Successive parts of the trackway and all individual tracks were photographed. A silicone cast of the whole trackway was made in situ in order to obtain a resin replica for laboratory studies. Then, the bed bearing the trackway was collected. The original trackway and its resin replica are housed in the Collections de Géologie de l'Université de Lyon (original = n° FSL 504919 a, resin replica = n° FSL 504919 b). Measurements of the whole trackway were made, using, after modification, the methodologies proposed for locomotion traces of arthropods (Trewin 1994; Braddy 2001) and vertebrate tetrapods (Haubold 1971; Leonardi 1987).

The limulid trackway was situated at the top of a thin, 1.25 mm thick limestone bed. It clearly corresponds to an epichnion, more precisely to an epichnial groove (Martinsson 1970). Goldring and Seilacher (1971) consider
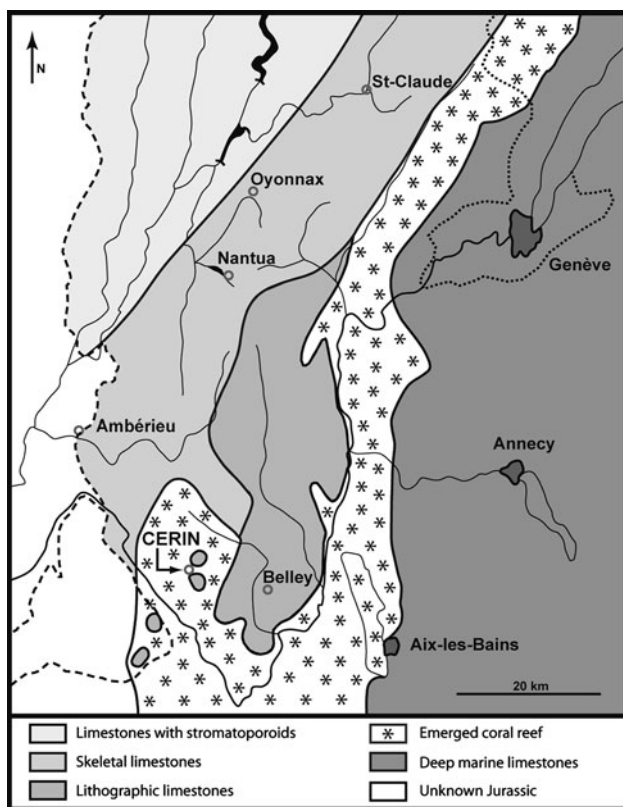
Fig. 2 Palaeogeography of the Southern Jura area during the Late Kimmeridgian (modified after Bernier 1984). The Cerin Lagerstätte corresponds to a small, isolated, marginal marine lagoon

that limulid trackways are commonly made of undertracks. The presence of undertracks is not so easy to prove as noted by Romano and Whyte (2003) and no evidence of such tracks has been found when studying the trackway. Moreover, the presence of surface tracks is likely in the studied case because the calcareous mud of the Cerin lagoon was commonly covered by a microbial mat providing a cohesive substrate. The occurrence of microbial mats is clearly proven for the Cerin Lagerstätte and they have a very important influence on taphonomy (Gall et al. 1985; Gaillard et al. 2006). The occurrence of microbial mats at the top of the bed containing the studied trackways is possible but, however, not really proven.

Taxonomic considerations

The systematic ichnology of limulid tracks is not straight forward, because diverse behaviours are commonly documented by traces which exhibit a wide morphological diversity. For example, these behaviours may form resting traces (Miller 1982), successions of resting traces (Hardy 1970; Eagar et al. 1985), slight burrowing activity (Romano and Whyte 1987; Wang 1993), regular locomotion (Oppel

1862; Nopsca 1923; Nielsen 1949; Kolb 1963; Frickhinger 1994; Schweigert 1998; Harris and Lacovara 2004) or slow dying locomotion (Malz 1964; Groiss 1975; Barthel 1978; Barthel et al. 1990; Frickhinger 1994). The preservation of these traces is often poor and, frequently, only more or less hazy trackways occur (Packard 1900; Bandel 1967; Chisholm 1983; Conti et al. 1991; Buatois et al. 1998; Harris and Lacovara 2004). As a consequence a considerable confusion surrounds the taxonomy of limulid traces and several ichnogenera have been proposed: *Kouphichnium* Nopsca 1923; *Micrichnus* Abel 1926; *Artiodactylus* Abel 1926, *Hypornithes* Jaekel 1929; *Ornichnites* Jaekel 1929; *Protornis* Jaekel 1929; *Paramphibius* Willard 1935; *Limuludichnulus* Linck 1943; *Limuludichnus* Linck 1949, *Limulicubichnus* Miller 1982; *Selenichnus* Romano and Whyte 1987; *Selenichnites* Romano and Whyte 1990. Most of the older ichnogenera are now considered as synonyms of *Kouphichnium* (Häntzschel 1975) which is actually the most widely used ichnotaxon covering a large morphological variability.

Ichnogenus *Kouphichnium* Nopsca 1923

Type ichnospecies Kouphichnium lithographicum (Oppel 1862)

In spite of some differences, the trackway described in this paper is rather similar to the type specimen illustrated by Oppel (1862) and can be related to the ichnogenus *Kouphichnium.* This ichnotaxon is relatively complex and its characterization is not easy because, as noted by Häntzschel (1975), it is a "heteropodous track of great variability". It corresponds to a complete or incomplete assemblage of very different traces made by different appendages which include two types of walking legs and a sword-like telson.

The ichnogenus *Kouphichnium* was introduced by Nopsca (1923) for very regular locomotion traces previously described by Oppel (1862) under the name "*Ichnites lithographicus*". The type species was discovered in the Upper Jurassic Solnhofen Lithographic Limestones (Bavaria, Germany) and was cited under different names such as "*Ichnites lithographica*" or "*Ichnium lithographicum*" (see Walther 1904). The ichnogenus *Kouphichnium* was later used for a wide range of traces made by limulids. For example, Hardy (1970) used the name *Kouphichnium rossendalensis* to describe very different trackways composed of a succession of resting traces. To clarify this problem, Romano and Whyte (1987, 1990) introduced the ichnogenus *Selenichnites* for traces characterized by a lunate part resulting from burrowing activity. *Limulicubichnus* is a true limulid resting trace (Miller 1982). All other above-cited ichnogenera may be considered as junior

synonyms of *Kouphichnium* or they are invalid as in the case of *Selenichnus* (Romano and Whyte 1990).

