

Limuloid trackways from Permian-Triassic continental successions of North China

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ABSTRACT

Forty-four well-preserved specimens of *Kouphichnium*, a typical limuloid (horseshoe crab) trackway, are reported and systematically studied for the first time from continental Upper Permian to Lower Triassic successions in North China. A new ichnotaxonomic system of *Kouphichnium* is proposed according to the ichnotaxobase of limuloid trackways, including simple foot imprints (T), pusher imprints (P), median impressions (M) and genal spine impressions (GS). In total, one ichnogenus and six ichnospecies are recognized, one of which is new: *Kouphichnium liulinensis* sp. nov. Ichnogenus *Paramphibius* is regarded as a synonym of *Kouphichnium* and the diagnoses of ichnogenus *Kouphichnium* and its two early ichnospecies, i.e. type ichnospecies *Kouphichnium lithographicum* Oppel, and *Kouphichnium didactylum* Willard, are revised. A morphological-palaeoethological pattern is proposed in reference to these ichnospecies from the continental Upper Permian to Lower Triassic successions in North China. These six ichnospecies are assigned to six types in the new ichnotaxonomic system and the locomotion rates of each type can be ranked by the possible speed index λ . The size of trackmaker is estimated from the external width of the trackway, and it shows a drastic decrease from the Late Permian to Early Triassic, followed by a gradual increase in the Early Triassic. This size variation of trackmakers (limuloids) during the Permian-Triassic transition, especially the drastic drop, probably reflects the intensive environmental stress during the biotic crisis. In addition, the analysis of the sizes of pusher imprints (P) from certain well-preserved trackways suggests a potential sexual dimorphism of limuloids.

1. Introduction

Limuloids (horseshoe crabs) are well-known as “living fossils” because they are descendants of a bradytelic lineage with little morphological variation from their earliest known occurrence in the Middle Ordovician to modern times (Størmer, 1952; Rudkin et al., 2008; Lamsdell, 2016). Limuloid body fossils are rare, whereas their trace fossils are more commonly reported in geological records (Gaillard, 2011; Chakraborty and Bhattacharya, 2012; Moreau et al., 2014). For a long time, the makers of these trackways were debated. For nearly 80 years, they were interpreted as having been produced by bipedal reptiles, the first bird *Archaeopteryx*, pterodactyls, amphibians, dinosaurs, or even jumping mammals (Oppel, 1862; Figuiet, 1866; Walther, 1904; Jaekel, 1929; Abel, 1935; Willard, 1935). Then, with the development of neoichnology and discoveries of the trackways with fossil limuloid corpses (e.g. the well-known *Kouphichnium walchi* Malz from Solnhofen that ends with its track maker, *Mesolimulus walchi*), more convincing evidence shows that these traces were made by

limuloids (Wilfarth, 1937; Caster, 1938, 1939, 1940, 1941, 1944; Malz, 1964; Lomax and Racay, 2012).

So far, four limuloid ichnogenera have been proposed, which demonstrate different behaviours, including *Kouphichnium Nopcea*, 1923 (re-pichnia, comprising all xiphosuran trackways, or mortichnia, trackways with prosoma marks), *Limulicubichnus* Miller, 1982 (cubichnia, resting traces of limuloids), *Selenichnites Romano and Whyte*, 1987 (domichnia, burrowing activity of limuloids, or fodinichnia, foraging traces), and some of *Crescentichnus Romano and Whyte*, 2015 (domichnia or fodinichnia) (Miller, 1982; Romano and Whyte, 1987, 1990, 2003, 2013, 2015; Romano and Taylor, 2016). Among these four ichnogenera, *Kouphichnium* trackways are the most common. The first specimen of the xiphosuran trackways was reported from the Upper Jurassic Solnhofen Lithographic Limestones (Bavaria, Germany) with the famous *Archaeopteryx* (Oppel, 1862). Ever since, more fossils of *Kouphichnium* have been recognized around the world. In total, nine ichnospecies of *Kouphichnium* have been recognized and described, including *Kouphichnium lithographicum* Oppel, 1862, *K. walchi* Malz,

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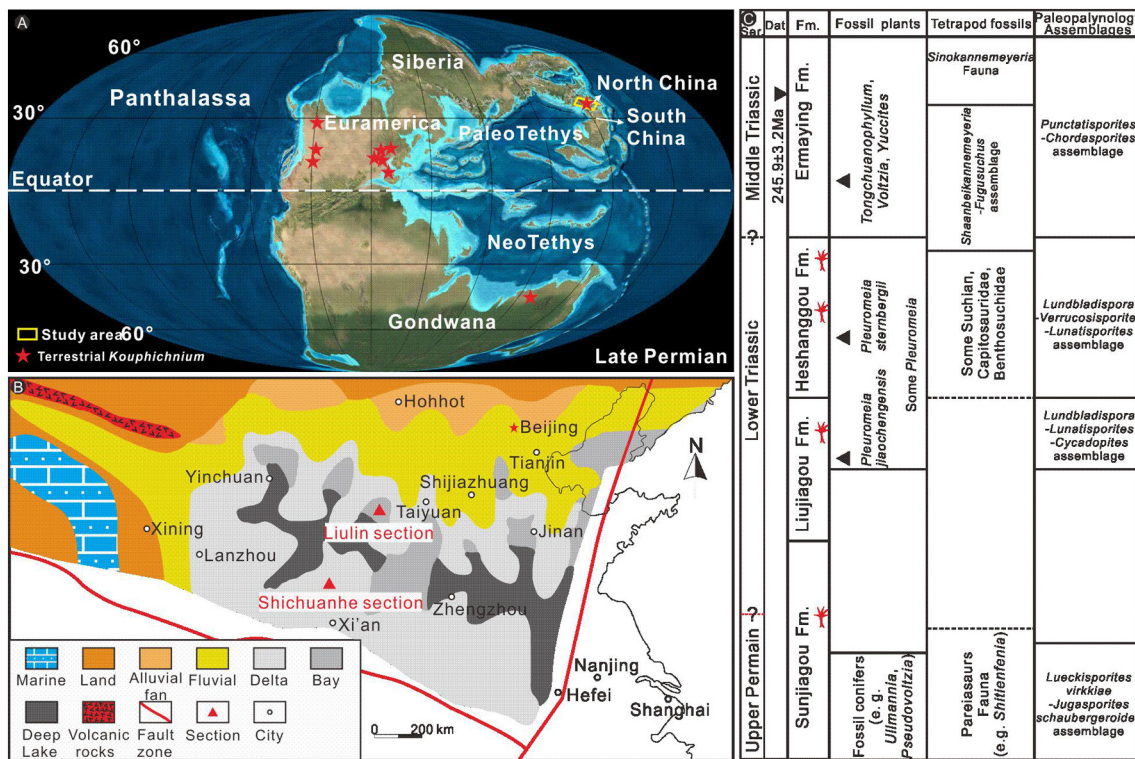


Fig. 1. Palaeogeographic maps and litho- and bio-stratigraphic units related to the studied fossils. A. Global palaeogeography during the Permian-Triassic transition (modified from Blakey, <http://jan.ucc.nau.edu/~rcb7/index.html>), showing the distribution of the Permian-Triassic transition terrestrial *Kouphichnium*, including Utah and Wyoming, USA (Mickelson et al., 2006; Mickelson, 2010; Lerner et al., 2007; Lovelace and Lovelace, 2012), Canada (Beatty et al., 2006; Zonneveld, 2007), Iberian peninsula (Mujal et al., 2018), France (Gall and Grauvogel-Stamm, 1993, 2005), Germany (Goldring and Seilacher, 1971; Pollard, 1981), Netherlands (Demathieu and Oosterink, 1988; Oosterink and Winkelhorst, 2013), Poland (Żyła et al., 2013), Australia (Lamsdell, 2016), and North China (this study); B. Late Permian palaeogeographic map of North China (after Zhu et al., 2007), showing locations of study sections; C. Simplified litho- and biostratigraphic successions in central North China from Late Permian to Middle Triassic, with Horizons 1 to 4 representing the main horizons of *Kouphichnium* ichnofossils.

1964, *K. aspodon* Aldrich, 1930, *K. arizonae* Caster, 1944, *K. variabilis* Linck, 1949, *K. gracilis* Linck, 1949, *K. didactylum* Willard, 1935, *K. fernandezii* Romano and Meléndez, 1985, and *K. pterodactyli* Malz, 1964. However, some of these ichnospecies were proposed based only upon poor-defined characteristics, e.g. a simple straight locomotion trace for *Kouphichnium lithographicum* Oppel, 1862 (Gaillard, 2011), a complex and variable trace for *K. variabilis* Linck, 1949 (Linck, 1949; Romano and Whyte, 2003; Gaillard, 2011), and even just a different number of simple tracks for *Kouphichnium didactylum* Willard, 1935 (Willard, 1935; Caster, 1938). Thus, the taxonomic system for the ichnospecies of *Kouphichnium* needs to be clarified.

As a typical trace of limuloids, *Kouphichnium* proliferated significantly from the latest Permian to the Early Triassic. Diverse occurrences of *Kouphichnium* have been reported from the uppermost Permian to Lower Triassic in various locations (Fig. 1A: North America: Beatty et al., 2006; Mickelson et al., 2006; Mickelson, 2010; Lerner et al., 2007; Zonneveld, 2007; Lovelace and Lovelace, 2012; Thomson et al., 2016; France: Gall and Grauvogel-Stamm, 1993, 2005; Germany: Goldring and Seilacher, 1971; Pollard, 1981; Poland: Żyła et al., 2013; Netherlands: Demathieu and Oosterink, 1988; Oosterink and Winkelhorst, 2013; Iberian peninsula: Mujal et al., 2018; South China: Bi et al., 1995; Australia: Lamsdell, 2016). However, only a few of these accounts recorded the systematic palaeontological diagnosis and additional information on valid stratigraphic correlation (e.g. Goldring and Seilacher, 1971; Pollard, 1981; Bi et al., 1995; Mujal et al., 2018). In particular, systematic palaeontological works at the level of ichnospecies of *Kouphichnium* were scarcely given attention. For example, most studies just reported specimens as *Kouphichnium*, without a specific name or any further details (e.g. Pollard, 1981; Demathieu and Oosterink, 1988; Gall and Grauvogel-Stamm, 1993; Beatty et al., 2006; Mickelson et al., 2006; Mickelson, 2010; Zonneveld, 2007; Lerner et al., 2007; Lovelace and Lovelace, 2012; Żyła et al., 2013; Oosterink and Winkelhorst,

2013). A few studies identified the ichnospecies, but with simple and sometimes unclear descriptions of specimens, such as *Kouphichnium lithographicum* (Bi et al., 1995; Thomson et al., 2016), *K. gracilis* Linck, 1949 (Gall and Grauvogel-Stamm, 2005) and *K. isp.* (Mujal et al., 2018). Thus, the ichnotaxa of *Kouphichnium* from the Upper Permian to Lower Triassic are still poorly understood, and there is a need to establish a constant approach to their systematic diagnoses. In addition, the greatest extinction event in the Phanerozoic, the Permian-Triassic mass extinction (PTME), led to a profound catastrophe for both marine and continental invertebrates (Erwin, 1993; Benton, 2001). The body fossil records suggest that limuloids diversified in the Early Triassic rather than suffering a severe crisis (Rudkin and Young, 2009; Moreau et al., 2014; Lamsdell, 2016), whereas evidence from their traces is still unclear during the PTME and its aftermath (Moreau et al., 2014).

Here, we present a systematic study of *Kouphichnium* from two continental sections in North China. Abundant *Kouphichnium* specimens were collected from the uppermost Permian to Lower Triassic, which provide important evidence for discussing the morphology of *Kouphichnium*, behaviour of the limuloids, locomotion rates and evolution of their sizes.

2. Geological setting

North China traversed low latitudes (about 30°N) in the northeastern part of the Palaeo-Tethys Ocean during the late Palaeozoic and early Mesozoic (Fig. 1A; Wang et al., 1998; Rees, 2002). The sedimentary sequences suggest there was a huge lake, about 1400 km long, in North China during the Triassic time (Fig. 1B; Zhu et al., 2007). The Upper Permian to Middle Triassic sequence is lithostratigraphically subdivided into the Sunjiagou, Liujiagou, Heshanggou and Ermaying formations (Fig. 1C). The Sunjiagou Formation is dominated by red thin- to medium-bedded

mudstone with numerous interbedded calcareous nodules. This stratigraphic unit has been interpreted as a deposit of deltas and lake shores (Zhu et al., 2007). Intermittently, it was influenced by marine flooding, indicated by marine fossil beds in the upper Sunjiagou Formation in the southwestern part of the study region (Yin and Lin, 1979; Chu et al., 2017). The overlying Liujiagou Formation is composed of massive red sandstone with a few interbedded mud-siltstones, occasionally bearing wrinkle structures, which are usually taken as the evidence of microbial mats over the surface (Chu et al., 2015a; Tu et al., 2016). This unit might be deposited in a fluvial or lake-shore environment. The Heshangou Formation consists of red siltstone interbedded with some thin sandstone beds and abundant bedded calcareous nodules. The Heshangou Formation is interpreted as the deposition in a shallow lake (Hu et al., 2009). The Ermaying Formation comprises greyish green, thick-bedded sandstone with greenish and reddish thin-bedded mudstone and was deposited in a fluvial-lacustrine facies.