Ichnospecies Kouphichnium lithographicum (Oppel 1862)

This ichnospecies was first proposed for simple straight locomotion traces found in the Solnhofen area. The type ichnospecies described by Oppel (1862) exhibits a median groove and repeated series of imprints including, on each side, a complex trifid imprint and only one simple imprint. Then, the famous traces with the dead limulid *Mesolimulus walchi* (Desmarest 1822) at the end have been described from the same Upper Jurassic deposits. These mortichnia have been consequently named *Kouphichnium walchi* by Malz (1964). This usage has some followers: for example, Groiss (1975) described a trackway referred to *Kouphichnium* (*Mesolimulus*) *walchi*. This ichnospecies is a curved complex trackway characterized by frequent disrupted imprints of the telson. Numerous trackways with intermediate characteristics have been discovered in the lithographic limestones from the Solnhofen area showing that the use of two distinct ichnotaxa is probably not a good choice. The limulid trackway from the lithographic limestones of Cerin is assigned to *Kouphichnium lithographicum* because it clearly corresponds to a simple straight locomotion trace.

Kouphichnium variabilis (Linck 1949) is a complex, variably defined ichnospecies (Romano and Whyte 2003) and *Kouphichnium rossendalensis* Hardy 1970 is a succession of resting traces now related to the ichnogenus *Selenichnites* (Romano and Whyte 1987, 1990). Other ichnospecies such as *K. didactylus* (Willard 1935), *K. arizonae* Caster 1944, *K. gracilis* (Linck 1949), and *K. cordiformis* Fischer 1978 are also quite different.

Trackway description

Kouphichnium is characterized by strongly heteropodous tracks because limulids have six pairs of appendages including a pair of chelicers and five heterogeneous pairs of legs (Størmer 1955; Malz 1964; Fig. 3). The pair of chelicers (I) is the smallest and is used only for ingestion whereas the next five pairs (II–VI) are mainly used for locomotion. Like chelicers, legs are chelate (II–V) except for the last pair (VI). The first pair (II) is smaller and corresponds to pedipalps. The next three pairs (III–V) are true walking legs. The last pair (VI) corresponds to complex legs which are used for locomotion as active "pushers" but also for digging. These hind-legs which are typical of horseshoe crabs have additional segments forming a fan-shaped structure. Limulids are also characterized by a two-part body consisting of a prosoma (head part) and an opisthosoma (abdominal part) ending in a long
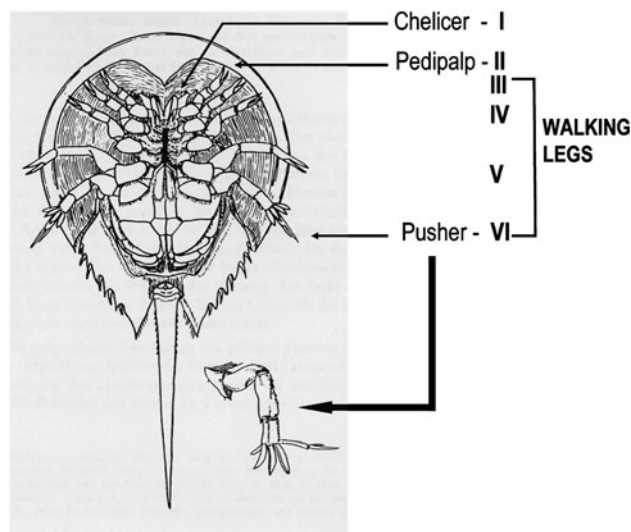

Fig. 3 Ventral view of a living limulid showing the different appendages (after Malz 1964). The leg VI, named "pusher" is detailed in another position

telson. Prosoma and telson are also potential trace-making organs.

The morphology of a complete or ideal trackway is now well established based on fossil and recent observations (Caster 1944). It is composed of two main lateral imprints (legs VI = "pushers"), eight small intermediate imprints (legs II–V), and one axial median imprint (telson). This pattern differs from the holotype drawn by Oppel (1862) which shows two main lateral imprints, only two small intermediate imprints, and one axial median imprint. *Kouphichnium* observed in the Upper Jurassic Lithographic Limestones of Cerin is an intermediate form between the two.

The studied trackway exhibits only tracks without any telson and prosoma imprints. It is a symmetric trackway exhibiting ten sets of imprints (Fig. 4). Each set shows a pair of well preserved main imprints and a variable number (mostly three pairs) of discrete intermediate imprints. The whole trackway is straight and three meters long. Several parameters have been measured (Figs. 5, 6). The internal width is 178 mm and the external width is 258 mm (Table 1). The mean stride or repeat distance is 314 mm (Table 2). The average series length is 343 mm (Table 3) and the mean set overlap is 6 mm (Table 4). The spacing of intermediate imprints is 89.5 mm (Table 5). The angle of intermediate imprints to the mid-line is 14° (Table 6).

Main imprints or "pusher imprints"

These are the largest and the most external imprints of the trackway. In a set, two main imprints are symmetrically opposed and clearly correspond to the pushers (leg VI).