The age assignments of these formations have long been disputed. Some sporadic evidence from fossil plants, palynology, fossil tetrapods and a few U-Pb dates may indicate rough ages. The occurrence of a fossil conifer macroflora (e.g. *Ullmannia* and *Pseudovoltzia*) and the *Lueckisporites virkkiae*–*Jugasporites schaubergeroides* sporomorph assemblage in the lower part of the Sunjiagou Formation suggests a Late Permian age (Fig. 1C; Li and Wu, 1989; Wang, 1993; Hou and Ouyang, 2000). The fossil plant *Pleuromeia* was collected from the middle part of the Liujiagou Formation and the Heshangou Formation (Wang et al., 1978; Wang, 1993). The *Lundladispora-Verrucosporites-Lunatisporites* sporomorph assemblage from the Heshangou Formation (Qu, 1982; Qu et al., 1983; Ouyang and Norris, 1988) is similar to the *Lundladispora-Lunatisporites-Cycadopites* palynomorph assemblage from the Liujiagou Formation (Qu, 1982; Qu et al., 1983). Thus, the fossil plants and palynoflora indicate that the upper part of the Liujiagou Formation and the Heshangou Formation belong to the Early Triassic in age (Fig. 1C). The *Punctatisporites-Chordasporites* palynofloral assemblage and some fossil plants (e.g. *Tongchuanophyllum*, *Voltzia* and *Yucites*) in the Ermaying Formation and the SHRIMP U-Pb zircon date of 245.9 ± 3.2 Ma suggest the Ermaying Formation of a Middle Triassic age (Qu et al., 1983; Wang and Wang, 1990; Liu et al., 2013). Moreover, several characteristic fossil tetrapods were discovered in the lower to middle part of the Sunjiagou Formation, the Heshangou Formation and the Ermaying Formation, indicating the Late Permian, Early Triassic and Middle Triassic age, respectively (Fig. 1C; Young and Yeh, 1959, 1963; Cheng, 1980; Yang et al., 1982; Lucas, 1993; Sterling et al., 2011; Liu and Li, 2013; Liu, 2015; Benton, 2016). Although the precise position of the Permian-Triassic boundary is unclear, the biostratigraphic evidence listed above places it within the upper Sunjiagou Formation.

The limuloid trace fossils in this study are collected from the reddish argillaceous siltstone in the upper part of the Sunjiagou Formation (Horizon 1), the upper part of the Liujiagou Formation (Horizon 2) and the middle to upper part of the Heshangou Formation (Horizons 3 and 4) (Figs. 2, 3). Thus, the samples are distributed at four horizons from the Upper Permian to the Lower Triassic (Figs. 1C, 2).

3. Materials and methods

All field works were done bed by bed in the Sunjiagou, Liujiagou and Heshangou formations, including stratigraphic studies and sample and fossil collections (Fig. 2). On the basis of a lithological analysis and some reported ichnofacies, the limuloid-living substrate can be identified as a firm ground. All successive parts of trackways and individual tracks were photographed with a Canon EOS 7D digital camera. Forty-four fossil specimens from this study are sampled and stored in the Yifu Museum, China University of Geosciences, Wuhan (CUGMUS).

3.1. Limuloid trackway terminology and measuring proxies

Since there is a great variety in the descriptive terminology of various authors, some terms used in the present study are firstly explained here, and this requires a consideration of the basic limuloid anatomy.

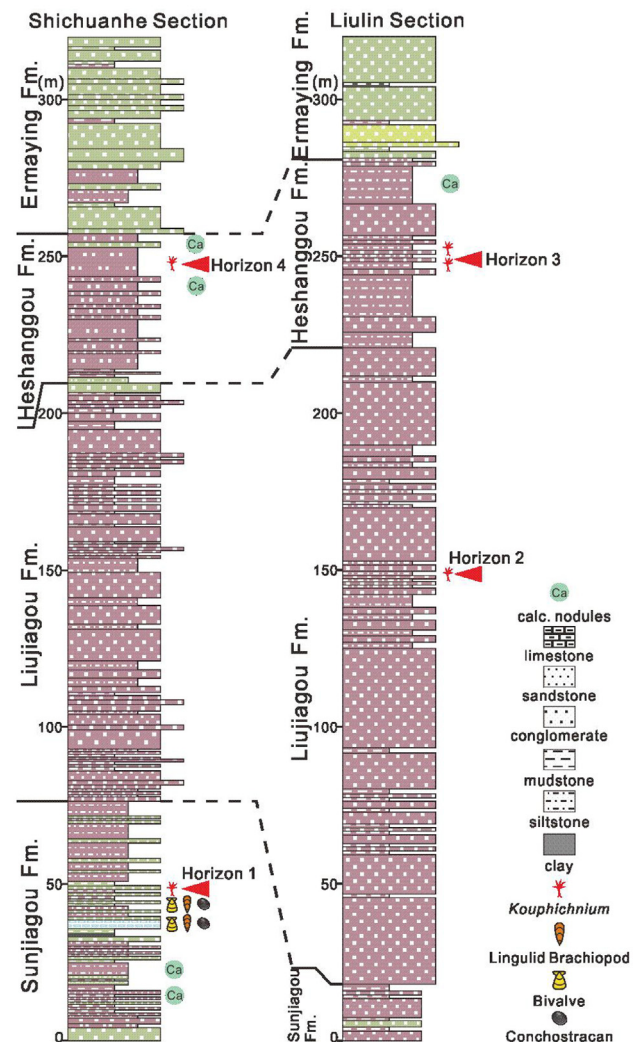


Fig. 2. Lithological columns of the studied sections showing the lithology and the position of the sampled horizons. Abbreviations: Fm., Formation.

A limuloid has six pairs of appendages (Fig. 4A): the first pair is used for feeding rather than for walking, so the true walking legs are the remaining five pairs of appendages (Caster, 1938, 1944; Minter et al., 2007). However, the sixth pair of appendages or the fifth pair of walking legs, commonly called “pushers” (Fig. 4A), possess patent and complex structures, which are modified by 4–5 movable fan-like blades at the termination of the antepenultimate segment, and these have the function of pushing while swimming, or digging (Caster, 1944; Gaillard, 2011).

The terminology for limuloid trackways is defined as follows (Fig. 4B): Marks (imprints if they are discrete or impressions if continuous) are caused by certain aspects of the potential producer's anatomy (e.g. tail or carapace). A simple foot imprint (T) is a mark comprising a discrete V/Y-shaped or nail-like anterior part and dot-like bulge posterior part, or just round imprints, which may be produced by a single locomotor appendage (usually one of the 2nd–5th pairs of appendages), while a pusher imprint (P) is exclusive to the potential producer (limuloids), with radiating blade imprints (trifid, quadrifid or quinquefid) or anterior radiating blade part and dot-like bulge, “one-digitate” or inverted “Y” posterior part, which may be produced by the sixth pair of appendages. A genal spine impression (GS) is a lateral continuous or intermittent and curved or straight mark, which may be made by the genal spine or the lateral side of the prosoma but here named as genal spine. A limuloid trackway is a repeated pattern of simple foot imprints (T), pusher imprints (P), median imprints or

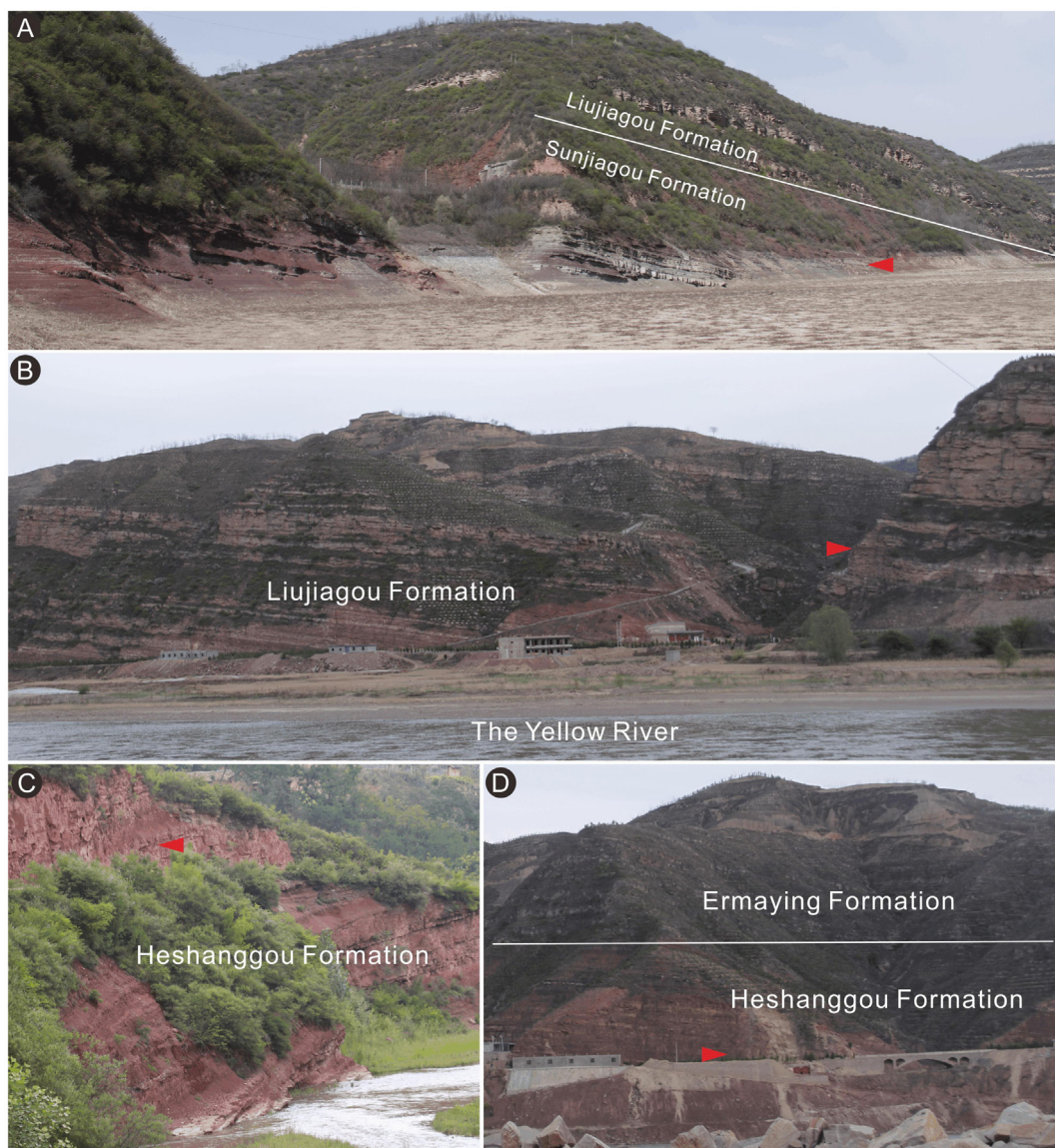


Fig. 3. Field photographs of the studied sections. A. Field photograph showing the boundary between the Sunjiagou and Liujiagou formations in the Shichuanhe section. The Permian-Triassic boundary is supposed to be in the upper part of the Sunjiagou Formation. The red arrow indicates Horizon 1 of limuloid trace fossils; B. Field photograph showing the Liujiagou Formation in the Liulin section along the Yellow River. The red arrow indicates Horizon 2 of limuloid trace fossils; C. Field photograph showing the Heshanggou formation in the Shichuanhe section. The red arrow indicates Horizon 4 of limuloid trace fossils; D. Field photograph showing the boundary between the Heshanggou and Ermaying formations in the Liulin section. The red arrow indicates Horizon 3 of limuloid trace fossils. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

impressions (M), and genal spine impressions (Frey, 1973; Seilacher, 2007). Here, a limuloid trackway does not include imprints attributed to gill flaps, which are here assigned to cubichnia (resting traces of limuloids). A trail is a continuous trace without discrete tracks, which might be produced by dragging the body on the substrate surface. A median imprint or impression (M) is a mid-line mark of the telson, representing the hypothetical axis of the trackway. A series is a discrete group of tracks that occurs on one side of the mid-line, and is equivalent to Anderson's (1975) 'natural tracks cycle' (Minter et al., 2007), which represents the grouping of tracks formed after each walking leg on one side of the body has been placed on the substrate once. However, it is extremely rare that a complete series is preserved, comprised of four simple foot imprints (T) (made by the first to fourth pairs of walking legs) and one pair of pusher imprints (P). The series length is the distance, parallel to the mid-line of the trackway, between the anterior and posterior tracks of a series. The series width is the distance, perpendicular to the mid-line of the trackway, from the outermost side to the

innermost side of a series. If the tracks of a bilateral series are bisymmetric, they should be called opposite (Braddy, 2007). If the tracks of a series are arranged in a relatively straight line, the series angle (i.e. the angle between a line intersecting the tracks and the mid-line) can be measured (Sadler, 1993). A set denotes a pair of series that occur on either side of the mid-line. The series overlap is the overlap length of a pair of series in a set, differing from the set overlap (in Gaillard, 2011 and Alberti et al., 2017), which denotes the overlap length between two adjacent series on the same side of the mid-line. The value of the series overlap ranges from zero to the series length, precisely equal to the series length in Fig. 4B. A stride is the distance, parallel to the mid-line of a trackway, between successive tracks of the same locomotor appendage, and is equivalent to the 'repeat distance' of Trewin (1995). The inter-series distance of Trewin (1995) is the distance between successive tracks in the same series. The external width is the distance, perpendicular to the mid-line of the trackway, between the outermost edges of the outer tracks (Braddy, 2007; Gaillard, 2011). The internal

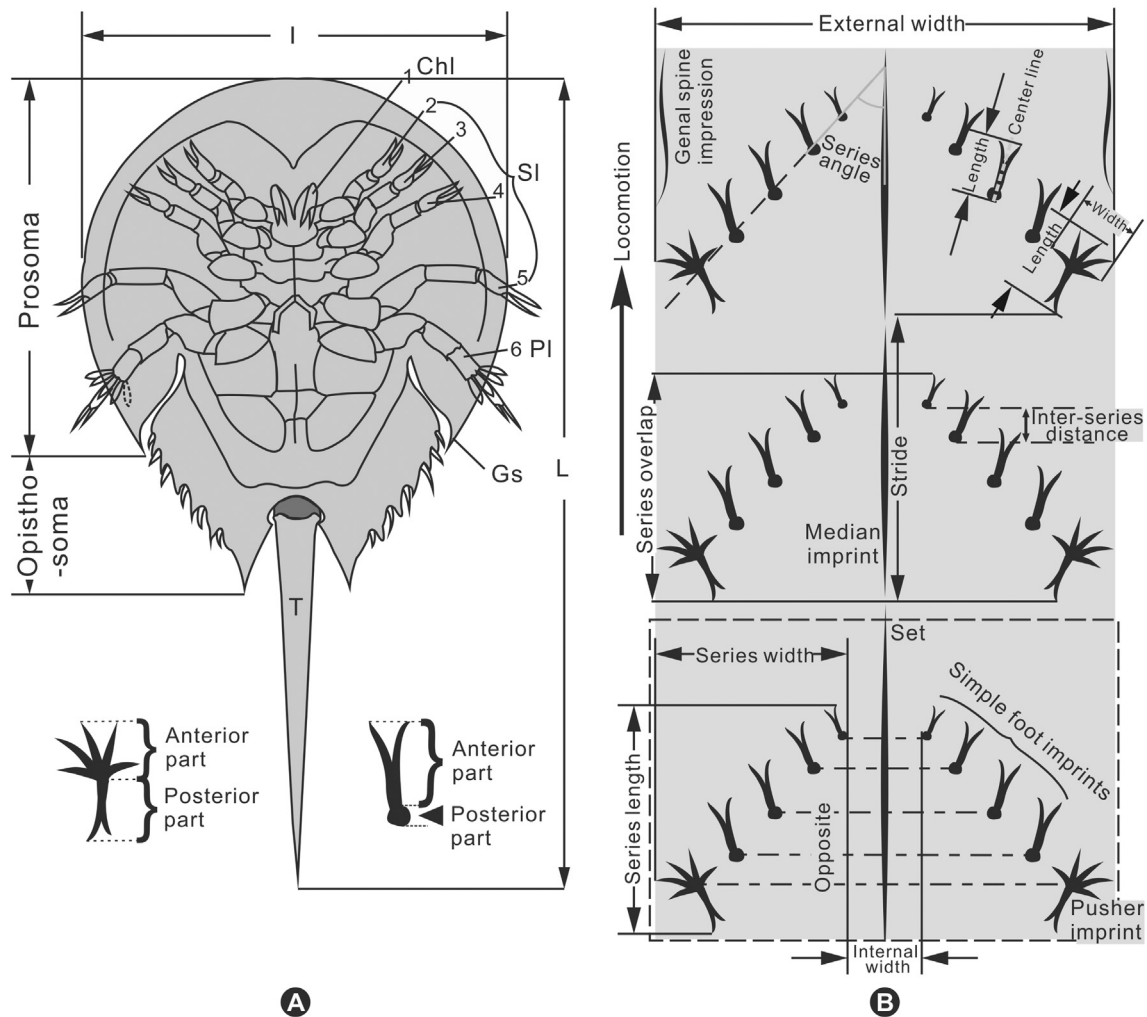


Fig. 4. A. Ventral view of a living limuloid animal (after Caster, 1938) and structures of simple foot imprints (T) and pusher imprints (P). 1. Chelicera (the first pair of appendages); 2, 3, 4, 5. The second to fifth pairs of appendages or the first to fourth pairs of walking legs; 6. The sixth pair of appendages or the fifth pair of walking legs or “pusher” legs. Chl., chelicera; PI., pusher walking legs; SL., simple walking legs; Gs, genal spine; I, width of prosoma; L, total length of limulid; T., telson.; B. Basic descriptive terminology and measuring proxies of limulid trackways.

width is the distance, perpendicular to the mid-line of the trackway, between the innermost edges of the inner tracks, but in relatively long trackways the external and internal widths may be averaged over several data sets to establish a range and a mean value (Gaillard, 2011).

Abbreviations: EW, external width of a trackway; GS, genal spine (or the lateral side of the prosoma) impressions; I-s d, inter-series distance; IW, internal width of a trackway; M, median impressions; NT, nail-like tracks; P, pusher imprints; PL, length of a pusher imprint; PW, width of a pusher imprint; SA, series angle; Sd, stride; SL, series length; SW, series width; T, simple foot imprint; TL, length of a simple foot imprint; VT, V-shaped tracks; YT, Y-shaped tracks.

3.2. Trace fossil classification

Kouphichnium can be identified as a limuloid trackway or limuloid trace, which includes the ichnogenera *Limulicubichnus* Miller, 1982 (Carboniferous to Triassic), *Selenichnites* Romano and Whyte, 1987 (Ordovician to Jurassic) and some of *Crescentichnus* Romano and Whyte, 2015. Alternatively, *Kouphichnium* can be also assigned to the group *Movichnia* (movement traces) of Seilacher (1953) and sub-group *Repichnia* (crawling) of Leipnitz and Müller (1982).

The concept of the ichnotaxobase has not been much discussed at the ichnospecies level of *Kouphichnium* (Romano and Whyte, 1987, 1990, 2015; Romano and Taylor, 2016). According to Minter et al.

(2007), the ichnotaxobase (morphology and substrate types) of an invertebrate ichnotaxon should incorporate three key components, i.e. the expressed behaviour (ethology), the producer (biotaxonomy) and the substrate (taphonomy). However, it has been suggested (Bertling et al., 2006; Bertling, 2007) that the expressed behaviour (ethology) and the producer (biotaxonomy) should be avoided as part of the definition of the ichnotaxobase because they are subjective. Further, the substrate (taphonomy) is also controversial as part of the ichnotaxobase (Buatois et al., 2017). Thus it was suggested that the ichnotaxobase should be founded only on morphology (Knaust, 2012, 2013; Romano and Whyte, 2015; Romano and Taylor, 2016; Buatois et al., 2017; Alberti et al., 2017). While it is more than likely that *Kouphichnium* Nopcsa was produced by limuloids, it is hard to identify a particular genus or species (Caster, 1938; Alberti et al., 2017), except for the rare cases such as the well-known *Kouphichnium walchi* Malz, 1964, which is preserved together with the limuloid body fossil *Mesolimulus walchi* (Malz, 1964; Lomax and Racay, 2012). Although the producer of *Kouphichnium* Nopcsa can be clearly regarded as one group of organisms (limuloids, Order Xiphosurida), the producer is not necessary to be a part of the ichnotaxobase at the level of ichnospecies. Secondly, the substrate for *Kouphichnium* Nopcsa can be mainly identified as lithic (as it does not occur in wood or bone etc.). So, the substrate might not be so important in the classification of ichnospecies of *Kouphichnium*. Thirdly, the expressed behaviour (ethology) is interpreted based on the

morphology and it should be avoided as a part of the ichnotaxobase of *Kouphichnium*. Thus, it seems reasonable that the ichnotaxobase of *Kouphichnium* is mainly based on the morphology. Based on the terminology system for limuloid trackways in this study, the ichnotaxobase at the ichnospecies level of *Kouphichnium* comprises four elements, including simple foot imprints (T), pusher imprints (P), median impressions (M), and genal spine impressions (GS).

Nine ichnospecies of *Kouphichnium* have been named, but their systematic palaeontological classification is unclear (Table 1). Based on the ichnotaxobase in this study, seven types can be identified for the classification of *Kouphichnium* (Fig. 5 and Table 1). Type a is made of simple foot imprints (T), pusher imprints (P) and median impressions (M), such as *Kouphichnium lithographicum*; type b made of simple foot imprints (T) and pusher imprints (P) or just simple foot imprints (T), such as *Kouphichnium didactylum*; type c made of simple foot imprints (T), median impressions (M) and genal spine impressions (GS), such as *Kouphichnium liulinensis* sp. nov.; type d made of simple foot imprints (T) and median impressions (M), such as *Kouphichnium aspodon* in previous studies and *K. cf. aspodon* in this study; type e made of simple foot imprints (T), pusher imprints (P) and genal spine impressions (GS), such as *Kouphichnium gracilis* in previous studies and *K. cf. gracilis* in this study; type f made of pusher imprints (P) and median impressions (M) or just pusher imprints (P), including *Kouphichnium fernandesi*, *K. pterodactyli* in previous studies and *K. isp. 1* in this study; and type g made of pusher imprints (P), median impressions (M) and genal spine impressions (GS). More work is needed on type g in the future.

Based on this new ichnotaxonomic system, 44 well-preserved specimens from the uppermost Permian to Lower Triassic strata of North China are assigned to six ichnospecies of *Kouphichnium*, namely *Kouphichnium lithographicum* Oppel, *K. didactylum* Willard, *K. liulinensis* sp. nov., *Kouphichnium cf. aspodon*, *K. cf. gracilis* and *K. isp. 1*. The first three ichnospecies with emended diagnosis and new diagnosis are described in detail in Section 4, and the last three ichnospecies described simply in Section 5.1.

Table 1
New proposed ichnotaxobases and standard of classification (types) in this study.

Ichnospecies	Components	Producers	References	Ichnotaxobases ^a	Types ^a
<i>Ichnites lithographicus</i> Oppel, 1862	Feet tracks; 3-toe feet tracks; median depression	<i>Archaeopteryx</i>	Oppel, 1862	Simple feet tracks; pusher imprint; median impressions	a
<i>Kouphichnium lithographicus</i> Oppel, 1862	Tetradiate “toe” impressions; roundish impressions; groove	Limuloids	Caster, 1941	Simple feet tracks; pusher imprint; median impressions	a
<i>K. lithographicum</i> Oppel, 1862	Simple imprints; trifold imprint; median groove	Limuloids	Gaillard, 2011	Simple feet tracks; pusher imprint; median impressions	a
<i>Bipedes aspodon</i> Aldrich, 1930	Two-toe feet tracks	Bipedal reptiles	Aldrich, 1930	Simple feet tracks; median impressions	d
<i>Kouphichnium aspodon</i> Aldrich, 1930	–	Limuloids	Buta et al., 2005	Simple feet tracks; median impressions	d
<i>K. arizonae</i> Caster, 1944	Middle groove; tracks; ectognath imprints	Limuloids	Caster, 1944	Simple feet tracks; pusher imprint; median impressions	a
<i>Paramphibius didactylus</i> Willard, 1935	Manus; Pes	<i>Paramphibius</i> (amphibians)	Willard, 1935	Simple feet tracks; pusher imprint	b
<i>P. didactylus</i> Willard, 1935	Simple tracks; pusher-prints	Limuloids	Caster, 1938	Simple feet tracks; pusher imprint	b
<i>Kouphichnium variabilis</i> Linck, 1949	V/hook/fork-shaped impressions; multi-grooved impressions; tail spiked track	Limuloids	Linck, 1949	Simple feet tracks; pusher imprint; median impressions	a
<i>K. gracilis</i> Linck, 1949	V-shaped kicks; 4-forked kicks; Trailing trace	Limuloids	Linck, 1949	Simple feet tracks; pusher imprint; genal spine impressions	e
<i>K. fernandesi</i> Romano and Meléndez, 1985	Pusher imprints	Limuloids	Romano and Meléndez, 1985	Pusher imprints	f
<i>K. pterodactyli</i> Malz, 1964	Three-toed feet track	Limuloids	Malz, 1964	Pusher imprints	f
<i>K. walchi</i> Malz, 1964	–	<i>Mesolimulus walchi</i>	Malz, 1964	–	–

^a Ichnotaxobases and types proposed in this study.

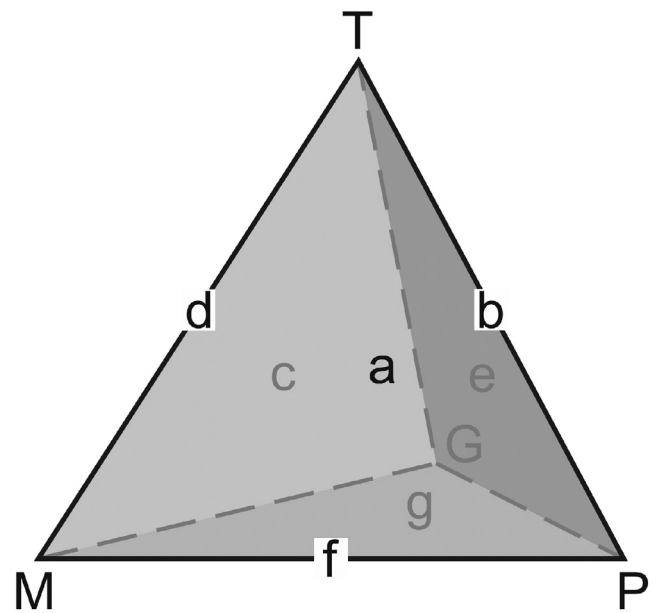


Fig. 5. A regular tetrahedron showing a new ichnotaxonomic system for the classification of *Kouphichnium*, based on four basic characters of *Kouphichnium* ichnotaxobases. Abbreviations: G, genal impressions; M, median impressions; P, pusher imprints; T, simple foot imprints. And a, b, c, d, e, f and g represent the seven ichnotaxa of *Kouphichnium*, respectively.

4. Systematic palaeoichnology

Ichnogenus *Kouphichnium* Nopcsa, 1923.

Type species. *Kouphichnium lithographicum* Oppel, 1862; from the Upper Jurassic Solnhofen Lithographic Limestones of Bavaria, Germany.