Fig. 4 Schematic drawing of the whole trackway with numbering of sets. The detailed photographic part shows some imprints of the series numbered L3 and L4 on the left side of the trackway
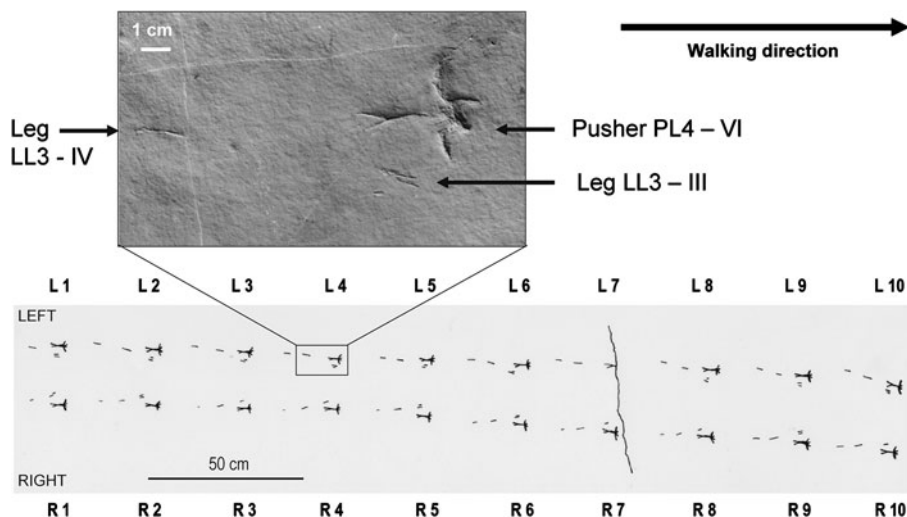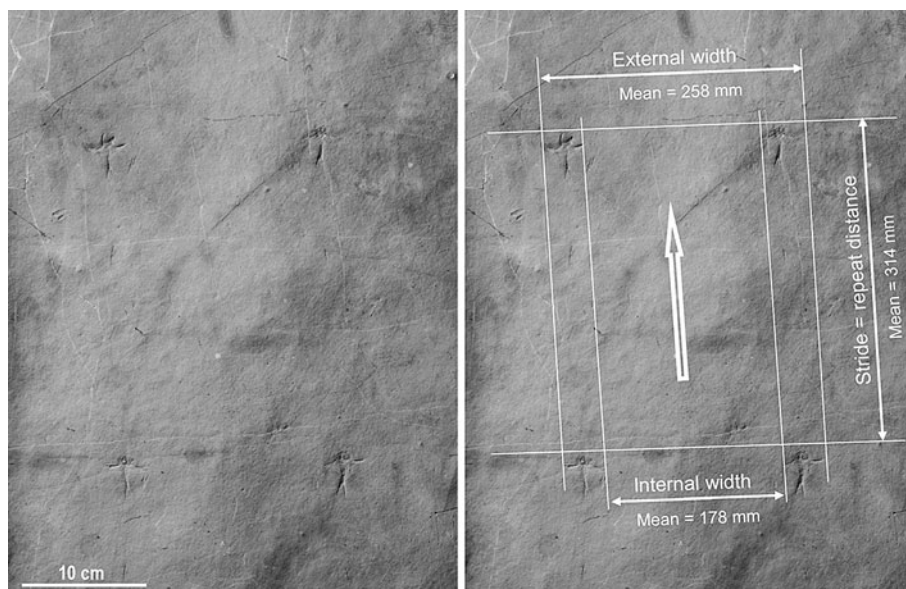
Fig. 5 Section of the trackway showing four pusher imprints and specifying the measurement of external width, internal width, and stride. Pusher imprints come from sets 3 and 4

These imprints exhibit a tetradactyl or 'quadrifid' wide anterior part and a didactyl or 'bifid' posterior part (Fig. 7). The four digit-like protuberances point forward and clearly correspond to the four blade-like appendices which characterize the anterior fan-structure of the hind-leg. The external digit is the longest. The posterior part is a thin elongate mark ending in a bifid tail. It corresponds to the longest and narrowest bifid segment which characterizes the extremity of the hind-leg. Three parameters have been measured (Fig. 8, Table 7). The mean width is 40.2 mm (37–44 mm) and the mean length is 45.8 mm (40–50 mm). The mean angle between the two parts of the bifid tail is 30.4° (28°–42°).

The tetradactyl or quadrifid aspect of the anterior part is quite original. The initial drawing of Oppel (1862) for *Kouphichnium lithographicum* only shows three digits. The drawing of Caster (1944) shows also a trifid part but with only one "digit" pointing forward. But some other prints are rather similar with four "digits" pointing forward, for example those illustrated by Schweigert (1998, Taf. 10, p. 47 and the very schematic drawing of Fig. 5, p. 18), the specimen illustrated by Kolb (1963), some specimens described as a "digitate track with four acuminate rays" by Nielsen (1949), pusher traces of the trackway described by Oishi et al. (1993), and even some specimens illustrated by Harris and Lacovara (2004, Fig. 5). The quite similar pusher imprint is shown by *Kouphichnium lithographicum* from the Upper Jurassic Nusplinger Plattenkalk (Schweigert and Dietl 2002). Imprints from Cerin never show five digits as seen in some Devonian limulid imprints reported as *Paramphibius*.
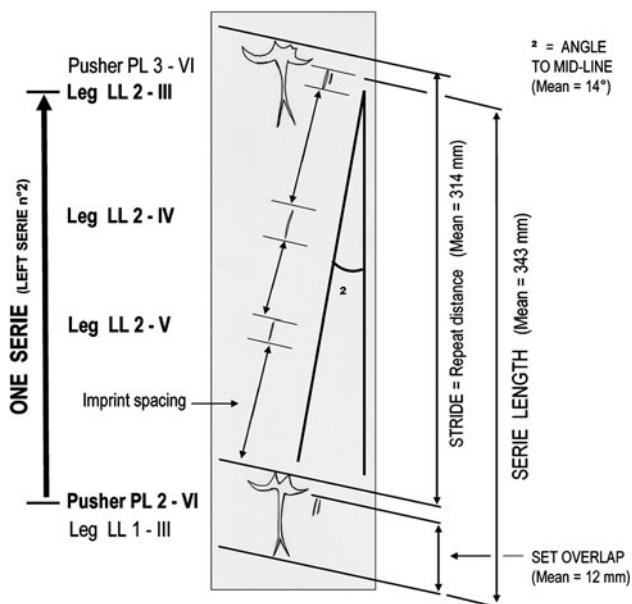
Fig. 6 Schematic drawing specifying the numbering of prints and the measurement of imprint spacing, serie length, stride, set overlap and angle to mid-line

Table 1 Measurements of internal width and external width of the trackway

	Internal width (mm)	External width (mm)
R1–L1	175	257
R2–L2	176	260
R3–L3	178	258
R4–L4	182	260
R5–L5	179	258
R6–L6	177	260
R7–L7	?	258
R8–L8	178	257
R9–L9	180	259
R10–L10	179	260
Mean	178.2	258.7

? data non available

Intermediate imprints or "simple tracks"

Three pairs of small intermediate imprints are visible in a set. They are elongate imprints appearing as single (IV, V) or eventually double scratch marks (III). The mean length of these imprints is 11.7 mm (Table 8). They are straight and very slightly oblique (mean angle to mid-line: 14°). These elongate imprints differ strongly from the circular or ellipsoidal imprints drawn by Oppel (1862) for *Kouphichnium lithographicum* and by Caster (1944). Double scratches underline the chelate nature of walking legs (Fig. 8). V-shaped furrows as observed by Schweigert (1998) are not present. The occurrence of three pairs of

Table 2 Measurements of repeat distances (stride)

Stride–repeat distance (mm)	
Right	
R1–R2	332
R2–R3	318
R3–R4	327
R4–R5	334
R5–R6	314
R6–R7	330
R7–R8	338
R8–R9	322
R9–R10	343
Left	
L1–L2	334
L2–L3	328
L3–L4	322
L4–L5	332
L5–L6	350
L6–L7	330
L7–L8	341
L8–L9	338
L9–L10	314
Mean	314.8