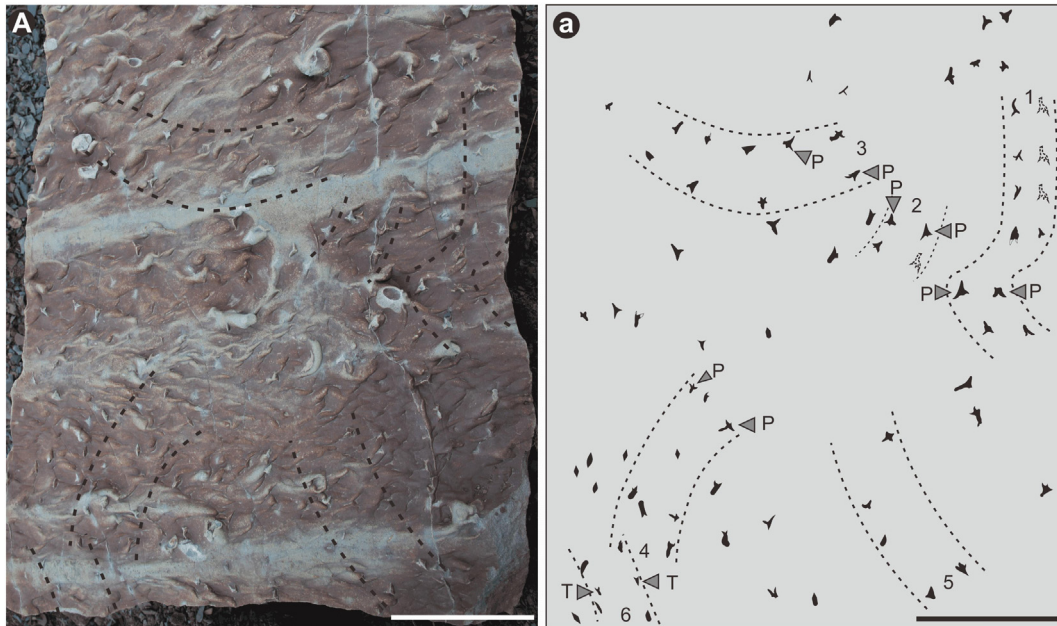


Fig. 6. *Koupichnium didactylum* (STS-1) from the upper part of the Sunjiagou Formation of North China. A. six trackways (1–6) can be identified and others are scattered simple foot imprints (T) and pusher imprints (P), from Horizon 1 in the upper part of the Sunjiagou Formation of the Shichuanhe section (Shaanxi Province, North China). a. Sketch of A. P, pusher imprints; T, simple foot imprints. Scale bar = 10 cm.

Diagnosis emended. (following Häntzschel, 1975: W75) Heteropodous tracks of great variability; complex tracks mainly 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; and (2) one pair of digitate or flabellar, toe-shaped or otherwise variable imprints. In addition, the complete trackway also includes the median impressions (M), maybe continuous or discrete; straight or curved. Sometimes, there are some genal spine impressions (GS) in the trackway, either arranged on the external side or cutting across previously formed tracks.

4.1. *Koupichnium lithographicum* (Oppel, 1862)

- Figs. 7A–C; 8A–D; 10A–C; 11A, C, E; 12 C-trackway C; 13D, G, H. 1862 *Ichnites lithographicum* Oppel, 1862; Oppel: 121–125, pl. 39. 1923 *Koupichnium lithographicum* Nopcsa; Nopcsa, 1923: 1–210. 1929 *Ichnites lithographicum* Oppel, 1862; Jaekel, 1929: 234, pl. 10, Fig. 2. 1929 *Ornichnites caudatus* Jaekel, 1929; Jaekel, 1929: 235, Abb. 19. 1938 *Koupichnium lithographicum* Oppel, 1862; Caster, 1938: Fig. 5. 1944 *Koupichnium arizonae* Caster, 1944; Caster, 1938: 80–81, pl. 1. 1949 *Koupichnium variabilis* Linck, 1949; Linck, 1949: 50, Abb. 2; 97: pl. 5, Fig. 1; 99: pl. 7, Fig. 1. 1975 *Ichnites lithographicum* Oppel, 1862; Häntzschel, 1975: W75. 1982 *Ichnites lithographicum* Oppel, 1862; Leipnitz and Müller, 1982: 11, Abb. 11. 2003 *Ichnites lithographicum* Oppel, 1862; Romano and Whyte, 2003: 259. 2011 *Koupichnium lithographicum* Oppel, 1862; Gaillard, 2011: 59–61, Figs. 4, 5. 2013 *Koupichnium lithographicum* Oppel, 1862; Fabrègues and Allain, 2013: 183–184, Figs. 2, 3. 2014 *Ichnites lithographicum* Oppel, 1862; Moreau et al., 2014: 5.

4.1.1. Diagnosis emended

This type ichnospecies was proposed by Oppel (1862) for simple straight locomotion traces (a median groove, a pusher imprint (P) and

only one simple foot imprint (T) found in the Solnhofen Limestone. It seems best to consider *Ichnites* as a synonym of *Koupichnium* (Caster, 1938, 1944; Gaillard, 2011) and the name of this ichnospecies should be *Koupichnium lithographicum* rather than *Koupichnium lithographicus* since the gender of the species name follows the gender of the genus. Because the diagnosis of Oppel (1862) is insufficient for all specimens assignable to the ichnospecies, we extend the definition here as follows.

Marks occur as epichnial impressions or can be moulded as convex hypichnia. It represents a straight trace or gently meandering trace containing several simple foot imprints (T) (one to four imprints, even rarely five imprints, in a series), pusher imprints (P) (only one pusher imprint (P) in a series) and median impressions (M). The form of the simple foot imprints (T) may be Y-shaped, V-shaped, or with a nail-like anterior part and a dot-like bulge at the posterior part, or just round imprints. In addition, the pusher imprints (P) also have diverse types, such as radiating blade imprints (trifid, quadrifid or quinquefid) or anterior radiating blade part with a dot-like bulge, “one-digitate” or inverted “Y” posterior part. In addition, the median impressions (M) may be curved or straight and continuous or intermittent. Ideally, the trackway should be an imprint series with opposite symmetry.

4.1.2. Material

Sixteen specimens, including six from Horizon 4 in the Heshanggou Formation at the Shichuanhe Section, three from Horizon 2 in the Liujiagou Formation, and seven from Horizon 3 in the Heshanggou Formation at the Liulin Section (Shanxi Province, North China). All specimens are preserved in the Yifu Museum of China University of Geosciences, Wuhan (CUGMUS).

4.1.3. Sample numbers

CUGMUS STS-2 (part, Fig. 7A and counterpart, Fig. 7B), STS-3 (Fig. 7C), STS-8 (Fig. 8A), STS-9 (Fig. 8B), STS-10 (Fig. 8C), STS-11 (Fig. 8D), SLL-1 (Fig. 10A), SLL-2 (Fig. 10B), SLL-3 (Fig. 10C), SLL-7 (Fig. 11A), SLL-9 (Fig. 11C), SLL-11 (Fig. 11E), SLL-18 (Fig. 12C), SLL-22 (Fig. 13D), SLL-25 (Fig. 13G) and SLL-26 (Fig. 13H).

4.1.4. Description

Trackways, some of nearly straight traces (lurching-type in Braddy,

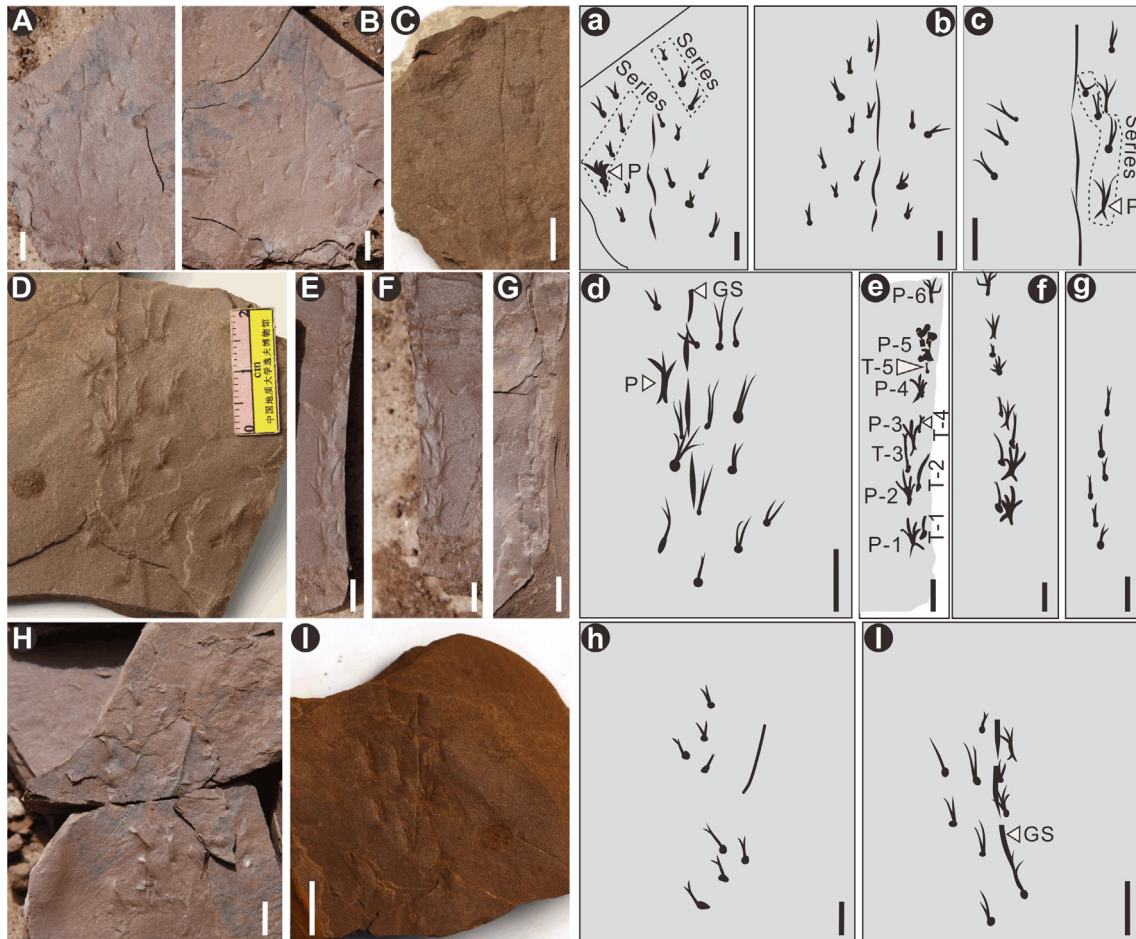


Fig. 7. *Kouphichnium* from Horizon 4 in the upper part of the Heshangou Formation of the Shichuanhe section (Lower Triassic, Shaanxi Province, North China). A. part of *Kouphichnium lithographicum* (STS-2, concave epichnia); B. counterpart of *Kouphichnium lithographicum* (STS-2, convex hypichnia); C. *Kouphichnium lithographicum* (STS-3) with a discernible series; DandI. *Kouphichnium cf. gracilis* (STS-4) with special genal spine impressions (GS) on one side, D. counterpart and I. part; E, F. *Kouphichnium didactylum* (STS-5) with pusher imprints (P-1 to P-6) and simple foot imprints (T-1 to T-5), E. part and F. counterpart; G. *Kouphichnium didactylum* (STS-6) with just simple foot imprints (T); H. *Kouphichnium cf. aspodon* (STS-7) with simple foot imprints (T) and median impressions (M). a–i, Sketches of A–I. All scale bars = 10 mm.

2007) occur on bedding planes of red siltstone. Some specimens are preserved as concave (negative) epichnia (Figs. 7A, C, 8B, 10B, 11C) while others as convex (positive) hypichnia (Figs. 7B, 8A, C, D, 10A, C, 11A, E, 12C (trackway C), 13D, G, H). Both types of preservation exhibit differing median impressions (M), including a discontinuous curved (Figs. 7A–C, 10B, C, 11C, 13D, G), continuous curved (Figs. 11E, 12C (trackway C)), or discontinuous straight (Figs. 8A–D, 10A, 11A, 13H) pattern, and the median impression (M) may be seen as a groove (Figs. 7A, C, 8B, 10B, 11C) or ridge (Figs. 7B, 8A, C, D, 9D, G, H, 10A, C, 11A, E, 12C (trackway C)). One to four sets of imprints were preserved in a trackway (Figs. 7A–C, 8A–B, 11A, E), including repeated series of imprints in paired rows on both sides of the median impression (M). Each series covers one to four simple foot imprints (T) and one pusher imprint (P). In detail, these epichnial series can be divided into two groups, one on the left of the median impression (M) (Left series, Ls) and the other on the right of the median impression (M) (Right series, Rs). Due to imperfect preservation, the symmetry of these trackways exhibits incomplete imprint series with opposite symmetry. Moreover, there are undertracks in some specimens (Figs. 11A, 13D, G (some pusher imprints (P))).

4.1.5. Simple foot imprints (T)

They are mainly composed of two parts in various forms, including V-shaped or Y-shaped bifid oblique imprints (e.g. Fig. 7A–C) and nail-

like tapered external (or comma external) imprints (e.g. Figs. 8A, B, 10C). The anterior part is a V-shaped, Y-shaped or nail-like imprint, while the posterior part is a round or ellipsoidal imprint. The open parts of simple foot imprints (T) indicate the forward moving direction.

4.1.6. Pusher imprint (P)

Pusher imprints (P) show a trifold (Fig. 7C), quadrifold (Fig. 10A–C) or quinquefid (Fig. 8B) anterior radiating blade part pointing forward, and ending with a visible oval-round dot-like bulge (Fig. 8H) or inverted “Y” imprints (Fig. 8I, J).

4.1.7. Dimensions

EW = 10.5–43.3 mm; IW = 2.2–11 mm; SL = 11.5–38.9 mm; SW = 5.6–13.7 mm; SA = 16.4–27.8°; Sd = 12.2–23.5 mm; I-s d = 1.1–11.4 mm; TL = 1.4–9.6 mm; PL = 2.5–11.3 mm; PW = 2.1–7.8 mm.