Table 3 Measurements of series length

Series length (mm)	
Right	
SR 1	333
SR 2	333
SR 3	340
SR 4	347
SR 5	330
SR 6	345
SR 7	345
SR 8	344
SR 9	348
Left	
SL 1	347
SL 2	352
SL 3	347
SL 4	352
SL 5	353
SL 6	340
SL 7	348
SL 8	356
SL 9	327
Mean	343.7

Table 4 Measurements of set overlaps

Set overlap (mm)	
Right	
R1–R2	2
R2–R3	20
R3–R4	7
R4–R5	11
R5–R6	16
R6–R7	10
R7–R8	6
R8–R9	20
R9–R10	1
Left	
L1–L2	17
L2–L3	28
L3–L4	23
L4–L5	18
L5–L6	0
L6–L7	5
L7–L8	8
L8–L9	18
L9–L10	8
Mean	12.1

Table 5 Measurements of imprint spacings

Imprint spacing (mm)			
Right		Left	
PR 1-VI–LR 1-V	125	PL 1-VI–LL 1-V	119
LR 1-V–LR 1-IV	59	LL 1-V–LL 1-IV	75
LR 1-IV–LR 1-III	72	LL 1-IV–LL 1-III	79
PR 2-VI–LR 2-V	110	PL 2-VI–LL 2-V	112
LR 2-V–LR 2-IV	72	LL 2-V–LL 2-IV	93
LR 2-IV–LR 2-III	77	LL 2-IV–LL 2-III	74
PR 3-VI–LR 3-V	130	PL 3-VI–LL 3-V	110
LR 3-V–LR 3-IV	58	LL 3-V–LL 3-IV	75
LR 3-IV–LR 3-III	80	LL 3-IV–LL 3-III	78
PR 4-VI–LR 4-V	125	PL 4-VI–LL 4-V	118
LR 4-V–LR 4-IV	79	LL 4-V–LL 4-IV	72
LR 4-IV–LR 4-III	82	LL 4-IV–LL 4-III	82
PR 5-VI–LR 5-V	108	PL 5-VI–LL 5-V	127
LR 5-V–LR 5-IV	72	LL 5-V–LL 5-IV	72
LR 5-IV–LR 5-III	73	LL 5-IV–LL 5-III	79
PR 6-VI–LR 6-V	132	PL 6-VI–LL 6-V	91
LR 6-V–LR 6-IV	62	LL 6-V–LL 6-IV	101
LR 6-IV–LR 6-III	79	LL 6-IV–LL 6-III	70
PR 7-VI–LR 7-V	108	PL 7-VI–LL 7-V	123
LR 7-V–LR 7-IV	68	LL 7-V–LL 7-IV	78
LR 7-IV–LR 7-III	80	LL 7-IV–LL 7-III	90
PR 8-VI–LR 8-V	112	PL 8-VI–LL 8-V	119
LR 8 V–LR 8-IV	74	LL 8-V–LL 8-IV	76
LR 8-IV–LR 8-III	80	LL 8-IV–LL 8-III	82
PR 9-VI–LR 9-V	135	PL 9-VI–LL 9-V	96
LR 9-V–LR 9-IV	57	LL 9-V–LL 9-IV	79
LR 9-IV–LR 9-III	80	LL 9-IV–LL 9III	75
Mean	88.4		90.5

imprints indicates a significant difference from the initial drawing of Oppel (1862) for *Kouphichnium litographicum* where only one pair is present. By contrast, the ideal set of Caster (1944) exhibits four pairs of intermediate imprints. Caster (1944) also noted that the first pair corresponding to pedipalps (legs II) is rarely preserved. The drawing of Abel (1926) for *Kouphichnium lithographicum* also illustrates only three pairs. Therefore, these imprints probably correspond to the walking legs III, IV and V.

Median imprint

The axial imprint, which is present in the type ichnospecies of *Kouphichnium lithographicum,* is completely absent in the studied trackway, indicating that the telson was not in contact with the sediment.

Size of the trackmaker

The size of the trackmaker can be deduced from the external width of the trackway. For this, the model proposed by Malz (1964) for limulids was used (Fig. 9a). It is based on data from Caster (1944), Størmer (1952) and Seilacher (1959) and leads to the following simple 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. Using this formula, the width of the prosoma of the limulid of Cerin is 387 mm. When considering the mean proportions of extant animals, for example *Limulus polyphemus* (Fig. 9b), the total length of the animal corresponds to the width of the prosoma multiplied by 2.12. Using this formula ($L = I \times 2.12$), the length of the trackmaker could be 820 mm. The mean proportions of other extant species (*Carcinoscorpius rotundicaudata, Tachypleus gigas* and *Tachypleus tridentatus*) are very similar with L/l ranging from 2 to 2.2 (Sekiguri 1988). The length of the limulid from Cerin probably ranges from 774 to 851 mm.

The size of the studied limulid is indubitably very important. First, it is larger than all limulids known from the recent. Among living species (*Carcinoscorpius rotundicaudata, Limulus polyphemus, Tachypleus gigas* and *Tachypleus tridentatus*), *T. gigas* is the largest with a carapace width reaching 250 mm (Vijayakumar et al. 2000).

Table 6 Measurements of angles to mid-line

Angle to mid-line (°)	
Right	
R1–R2	15°
R2–R3	15°
R3–R4	12°
R4–R5	14°
R5–R6	12°
R6–R7	14°
R7–R8	13°
R8–R9	15°
R9–R10	15°
Left	
L1–L2	15°
L2–L3	14°
L3–L4	13°
L4–L5	15°
L5–L6	15°
L6–L7	16°
L7–L8	16°
L8–L9	13°
L9–L10	15°
Mean	14.2°

trackways, their external width is never very large. Measurements from the literature are for example 19.6–51.1 mm in Carboniferous deposits (Buatois et al. 1998), 35–75 mm in Triassic deposits (Nielsen 1949), and 170 mm in Middle Jurassic deposits (Romano and Whyte 2003). The width of the similar pusher imprints is only 6.9–12.6 mm (Buatois et al. 1998) and 11–18 mm (Nielsen 1949). Only Late Jurassic limulid traces from France and Germany and the Oligocene example from Japan indicate much larger sizes. Solnhofen mortichnia are relatively narrow, with an external width of about 100 mm (Groiss 1975) but some other locomotion traces are wider. For example, Kolb (1963), Schweigert (1998) and Frickhinger (1994) noted the occurrence of trackways, respectively, 225, 260, and 330 mm wide from Solnhofen and Nusplingen Lithographic Limestones. The pusher imprint schematically drawn by Schweigert (Schweigert 1998, Fig. 5) is probably one of the largest previously described (35 mm width). The average width of the pusher imprints is about 40 mm in the studied trackway from Cerin. Clearly, Late Jurassic limulids from Lithographic Limestones of Germany (Solnhofen, Nusplingen) and France (Cerin) are giant limulids.

Behavioural considerations

The absence of median imprint clearly documents that the telson has not been in contact with the sea floor. The total absence of imprints of the telson and also of the prosoma indicates an underwater trace made by walking on the sea floor. Only locomotion appendages are used. The very well marked imprints of hind legs underline the main role of the "pushers" for locomotion. Its anterior digital aspect indicates a clear support by the fan structure of this specialized leg. The bifid aspect of the prints posterior part also proves the contact to the sea floor of the whole two parts of the opposite longer segment. The print of all these segments indicates that anterior and posterior segments of the pushers are shallower impressed as previously noted by Caster (1944) for some kinds of limulid imprints. By contrast, the intermediate imprints have probably a minor role because they are small and the traces are very discrete.

Their elongate straight shape indicates a light contact with the sea floor and not a true support. The very regular repetition of the imprints probably resulted from normal locomotion. The significant distance between two pairs of pushers imprints (repeat distance) indicates that locomotion was efficient and probably rather rapid. Fast locomotion is also suggested by the very straight line of the trackway. All these aspects could characterize a normal, but fast locomotion by walking on the sea floor. These ichnological deductions are fully consistent with personal
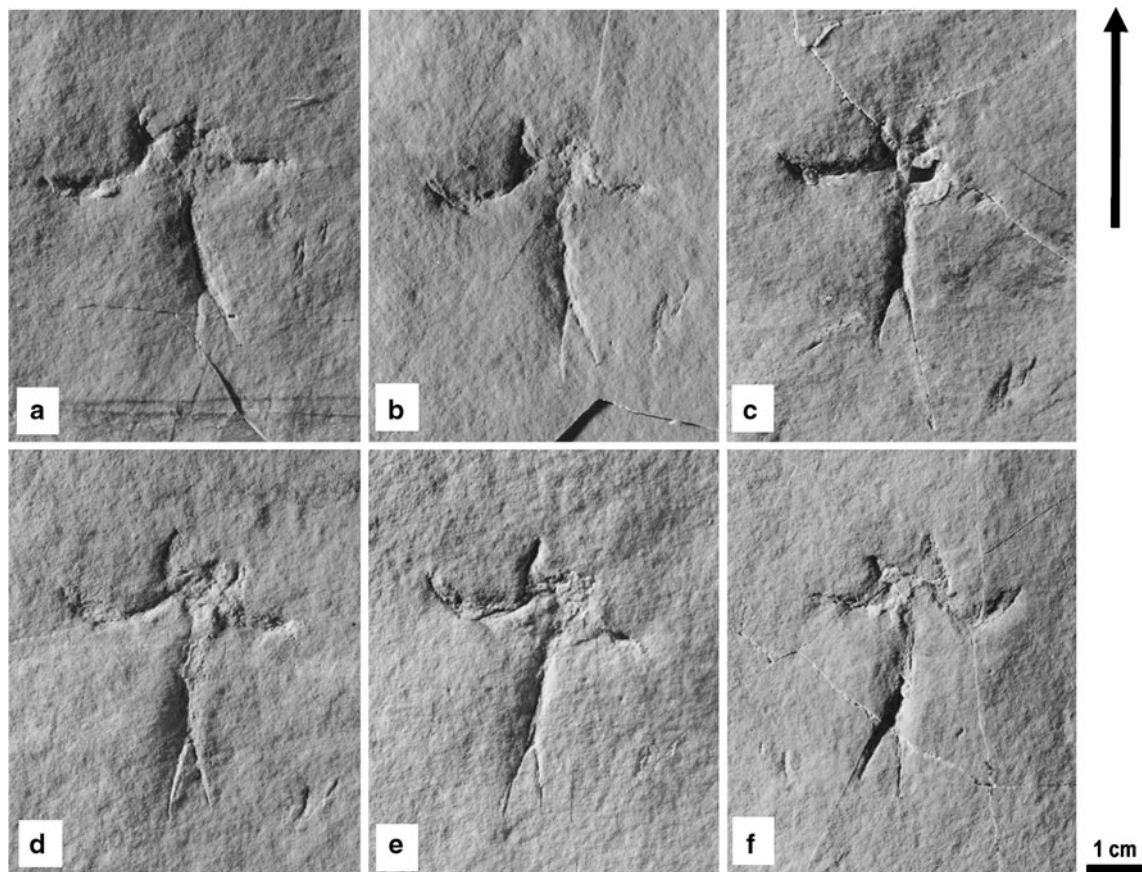
Females are larger than males. For example, concerning *Limulus polyphemus*, the mean prosomal width is 220 mm for females and 166 mm for males (Shuster 1982). Fossil limulids are never very long and the width of the carapace rarely reaches 200 mm. Many fossil limulids are only a few centimetres long (Hardy 1970; Riek and Gill 1971; Pickett 1984; Babcock et al. 2000). *Heterolimulus gadeai* is a large limulid from the Triassic of Spain, but the width of the carapace is smaller than 200 mm (Via Boada and de Villalta 1966). Siveter and Selden (1987) described a giant xiphosurid from the lower Namurian and wrote that it was one of the largest specimens known from the fossil record but the width of the carapace only reaches approximately 150 mm. These authors also stated that only *Tachypleus decheni* (Zincken 1862) from the German Miocene is larger (Böhm 1905). Jurassic limulids from lithographic limestones (*Mesolimulus walchi*) exhibit also a relatively large width of up to 235 mm in the Solnhofen Lagerstätte and ranging from 90 to 160 mm in the Cerin Lagerstätte (Gall et al. 1996). The tertiary trackway described by Oishi et al. (1993) and re-illustrated by Lockley and Matsukawa (2009) averages 246 mm in width.

The size of limulid trace fossils leads to the same conclusions. Limulids resting traces provide direct information about the prosoma width. It is 16 to 17 mm (Hardy 1970), 28 mm (Eagar et al. 1985), up to 110 mm (Miller 1982) for Carboniferous specimens and 70–80 mm for Rhaetian specimens (Wang 1993). When considering the described

Fig. 7 Six pusher imprints showing the four digit anterior part and the long bifid posterior part. **a** PL1; **b** PL2; **c** PL6; **d** PL8; **e** PL9; **f** PR5. The longer digit of the anterior part points out of the trackway. The arrow indicates the walking direction

observations made on a living adult of *Limulus polyphemus* in an aquarium. Swimming corresponds to another fast locomotion of limulids. Indeed, limulids can swim upside-down, using their book gills to propel themselves through the water (Shuster and 1982) but then they probably do not produce traces or quite different ones.