4.1.8. Remarks

The type specimen of Ooppel (1862) from the Solnhofen Lithographic Limestone (Solnhofener Plattenkalk) (Leipnitz and Müller, 1982: 11, Abb.11) also exhibits simple foot imprints (T), pusher imprints (P) and median imprints. But the simple foot imprints (T) are round-ellipsoidal imprints and there is just one simple foot imprint (T) in a series. Besides, several former ichnospecies should be reassigned to *Kouphichnium lithographicum* Ooppel, such as *Ornichnites caudatus* Jaekel, 1929,

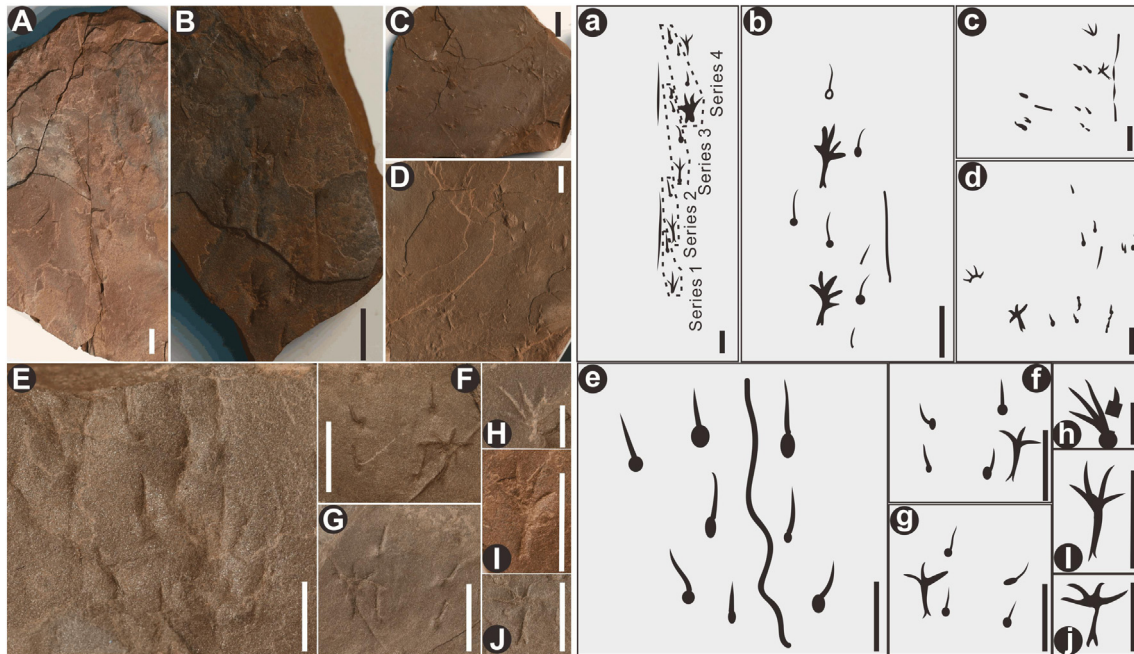


Fig. 8. *Koupichnium* and three single kinds of pusher imprints (P) from Horizon 4 in the upper part of the Heshanggou Formation of the Shichuanhe section (Lower Triassic, Shaanxi Province, North China). A. *Koupichnium lithographicum* (STS-8) with at least four series (series 1–4); B. *Koupichnium lithographicum* (STS-9) with nail-like simple foot imprints (NT), pusher imprints (P) and median impressions (M); C. *Koupichnium lithographicum* (STS-10) with V-shaped/nail-like simple foot imprints (VT/NT), pusher imprints (P) and median impressions (M); D. *Koupichnium lithographicum* (STS-11); E. *Koupichnium cf. aspodon* (STS-12) with nail-like simple foot imprints (NT) and median impressions (M); F and G, *Koupichnium didactylum* (STS-13) with nail-like simple foot imprints (NT) and pusher imprints (P), F, counterpart and G, part; H, I, J, single pusher imprints (P). a–j, Sketches of A–J. All scale bars = 10 mm.

Koupichnium arizonae Caster, 1944 (previous description as middle groove, tracks and ectognath imprints in Table 1) and *Koupichnium variabilis* Linck, 1949 (previous description as V/hook/fork-shaped impressions, multi-grooved impressions and tail spiked track in Table 1). However, *Koupichnium lithographicum* Oppel, 1862 in Gaillard (2011) and Fabrègues and Allain (2013) does not exhibit the median groove. They might be influenced by the different substrate or might be assigned to *Koupichnium didactylum*.

4.2. *Koupichnium didactylum* (Willard, 1935)

Figs. 6A, 7E–G, 8F, G, 9A–E, 10D, E, 11B, 12A, B, C (trackway A and B), 13A, C, F, I, J.

1935 *Paramphibius didactylus* Willard, 1935; Willard: 47, pl. 10, Figs. 1, 3.

1935 *Paramphibius tridactylus* Willard, 1935; Willard: 48, pl. 11, Figs. 2, 3.

1938 *Paramphibius didactylus* Willard, 1935; Caster, 1938: 6, Fig. 1a, aa, ab, ac, b, c, d and l.

4.2.1. Diagnosis emended

This ichnospecies was first described by Willard (1935) as the amphibian tracks, *Paramphibius*, with two species, *Paramphibius didactylus* Willard and *P. tridactylus* Willard. Caster (1938) restudied the material, and corrected the identification of the track-maker to a limuloid rather than an amphibian. According to Häntzschel (1975: W75), it seems best to consider *Paramphibius* as a synonym of *Koupichnium*. Further, Caster (1938) said that *Paramphibius tridactylus* is a synonym by page priority of *Paramphibius didactylus*, because it is inappropriate to distinguish two species of *Paramphibius* just according to the number of simple foot imprints (T). Other species of *Paramphibius* also should be rechecked in the future. Moreover, the name of this ichnospecies should be *Koupichnium didactylum* rather than *Koupichnium didactylus* since the gender of the species name follows the gender of the genus.

Here, the diagnosis of *Koupichnium didactylum* Willard is revised. Marks occur as epichnial impressions, or moulded as convex hypichnia. It is always a simple trackway, symmetrical or asymmetrical, containing simple foot imprints (T) with or without pusher imprints (P), but no median impressions. In a series, the number of simple foot imprints (T) varies from one to five imprints, but the number of the pusher imprints (P) is only one. The simple foot imprints (T) can be of various forms, such as Y/V/Nail-like types or just round imprints. In addition, pusher imprints (P) can also be of different types, including different anterior radiating blade parts (trifid, quadrifid or quinquefid), various posterior parts (dot-like, one-digitate or inverted-Y-shaped imprints) or even just the anterior radiating blade part without the posterior part.

4.2.2. Material

Seventeen specimens, including one from Horizon 1 in the Sunjiagou Formation and seven from Horizon 4 in the Heshanggou Formation at the Shichuanhe section, one from Horizon 2 in the Liujiagou Formation and nine from Horizon 3 in the Heshanggou Formation at the Liulin section. All specimens are preserved in the Yifu Museum of China University of Geosciences, Wuhan (CUGMUS).

4.2.3. Sample numbers

CUGMUS STS-1 (Fig. 6A), STS-5 (Fig. 7E, part and F, counterpart), STS-6 (Fig. 7G), STS-13 (Fig. 8F, counterpart and G, part), STS-14 (Fig. 9A, counterpart and B, part), STS-15 (Fig. 9C), STS-16 (Fig. 9D, counterpart and E, part), SLL-4 (Fig. 10D, counterpart and E, part), SLL-8 (Fig. 11B), SLL-16 (Fig. 12A), SLL-17 (Fig. 12B), SLL-18 (Fig. 12, C (trackway A and B)), SLL-19 (Fig. 13A), SLL-21 (Fig. 13C), SLL-24 (Fig. 13F), SLL-27 (Fig. 13I) and SLL-28 (Fig. 13J).

4.2.4. Description

Trackways were formed as concave epichnial traces (Figs. 7E, G, 8G, 9B, E, 10E, 11B, 12A, 13A, J) or moulded as convex hypichnia (Figs. 6A, 7F, 8F, 9A, C, D, 10D, 12B, C (trackway A and B), Fig. 13C, F,

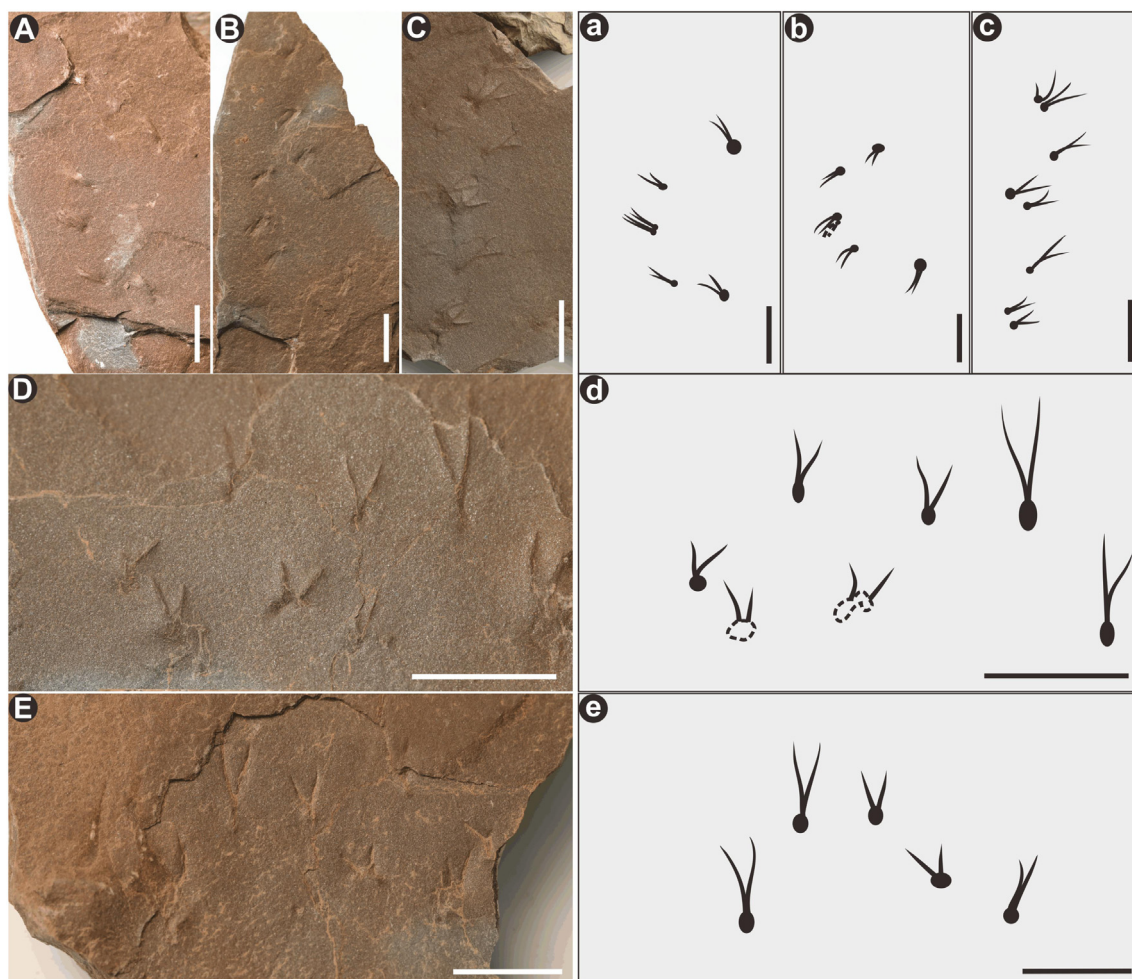


Fig. 9. Some scattered asymmetric trackways of *Kouphichnium didactylum* from Horizon 4 in the upper part of the Heshanggou Formation of the Shichuanhe section (Lower Triassic, Shaanxi Province, North China). A, B. several simple foot imprints (T) on the right side of the trackways (STS-14), A. counterpart and B. part; C. several simple foot imprints (T) on the left side of the trackways and each two appressed simple foot imprints (T) as a group with one simple foot imprint (T) between two groups (STS-15); D, E. several scattered simple foot imprints (T) in trackways (STS-16), D. counterpart and E. part. a–e, Sketches of A–E. All scale bars = 10 mm.

D). These trackways show a complex, barely regular and usually asymmetric (or just very few sporadic pairs of series in a trackway) pattern or consist only of several scattered simple foot imprints (T). The remarkable and typical feature of this type is the lack of median imprints and just composed of several series of simple foot imprints (T) with or without pusher imprints (P).

Most of the simple foot imprints (T) in these trackways are of V/Y-shape and end with a round or oval dot-like imprint. The opening of the V/Y-shaped part indicates the forward direction of locomotion. Some of them are tapered or comma-shaped externally, with a round or oval dot-like termination, which may indicate sexual dimorphism. The tips of the tapered external or comma external parts indicate the forward direction of movement.

Pusher imprints (P), typically in the relatively complete specimens, are divided into two parts, i.e. a trifid or quadrifid digitate or flabellar radiating anterior part linking with the inverted Y-shaped or inverted clavate marks in the posterior part.

4.2.5. Dimensions

EW = 12.5–46.9 mm; IW = 3.2–20.3 mm; SL = 3.5–5.7 mm; SW = 5.9–7.4 mm; SA = 47.2–63.3°; Sd = 4.4–34.8 mm; TL = 3.4–10.97 mm; PL = 2.7–11.4 mm; PW = 2.1–8.6 mm.

4.2.6. Remarks

The most important difference from *Kouphichnium lithographicum* is

that this ichnospecies is produced without the median impressions (M). In addition, the irregularity or asymmetry in trackways is also diagnostic. But the specimen with median imprints in Willard (1935, 47, pl. 10, Fig. 2) is different from this ichnospecies.

4.3. *Kouphichnium liulinensis* isp. nov.

Fig. 11D.