The studied trackway fundamentally differs from the famous mortichnia of Solnhofen. These mortichnia are not straight, but strongly meandering and characterized by a short repeat distance, well marked telson imprints, occasionally prosoma imprints and poorly-preserved leg imprints. Walking legs, and notably pushers, provide poorly preserved imprints because of their probable oblique position relative to the sea floor, and because of the reduced stride. By comparison, it is assumed that the flat 'plantigrade' impression of the pushers, the absence of the contact of the telson with the sea floor and the large repeat distance are the main characteristics of a normal, but fast locomotion. At least, when considering the previously described trackways, four main types of clear limulid traces could be proposed (Fig. 10):

1. Walking trackways: characterized by prints of legs (pushers and other legs) only. The stride is long and the angle to the midline is small. The animal walks relatively fast on the sea-floor. The studied trackway from Cerin, some Jurassic *Kouphichnium lithographicum* from Solnhofen (Schweigert 1998) and the Oligocene trackway from Japan (Oishi et al. 1993) are typical walking trackways.

2. Crawling trackways: characterized by prints of both, legs and telson. The stride is short and the angle to midline is high. The animal crawls slowly grooving the sediment with its telson. Some Jurassic *Kouphichnium lithographicum* from Solnhofen (Kolb 1963) are good examples.

3. Trackways of dying limulids (mortichnia): characterized by prints of legs, telson, and prosoma. The prints of legs are close scratches and the prosoma is slightly marked. The print of the telson is well marked. The trackway is sinuous and ends with the whole limulid imprint. This type of crawling characterizes the slow last locomotion trace made by a dying animal. The
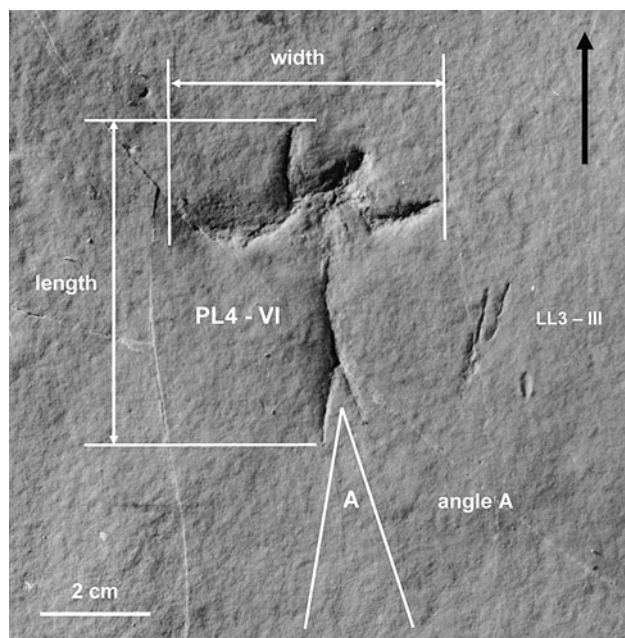
Fig. 8 Morphology of a pusher imprint and measurement of length, width and angle formed by the bifid posterior part. The picture shows the pusher imprint PL4-VI and the double scratched leg imprint LL3-III. The arrow indicates the walking direction

Limulicubichnus rossendalensis (Hardy 1970) and the Jurassic *Selenichnites hundalensis* (Romano and Whyte 1987, 1990) provide good fossil examples.

Parameters usually visible in limulid trackways and supporting this classification are listed and characterized in Table 9. Trackways considered in this classification certainly do not illustrate all locomotion activities of limulids. For example, crawling traces of juvenile limulids may have a very different *Nereites*-like morphology (Babcock et al. 2000; Martin and Rindsberg 2007). Of course, limulids also commonly swim without leaving traces on the sea floor (Shuster and 1982; Vosatka 1970).

Environmental considerations

Recent limulids are marine animals living in beach (spawning) to continental shelf (Shuster and 1982; Sekiguri 1988) environments. Many ancient limulids from Paleozoic and Triassic times are considered as freshwater animals because they are commonly found in continental deposits. Indeed, they are known from lacustrine, estuarine, and deltaic environments (Willard 1935; Caster, 1944; Bandel 1967; Hardy 1970; Eagar et al. 1985; Buatois et al. 1998; Babcock et al. 2000). Since the Jurassic, marine occurrences of limulids are commonly reported, and limulids in freshwater settings are still well established during the Cretaceous (Riek and Gill, 1971). These occurrences are related to episodic marine influences on a coastal plain (Romano and Whyte 2003) or tidal flat environments (Harris and Lacovara 2004). It is well established that, like Solnhofen, the Cerin lagoon represents a marginal marine environment. As a consequence, limulids from Cerin like recent

resulting trace is a typical mortichnia. The best example is *Kouphichnium walchi*, a Jurassic trackway from Solnhofen (Barthel 1978; Barthel et al. 1990).

4. Ploughing trackways: mainly characterized by deep prints of the prosoma. Telson traces may be poorly impressed and leg traces indistinct. The traces clearly indicate a superficial ploughing of the sediment. The recent species *Limulus polyphemus* commonly shows this behaviour (Eldredge 1970). The Carboniferous

Table 7 Measurements of length, width and angle A of pushers

Right	Length L (mm)	Width w (mm)	Angle A (°)	Left	Length L (mm)	Width w (mm)	Angle A (°)
PR 1	46	38	30	PL 1	40	44	33
PR 2	45	42	29	PL 2	46	42	30
PR 3	46	40	30	PL 3	47	40	29
PR 4	45	37	32	PL 4	49	41	30
PR 5	50	38	31	PL 5	49	41	24
PR 6	41	41	31	PL 6	46	42	26
PR 7	46	39	30	PL 7	?	?	28
PR 8	47	39	30	PL 8	48	40	30
PR 9	44	41	32	PL 9	47	38	30
PR 10	44	41	31	PL 10	45	40	42
Mean	45.4	39.6	30.6	Mean	46.3	40.8	30.2

P Pushers

Table 8 Measurements of length of leg imprints with indication of bifid imprints (b)

Right	Length L (mm)	Left	Length L (mm)
LR 1-V	10	LL 1-V	10
LR 1-IV	17	LL 1-IV	14
LR 1-III	12 b	LL 1-III	15 b
LR 2-V	8	LL 2-V	6
LR 2-IV	10	LL 2-IV	13
LR 2-III	18 b	LL 2-III	15 b
LR 3-V	7	LL 3-V	6
LR 3-IV	14	LL 3-IV	20
LR 3-III	11	LL 3-III	17 b
LR 4-V	8	LL 4-V	11
LR 4-IV	11	LL 4-IV	17
LR 4-III	9 b	LL 4-III	14 b
LR 5-V	4	LL 5-V	9
LR 5-IV	16	LL 5-IV	11
LR 5-III	12	LL 5-III	12 b
LR 6-V	10	LL 6-V	6
LR 6-IV	15	LL 6-IV	16
LR 6-III	6 b	LL 6-III	13
LR 7-V	9	LL 7-V	7
LR 7-IV	17	LL 7-IV	6
LR 7-III	11 b	LL 7-III	10 b
LR 8-V	6	LL 8-V	10
LR 8-IV	18	LL 8-IV	20
LR 8-III	14 b	LL 8-III	10 b
LR 9-V	14	LL 9-V	6
LR 9-IV	20	LL 9-IV	14
LR 9-III	14 b	LL 9-III	16 b
Mean	11.8		11.6

L legs, b bifid

limulids are probably true marine animals. Fossil freshwater limulids are generally smaller than marine limulids (Hauschke and Wilde 1991) and this is also consistent with the large size of the limulids from Cerin. Recent limulids show some euryhaline tendencies (Shuster and 1982) and this is also consistent with possible salinity conditions in the marginal marine environment of Cerin.

Most of the fossilized animals of Cerin came from various environments, and were occasionally introduced and gathered in the lagoon where they died after a relatively short time in poisonous water (Barale et al. 1985; Bernier and Gaillard 1990). According to this hypothesis, adult limulids could have been passively introduced into the lagoon. The occurrence of a large adult rapidly walking on the sea floor of the Cerin lagoon and the absence of limulid mortichnia probably illustrates short-term favourable environmental conditions allowing benthic life. This situation could correspond to short periods with a better connection between the open sea and the lagoon. This is a clear difference to the Solnhofen lagoon where juveniles are commonly preserved at the end of their mortichnia indicating that the environment was hostile (Seilacher 2007).

Fossil limulids from Cerin are rare. They were not discovered while the Lithographic Limestones of Cerin were intensively quarried and Van Straelen (1924) noted the total absence of limulids. Only two poorly-preserved specimens of *Mesolimulus walchi* were recently collected during the scientific excavation (Gall et al. 1996). At least, two specimens are known as body fossils and only one as trace fossil (this paper). All have been discovered at the base of the Lithographic Limestones. This clearly confirms the previously supposed history of the Cerin lagoon with early dominant marine influences marked by jellyfish, fish and ammonites and later dominant terrestrial influences marked by autochthonous marginal marine burrows (*Tubularina lithographica*) and allochthonous terrestrial plants (*Zamites*) (Gaillard et al. 2006). Nevertheless, the rare occurrence of limulids suggests the generally very poor connection between the Cerin lagoon and the open sea.

Recent limulids feed mainly on bivalves but also on polychaete worms that they dig out of the sediment (Shuster and 1982; Botton 1984; Botton and Ropes 1989; Botton et al. 2003). Infaunal bivalves are extremely rare in the Lithographic Limestone Unit of Cerin and polychaete worms, which are the probable trace makers of *Tubularina,* occur only in the upper part (Gaillard et al. 1994b), where limulids are absent. Probably, limulids, like many other organisms found in the Lithographic Limestones, did not habitually live in the Cerin lagoon. Recent limulids, such as *L. polyphemus,* spend most of their life in the subtidal zone, except of annual spawning migrations (Botton and Ropes 1987). Females lay their eggs in shallow nests on the beach and some days after hatching, juveniles have a benthic life in the intertidal zone for two years before moving into deeper environments (Rudloe 1981; Shuster and 1982; Sekiguri 1988; Brockmann 1990, 2003). Considering the Cerin environment, the occurrence of living adults in shallow waters and in a typical marginal marine environment could point to a spawning behaviour on the sandy beaches surrounding the lagoon. However, concrete evidence to support this spawning hypothesis is missing. Traces of juvenile limulids, which show similarities with *Nereites* (Martin and Rindsberg, 2007), are absent in the Lithographic Limestones of Cerin. Nevertheless, it is interesting to note that the surrounding area of

Fig. 9 Data used for the estimation of the trackmaker length. **a** Correspondence between the width of the prosoma and the external width of *Kouphichnium*. *I* width of the prosoma; *W* external width of the trackway (after Malz 1964). **b** Proportions of the living *Limulus polyphemus*. *L* total length; *l* width of the prosoma (after Pechenik 2000)
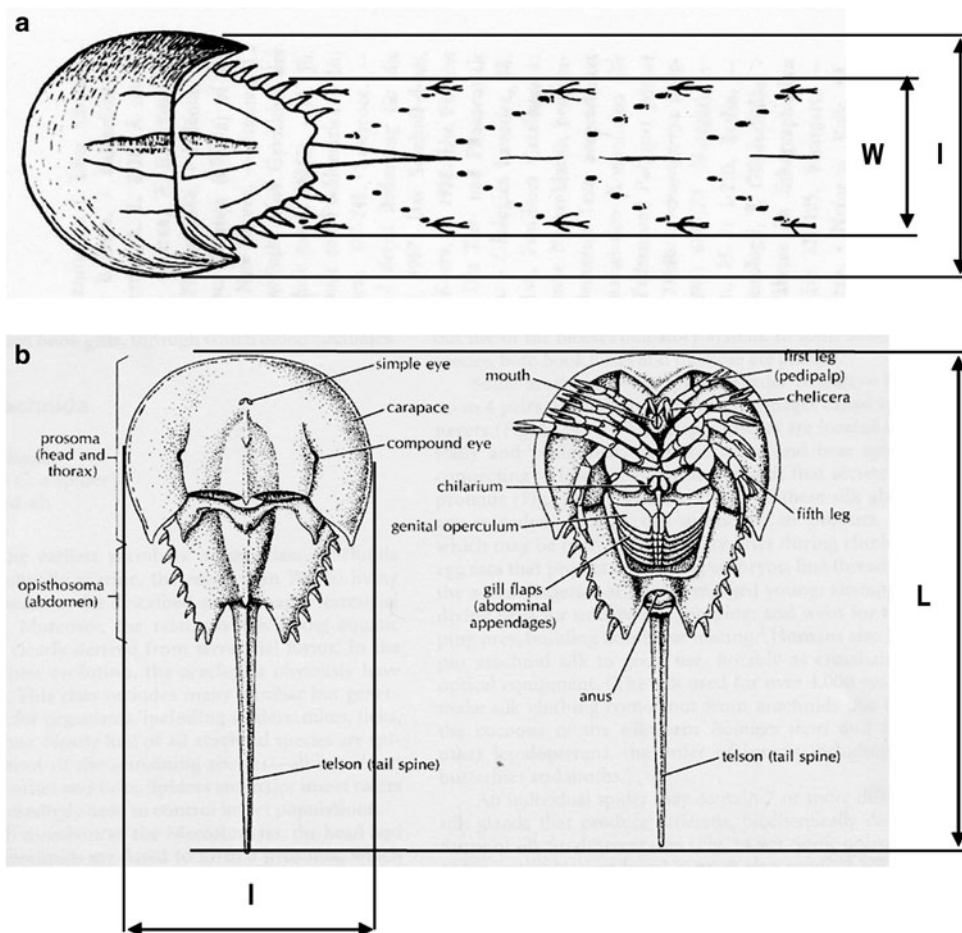
the Cerin lagoon has been considered as a possible nesting area for sea turtles (Gaillard et al. 2003). The co-occurrence of limulids and sea turtles in the surroundings of the lagoon of Cerin is also interesting because limulids were probably a prey of sea turtles. Recent data show that limulids play an important ecological role in the food web of sea turtles. For example loggerhead turtles (*Caretta caretta*) feed extensively on horseshoe crabs (Lutcavage and Musick 1985; Keinath 2003). Following these considerations, limulids and sea-turtles were possibly active animals within the Cerin ecosystem.