4.3.1. Diagnosis

Bilaterally symmetrical. A little complex straight trackway formed as concave epichnia or convex hypichnia, usually consisting of several simple foot imprints (T) (normally one or two imprints in a series) but no the pusher imprints (P), continuous or intermittent median impressions (M) and curved continuous sigmoidal genal spine impressions (GS). The anterior parts of the simple foot imprints (T) may be Y-shaped, V-shaped or nail-like imprints.

4.3.2. Derivation of name

From the name of the collection site, Liulin, Shanxi Province, China. Holotype. CUGMUS-SLL-10, Fig. 11D.

Material. One specimen from Horizon 3 in the Heshanggou Formation at the Liulin section (North China). The specimen is preserved in the Yifu Museum of China University of Geosciences, Wuhan (CUGMUS).

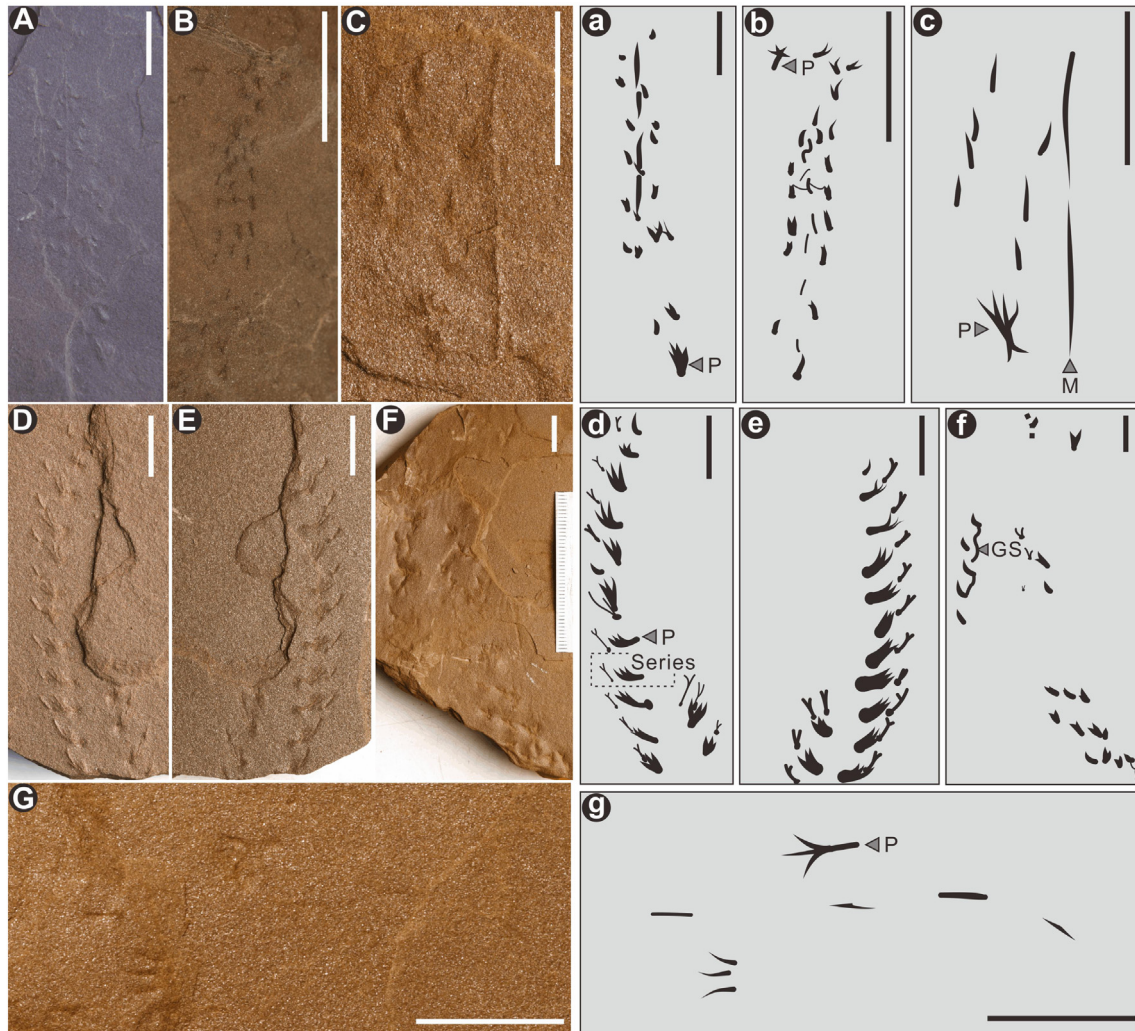


Fig. 10. *Kouphichnium* from Horizon 2 in the upper part of the Liujiagou Formation of Liulin section (Lower Triassic, Shanxi Province, North China). A. *Kouphichnium lithographicum* (SLL-1); B. *Kouphichnium lithographicum* (SLL-2); C. *Kouphichnium lithographicum* (SLL-3); D and E. *Kouphichnium didactylum* (SLL-4) with simple foot imprints (T) and a pusher imprint (P) in a series, D. counterpart and E. part; F. *Kouphichnium* cf. *gracilis* with genal spine impressions (GS) on one side (GS) (SLL-5); G. *Kouphichnium* isp. 1 with two pusher imprints (P) and median impressions (M) (SLL-6). a–g, Sketches of A–G. All scale bars = 10 mm.

4.3.3. Description

The trackway is moulded as a convex hypichnion. It is a slightly complex but symmetrical trackway, preserved on a bedding plane of reddish siltstone. It comprises V/Y/nail-shaped simple foot imprints (T), median impressions (M) and genal spine impressions (GS). The genal spine impressions (GS) are recorded on each side of the trackway, and as a continuous curved trace. Moreover, the median impressions (M) are relatively continuous and straight marks.

Simple foot imprints (T) in the trackway are recorded as several series. The first right series (= the first left one in Fig. 11D) without the left coupled series exhibits two V/Y-shaped bifid imprints and one nail-like imprint. However, it shows just two V/Y-shaped bifid imprints in the first pair of the series. In addition, the remaining series consists of just one V/Y-shaped bifid imprint.

4.3.4. Dimensions

EW = 11.9 mm; IW = 3.2 mm; SL = 7.4 mm; SA = 43.3°; Sd = 2.7–4.9 mm; I-s d = 0.7 mm; TL = 2.5–2.9 mm.

4.3.5. Remarks

This new ichnospecies can be distinguished from the other ichnospecies of *Kouphichnium* by the coupled genal spine impressions (GS) and bilateral symmetry. It is somewhat similar to *Mortichnia Kouphichnium* isp. (Alberti

et al., 2017, Fig. 7f), but the latter has pusher imprints (P) and discrete arc-shaped prosoma imprints rather than relatively continuous straight/S-shaped genal spine or lateral side of the prosoma impressions, especially with the dying trackmaker at the end. Genal spine (or the lateral side of the prosoma) impressions were described in the walking trail of *Paramphibius* by Caster (1938: 23, Fig. 5, Sg). However, this was an integrated sketch of all possible marks from a whole limuloid body without considering the classification of the traces. In addition, in the new ichnospecies, the genal spine impressions (GS) are marked on each lateral side of the trackway, with mostly just one or two simple foot imprints (T) in a series and without pusher imprints (P). What is more, the median impressions (M) are relatively straight and continuous.

5. Discussion

The observations and measurements presented above provide evidence on the palaeoethology and morphology (size and sexual dimorphism) of the *Kouphichnium* track makers. Studies of the neoichnology of modern horseshoes crabs (Caster, 1938; Martin and Rindsberg, 2007) suggest how the diverse traces of limuloids indicate various behaviours, and the relative locomotion rate could be estimated using Index λ (Gaillard, 2011; Alberti et al., 2017). In addition, the size of the limuloids can be reconstructed from their traces based on the

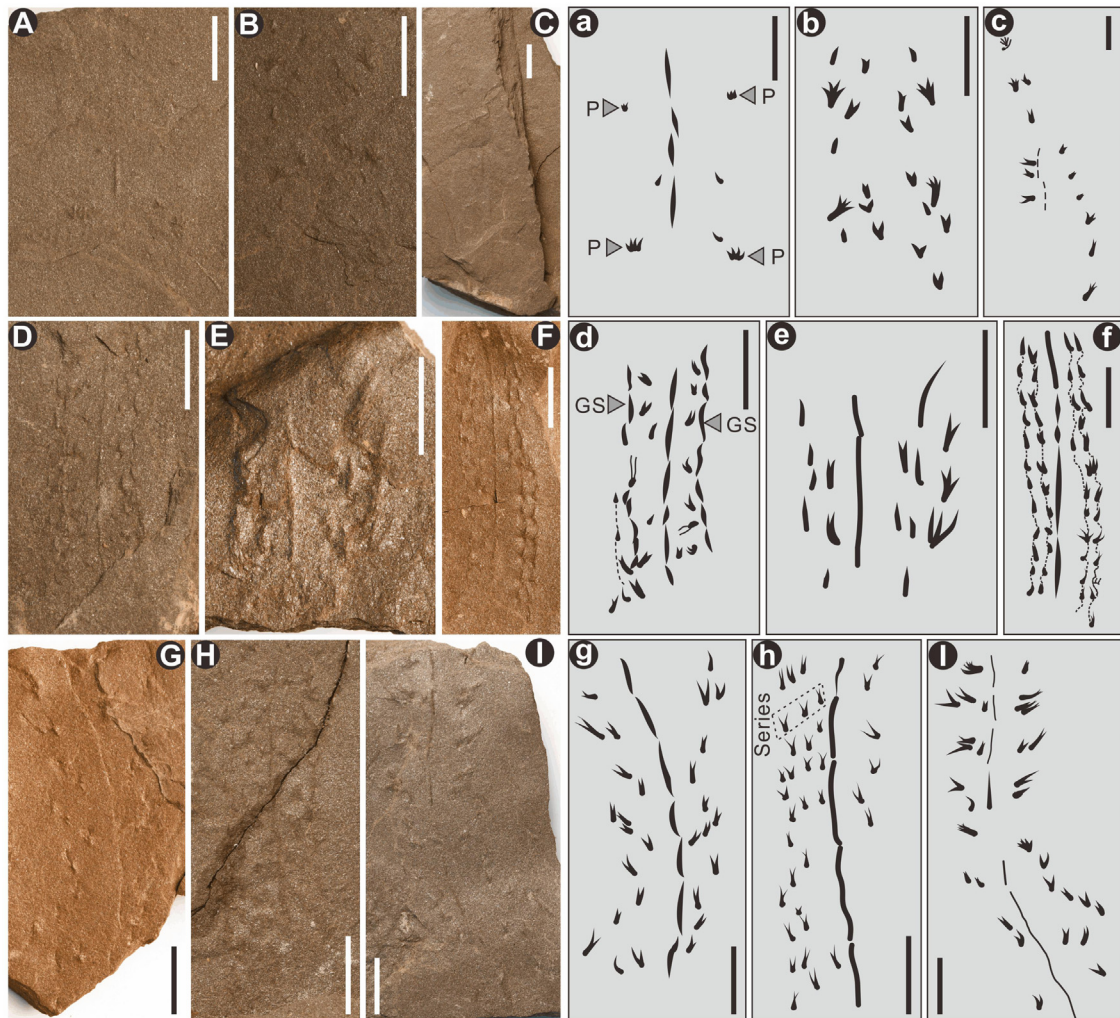


Fig. 11. *Koupichnium* from Horizon 3 in the middle-upper part of the Heshangou Formation of the Liulin section (Lower Triassic, Shanxi Province, North China). A. Possible undertracks of *Koupichnium lithographicum* (SLL-7); B. *Koupichnium didactylum* (SLL-8) with V-shaped/Nail-like simple foot imprints (T) and pusher imprints (P); C. possible undertracks of *Koupichnium lithographicum* (SLL-9); D. *Koupichnium liulinensis* sp. nov. (SLL-10) with genal spine impressions (GS) on both sides of trackways; E. *Koupichnium lithographicum* (SLL-11); F. *Koupichnium* cf. *aspodon* (SLL-12) with some drag traces between simple foot imprints (T); G. *Koupichnium* cf. *aspodon* (SLL-13) with just V-shaped/Y-shaped simple foot imprints (T); H. *Koupichnium* cf. *aspodon* (SLL-14) with just V-shaped/Y-shaped simple foot imprints (T); I. *Koupichnium* cf. *aspodon* (SLL-15) with just V-shaped/Y-shaped/nail-like simple foot imprints (T) and one pair of pusher imprints (P). a–i, Sketches of A–I. All scale bars = 10 mm.

formula proposed by Malz (1964), thereby enabling the study of temporal size variations from the Late Permian to Early Triassic in the study area. Modern limuloids show obvious sexual dimorphism, in which the females are larger than males (Moreau et al., 2014), and sexual dimorphism is also recognized in some well-preserved fossil specimens from North China.

5.1. Palaeoethological interpretations of *Koupichnium* and taphonomy

In the present study, the diagnosis of ichnogenus *Koupichnium* Nopcsa, including two ichnospecies (*K. lithographicum* and *K. didactylum*), is revised. Meanwhile, a new ichnospecies is proposed for the limuloid trackways with genal spine impressions (GS) here.

In addition, a general morphological-palaeoethological pattern is proposed to summarize the six *Koupichnium* ichnospecies from the uppermost Permian to Lower Triassic strata in North China and the palaeoethological interpretation is introduced below (type a', b', c', d', e' and f' of this study are respectively corresponding to type a, b, c, d, e and f in Fig. 5, respectively):

Type a' (Fig. 14A) is represented by *Koupichnium lithographicum* Oppel (here YT/VT/NT + P + M), and comprises simple foot imprints

(T) (at least one in a series), pusher imprints (P) (only one in a series) and a telson-drag impression (nearly continuous and straight or curved). Three basic marks appear concurrently in a trackway, which indicates the behaviour of crawling on the bottom. This relationship between morphology and behaviour was concluded by Gaillard (2011, p. 69, Fig. 10) and Alberti et al. (2017, Fig. 7d). But type a' has different series angles. The average of series angles of type a' is about 22.1° while the average of series angles in that “crawling specimen” of Gaillard (2011, p. 69, Fig. 10) is about 47.0°. According to Gaillard (2011, p. 69, Table 9) and Alberti et al. (2017, pp. 10–11), the relatively small series angle may correspond to the relatively high locomotion rate. So, the behaviour of type a' should be quick crawling. Moreover, if the telson-drag impression is curved, the trackmaker is suggested to wag its telson for more power of locomotion. Otherwise, if the telson-drag impression is straight, the power for quick crawling was produced simply by foot and pusher foot. So, the speed of quick crawling in trackways with curved telson-drag impressions is faster than in those with straight telson-drag impressions.

Type b' (Fig. 14B), represented by *Koupichnium didactylum*, is either symmetric or asymmetric. They are mainly composed of simple foot imprints (T) with or without pusher imprints (P) (here YT/VT/



Fig. 12. Some long *Kouphichnium* and some asymmetric *Kouphichnium* from Horizon 3 in the middle-upper part of the the Heshanggou Formation of the Liulin section (Lower Triassic, Shanxi Province, North China). A. *Kouphichnium didactylum* (SLL-16); B. *Kouphichnium didactylum* (SLL-17); C. three long trackways on a specimen (SLL-18) and trackway C lies over trackway B, trackway A and B are *Kouphichnium didactylum* without median impressions (M), and trackway C is *Kouphichnium lithographicum* with median impressions (M). a–b, Sketches of A–B. All scale bars, except C, are 10 mm and the scale bar of C is 10 cm.

NT + P or YT/VT/NT). All simple foot imprints of this type were produced by walking feet, including simple walking feet and sometimes a pusher foot that also worked as a walking foot here. However, none of them has a median impression (M), which suggests that the telson could not touch the bottom in the production of this trace, but might have worked in the water to control the direction of locomotion and produced a little power for slow movement of simple feet on the bottom. This relationship between morphology and behaviour was interpreted as walking by Gaillard (2011, p. 69, Fig. 10) and Alberti et al. (2017, Fig. 7c). But there are some differences in the series angle. The average of series angles of type b' is about 55.46° while the average of series angles in the “walking specimen” of Gaillard (2011, p. 69, Fig. 10 and Table 6) is about 14.2° . Thus, type b' may be formed from casual or

purposive wandering in water by trackmakers.

Type c' (Fig. 14C), expressed by *Kouphichnium liulinensis* sp. nov., comprises simple foot imprints (T) (just one or two in a series), short but slightly curved median impressions (M) and especially genal spine impressions (GS) on each lateral side (here YT/VT/NT + M + GS (each side)). The median impressions (M) indicate a high-frequency wag of the trackmaker's telson. In addition, sporadic simple foot imprints (T) and no pusher imprints (P) appear in a trackway, which may indicate the movement mainly in the water and the pusher foot working in pushing. Moreover, the special genal spine impressions (GS) on each lateral side indicate locomotion near the bottom. This morphology seems to be related to the behaviour of dying in Gaillard (2011, p. 69, Fig. 10) and Alberti et al. (2017, Fig. 7f). However, it does not exhibit a dying trackmaker but an active trackmaker because this type

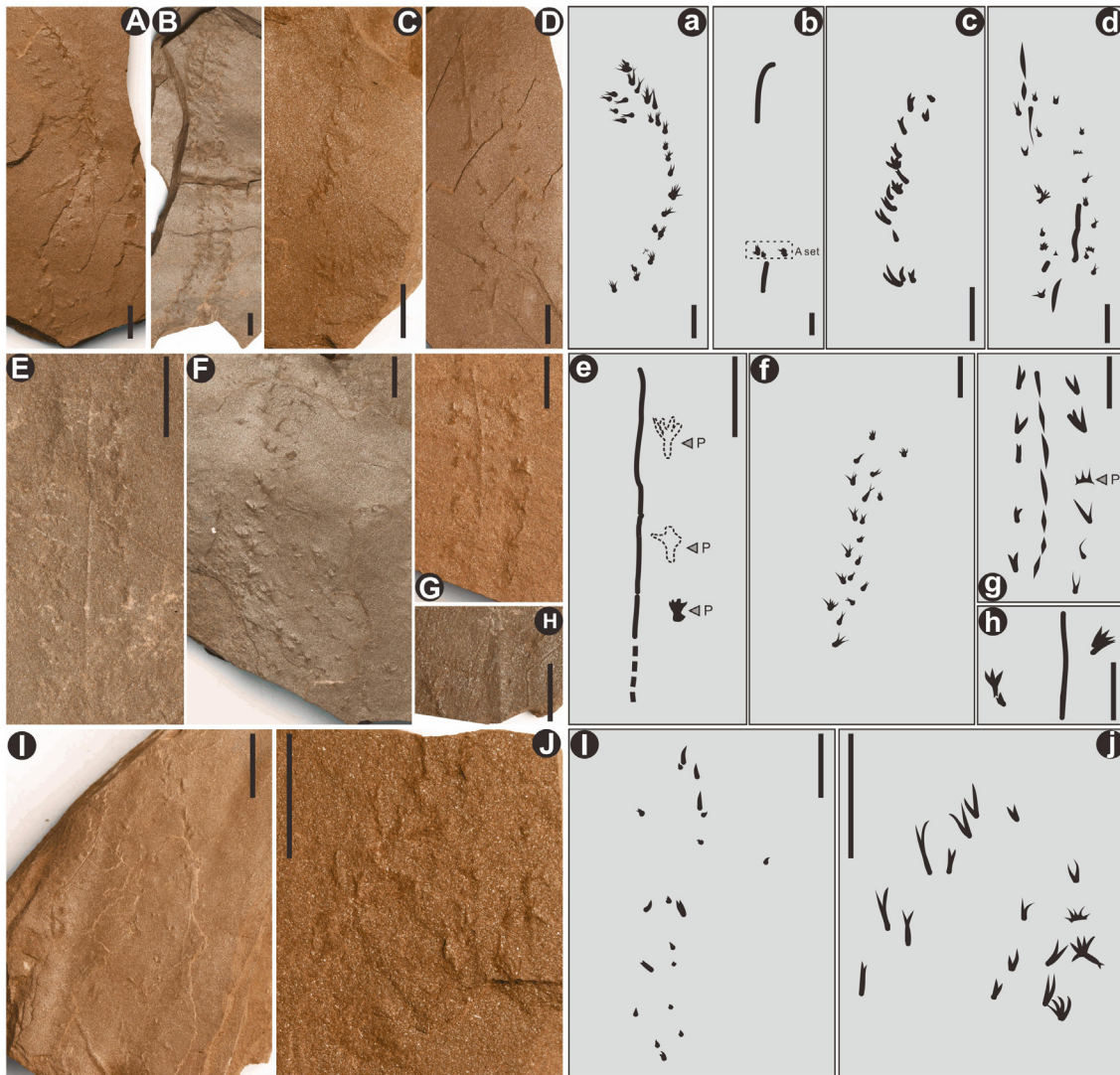


Fig. 13. Most trackways are the true surface tracks of *Kouphichnium* and some trackways are undertracks of *Kouphichnium* from Horizon 3 in the middle-upper part of the Heshanggou Formation of the Liulin section (Lower Triassic, Shanxi Province, North China). A. possible undertracks of *Kouphichnium didactylum* (SLL-19); B. *Kouphichnium* cf. *aspodon* (SLL-20) with an identified set; C. *Kouphichnium didactylum* (SLL-21) with an oblique row of simple foot imprints (T); D. *Kouphichnium lithographicum* (SLL-22) with off-centre median impressions (M); E. *Kouphichnium* isp. 1 (SLL-23) with just pusher imprints (P) and the median impressions (M); F. possible undertracks of *Kouphichnium didactylum* (SLL-24); G. *Kouphichnium lithographicum* (SLL-25); H. part of *Kouphichnium lithographicum* (SLL-26) preserved; I. possible undertracks of *Kouphichnium didactylum* (SLL-27); J. asymmetric *Kouphichnium didactylum* (SLL-28). a–j, Sketches of A–I. All scale bars = 10 mm.

consists of regular simple foot imprints, regular slightly curved median impressions, regular genal spine impressions but no pusher imprints. On the other hand, the “dying” type of Alberti et al. (2017, Fig. 7f) comprises irregular simple foot imprints, irregular median impressions, irregular genal spine impressions and irregular pusher imprints. Thus, this type should be formed by the trackmaker dragging its body and clinging to the bottom.

Type d' (Fig. 14D), namely *Kouphichnium* cf. *aspodon* (Figs. 7H, 8E, 11F–I, 13B), is similar to some specimens of *Kouphichnium aspodon* Aldrich, 1930 (Aldrich, 1930: pl. 5; Buta et al., 2005: pl. 64A, 65A–C), lacking pusher imprints (P) and always comprises several simple foot imprints (T) and short slightly curved median impressions (M) (here NT/YT/VT + M), which are very similar to type b', but have no pusher imprints (P) instead of median impressions (M). Thus, this type reflects half-crawling and half-walking near the bottom, sometimes with regularly simple feet and telson touching the bottom.

Type e' (Fig. 14E) is characterized by the occurrence of genal spine impressions (GS) on one side only (Figs. 7D, I, 10F; here YT/VT/NT + P + GS (one side)), and assigned to *Kouphichnium* cf. *gracilis* (similar to Linck, 1949: Taf. VI). The trackways are asymmetrical. These

unexpected features may reveal a sudden turn, when the trackmakers were chasing or chased.

Type f' (Fig. 14F), namely *Kouphichnium* isp. 1 (Figs. 10G, 13E), is relatively simple, including pusher imprints (P) and intermittent telson-drag impressions (here P + M). It may reflect a regular jumping in water with regular hits on the bottom by the pusher feet and telson, which differs from the “running” of Alberti et al. (2017, p. 10, Fig. 7b) that lacks the median impressions (M).

Meanwhile, the direction of movement can be identified from the simple foot imprints (T) or the pusher imprints (P). The V-shaped opening part of V/Y-shaped simple foot imprints (T) (Fig. 15A), the nail-head part of the nail-head that might be produced by a male limuloid's falcular appendages (Fig. 15C) or a female limuloid's closed chela (Fig. 15B), simple foot imprints (T), and the fan-like part of the pusher imprints (P) all indicate the forward direction (Romano and Whyte, 2003), contrasting to the V-shaped simple foot imprints of trilobites, which point backwards (Osgood, 1970). The different forms of pusher imprints (P) also reflect the variable locomotion of the pusher on the substrate, such as scratching in Fig. 15D or pressing totally on

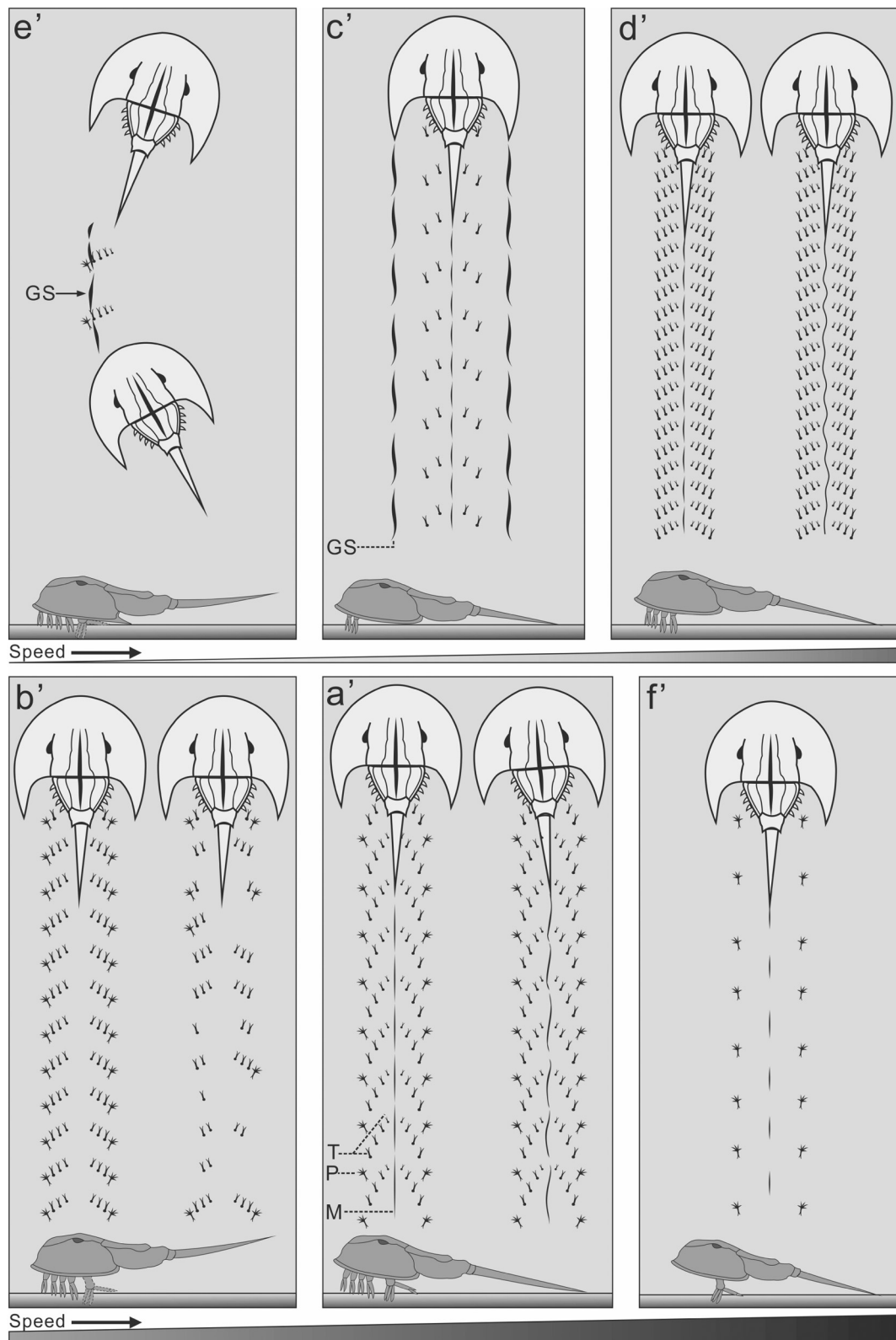


Fig. 14. Sketch maps of the morphological-palaeoethological pattern showing the relationship between limuloid palaeoethology and trackways' morphology. a'. quick crawling; b'. wandering in water near the bottom; c'. dragging clinging to the bottom; d'. half-crawling and half-walking near the bottom; e'. a sudden turn on the bottom when chasing or being chased; f'. jumping in water. Arrow indicates increasing speed of locomotion. Abbreviations: GS, genal spine impressions (GS); M, median impressions; P, pusher imprints; T, simple foot imprints. Sketches of A–J. All scale bars = 10 mm.

substrate in Fig. 15E (Caster, 1938, 1944; Seilacher, 2007).