Conclusions

The studied trackway was made by a very large marine limulid about 38 cm wide and 80 cm long, when compared to the proportions of the modern *Limulus polyphemus*. Most likely, the trackway indicates a normal but rapid locomotion of the trackmaker on the sea floor.

The main characteristics of the trackway are: straightness; well-marked tetradactyl or quadrigid imprints of external legs (VI) named pushers; discrete and straight intermediate imprints (legs III–V); absence of leg II imprint (pedipalp); low angle of leg traces to the mid-line; absence of median imprint (telson); great repeat distance (stride).

This trackway illustrates walking behaviour quite different from crawling, dying or ploughing activities commonly indicated by other fossil limulid trackways. The main characteristics of these different trackways can easily be differentiated.

The behaviour documented by the studied trackway indicates that normal marine conditions occasionally occurred in the Cerin lagoon, at least during short time intervals. This could indicate the occurrence of short-term connections between the restricted lagoon and the open sea. This trackway associated with two fossil limulids at the base of the Lithographic Limestones Unit of Cerin testifies a decrease of the marine influence in the Cerin lagoon, as previously noted using other sedimentological, paleontological, and palichnological evidence.
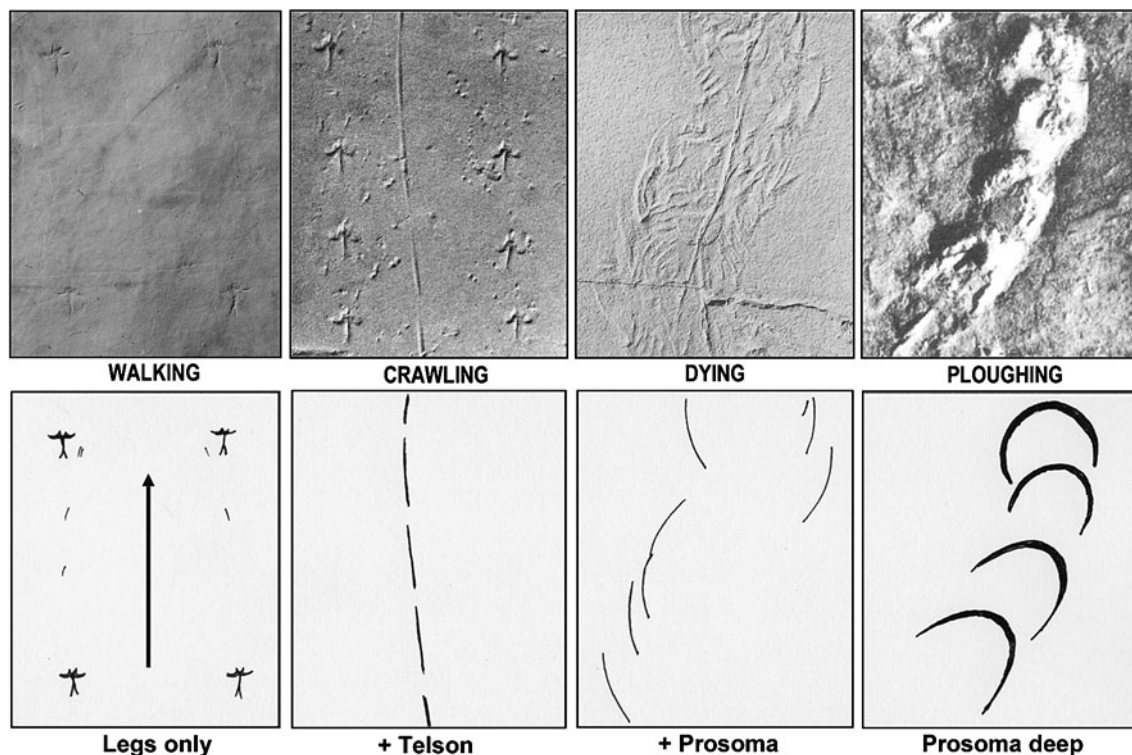
Fig. 10 Different fossil limulid trackways and their relation between morphology and behaviour. Walking: this work; crawling: after Kolb (1963); dying after Barthel et al. (1990); ploughing after Hardy (1970)

Table 9 Characterization of trackways corresponding to the four main locomotion styles of limulids

Behaviour				
Locomotion style	WALKING	CRAWLING	DYING	PLOUGHING
Locomotion rate	High	Medium	Low	Very low
Resulting traces				
Trackway	Straight	Straight	Sinuous	Sinuous
Prosoma imprints	Absent	Absent	Slight	Deep
Telson imprints	Absent	Continuous	Interrupted	Interrupted
Pushers imprints	Well marked	Well marked	Slight	Absent
Walking legs imprints	Short	Short	Long	Absent
Series length	High	Medium	Low	X
Repeat distance	High	Medium	Low	X
Imprint spacing	High	Medium	Low	X
Angle to mid-line	Low	Medium	High	X

The occurrence of adult limulids in a typical marginal marine environment could indicate spawning behaviour, but compelling arguments for this hypothesis are still lacking.

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