All the above-mentioned behaviours are also expressed from the various kinds of trackways with different speeds. As was mentioned by Gaillard

(2011, p. 69, table 9) and Alberti et al. (2017, pp. 10–11), the locomotion rates of different behaviours are mainly related to the series angles (or the angle of the simple foot imprints towards the midline), the length of series

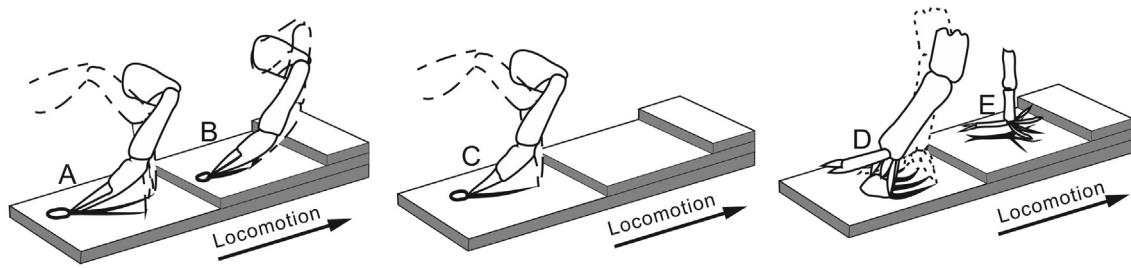


Fig. 15. Sketch showing the formation of various simple foot imprints (T) and pusher imprints (P). A. The production of V-shaped and Y-shaped simple foot imprints (T); B, C. The different possible causes of Nail-head simple foot imprints (T); D. Possible cause of pusher imprints (P) with dot-like bulge; E. Possible cause of pusher imprints (P) without dot-like bulge (the rear part may be inverse Y-shaped, short straight rod-shaped or even V-shaped). The front parts of these two types maybe had 3–5 digits, shaped by different number of blades on the substrate. The movement path runs from the dashed line to the solid line.

and the length of strides. In addition, it is implied that larger lengths of strides and smaller series angles generally indicate higher locomotion rates (Alberti et al., 2017, pp. 10–11). Although the length of stride may vary according to the size of the trackmakers, the ratio of the length of stride and the length of series (Sd/SL), here supposing α is equal to Sd divided by SL ($\alpha = Sd/SL$), is believed to be the key index to alleviate or even overcome this influence. Besides, the ratio α is closely related to the locomotion rate: $\alpha^{("swimming")} > \alpha^{("running")} > 1 > \alpha^{("walking")} (\sim 0.92) > \alpha^{("crawling")} (\sim 0.63)$ in Gaillard (2011, p. 69, Fig. 10) and Alberti et al. (2017, Fig. 7f) [$\alpha^{("walking")} = Av. Sd/Av. SL = 314.8\text{ mm}/343.7\text{ mm} = 0.92$, Av. Sd = 314.8 mm from Gaillard (2011, p. 62, Table 2), Av. SL = 343.7 mm from Gaillard (2011, p. 62, Table 3); $\alpha^{("crawling")}$ was directly measured from that "crawling specimen" of Gaillard (2011, p. 69, Fig. 10)]. The locomotion rate has a strong relation to the series angle (SA) except for the ratio α . According to the trigonometric functions, the actual series length (ASL) can be calculated by taking the series length (SL) divided by the cosine of the series angle (SA) (ASL = SL/cos (SA), supposing $\beta = \cos (SA)$). So, the ratio α could be improved by replacing the ratio of Sd and ASL (here supposing λ is equal to Sd divided by ASL, $\lambda = Sd/ASL = \alpha \cdot \beta$). The locomotion rate of Gaillard (2011, p. 69, Fig. 10) and Alberti et al. (2017, Fig. 7f) is also well-related to the ratio λ : $\lambda^{("swimming")} > \lambda^{("running")} > 1 > \lambda^{("walking")} (\sim 0.89) > \lambda^{("crawling")} (\sim 0.43)$ [$\beta^{("swimming")} = \beta^{("running")} = 1$; $\beta^{("walking")} = \cos 14.2^\circ = 0.97$, SA = 14.2° from that "walking specimen" of Gaillard (2011, p. 69, Fig. 10 and Table 6); $\beta^{("crawling")} = \cos 47.0^\circ = 0.68$, SA = 47.0° from that "crawling specimen" of Gaillard (2011, p. 69, Fig. 10)]. Thus, the ratio λ should be an index of the relative locomotion rate, if excluding other complex environmental influence, such as the direction of current, current rate and others. The locomotion rate (R) of types (a', b', c', d', e', and f) can be evaluated by the ratio λ (Table 2): $\lambda^{(type\ e')} > \lambda^{(type\ c')} > \lambda^{(type\ d')} > \lambda^{(type\ b')} > \lambda^{(type\ a')} > \lambda^{(type\ f)}$ and $R^{(type\ e')} > R^{(type\ c')} > R^{(type\ d')} > R^{(type\ b')} > R^{(type\ a')} > R^{(type\ f)}$ (Fig. 14).

5.2. Potential size difference indicating sexual dimorphism

Modern limuloids are sexually dimorphic and females are usually larger than males, with a mean female/male size ratio of 1.29 (Wenner and Thompson, 2000; Brockmann and Smith, 2009). This sexual size dimorphism is also reflected in limuloid trackways (Moreau et al., 2014). Our specimens exhibit a wide range of sizes at each horizon (e.g. Table 3), probably in part reflecting sexual dimorphism as well as maturity. The exceptionally well-preserved *Kouphichnium* at Horizon 4 in the Heshangou Formation at the Shichuanhe section (Tables 3; Figs. 7–9) allows the estimation of sexual dimorphism by the size of pusher imprints (P) (especially the length), since the cause of sexual size dimorphism in limuloids is a result of the different number of moults, or a different time to reach the adult state, in males and females (Wenner and Thompson, 2000; Brockmann and Smith, 2009).

The size distribution of the pusher imprints (P) from Horizon 4 (Table 3; Fig. 16A, B) clearly shows two separate groups: one from 11.0–11.4 mm and the other from 8.3–9.6 mm (Fig. 16A, B). This

Table 2

Measurements and indexes for the relative speed of different locomotion styles.

Types	Type a'	Type b'	Type c'	Type d'	Type e'	Type f'
SA	22.1	55.5	43.3	57.0	64.9	0.0
$\alpha = Sd/SL$	0.72	1.02	0.49	1.01	0.63	1.79
$\beta = \cos (SA)$	0.93	0.57	0.73	0.54	0.42	1.00
$\lambda = \alpha \cdot \beta$	0.67	0.58	0.36	0.55	0.26	1.79
Locomotion style	Quick crawling	Wandering	Dragging	Half-crawling & half-walking	A sudden turn	Jumping
Speed (rising trend)	Type e'	Type c'	Type d'	Type b'	Type a'	Type f'

Abbreviations: Sd, stride length; SL, series length.

distinct size differentiation might be explained by sexual dimorphism. Further, except for the mature female pusher imprints (P) with stable large values, the other lengths show a gradual increase that might indicate pusher imprints (P) from different immature age groups and a mature male group.

Table 3

Length and width of all pusher imprints in each specimen from Horizon 4.

No.	Length (mm)	Width (mm)
STS-2	11.3	7.5
Maximum one	11.3	7.5
STS-3	11.0	5.7
Maximum one	8.6	5.7
STS-4	11.0	5.7
Maximum one	9.0	5.6
STS-5	7.7	6.2
Maximum one	9.0	5.6
STS-5	10.8	7.0
Maximum one	11.4	7.2
STS-5	11.2	5.2
Maximum one	7.2	6.4
STS-5	9.6	5.2
Maximum one	8.8	6.8
STS-8	11.4	7.2
Maximum one	7.0	5.6
STS-8	11.4	5.5
Maximum one	9.6	7.0
STS-8	10.5	5.2
Maximum one	9.3	7.0
STS-9	11.4	5.5
Maximum one	11.2	6.8
STS-9	11.2	6.1
Maximum one	11.2	6.8
STS-10	9.6	7.8
Maximum one	9.6	7.8
STS-12	8.3	6.7
Maximum one	8.3	6.7

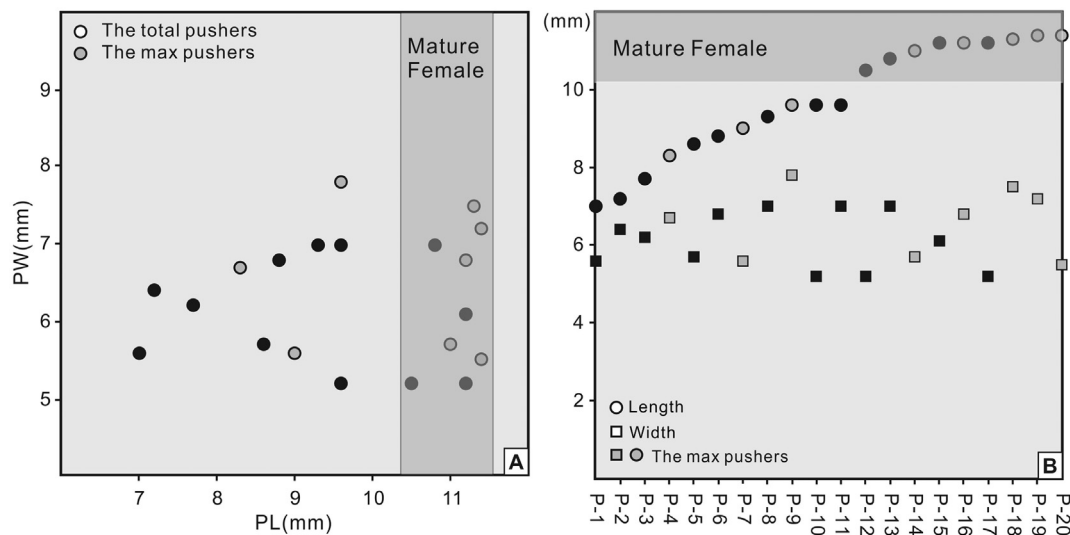


Fig. 16. Measurement of pushers from Horizon 4 of the Heshanggou Formation at the Shichuanhe section, showing the length of pushers related to sexual dimorphism of trackmakers. Abbreviations: PL, length of pusher imprints; P. No., number of pusher imprints; PW, width of pusher imprints; the total pushers refers to all pushers appearing in all specimens; the max. Pusher refers to the pusher with the maximum size in each specimen.

5.3. Variation in limuloid sizes from Late Permian to Early Triassic and implication for the PTME and following recovery

According to the model proposed by Malz (1964), it is possible to estimate size characteristics of limuloids from their tracks, where *I* is the width of the prosoma, *EW* the external width of the trackway, and *L* the total length of the trackmaker. Gaillard (2011) gave two formulae, $I = EW \times 1.5$ and the *I/EW* ratio, calculated from data of modern and fossil limuloids, and limuloid trackways from Caster (1944), Störmer (1952), Malz (1964), and Gaillard (2011). Further, $L = I \times 2.12$ and the *L/I* ratio were based on extant limuloids (Gaillard, 2011). The size of the trackmaker can therefore be deduced from the external width (*EW*) of a limuloid trackway.

The *EW* of trackways is 34.7–46.9 mm in Horizon 1, 8.4–16.7 mm in Horizon 2, 11.8–23.6 mm in Horizon 3, and 24.2–43.3 mm in Horizon 4. So, the sizes of trackmakers in Horizon 1 is estimated at 110.3–149.1 mm in length and 52.1–70.4 mm in width, and it is 26.7–53.1 mm long and 12.6–25.1 mm wide in Horizon 2, 37.5–75.0 mm long and 17.7–35.4 mm wide in Horizon 3, and 77.0–137.7 mm long and 36.3–65.0 mm wide in Horizon 4 (Table 4).

Previous studies demonstrated that the size of *Kouphichnium* in the Early Triassic was more or less larger than that in the Permian, implying a gradual increase from Permian to Triassic (Nielsen, 1949; Beatty et al., 2006; Moreau et al., 2014). However, our study shows a more complex pattern, with the size of limuloids undergoing a drastic decline from the Late Permian to Early Triassic, and then a gradual increase through the Early Triassic (Fig. 17). The temporal size variation through the Permian-Triassic transition in North China sections looks like the “Lilliput effect” phenomenon in some body fossil groups, such as foraminifers, ostracods, gastropods and others (Twitchett, 2007; Forel et al., 2015; Brayard et al., 2011; Payne, 2005; Song et al., 2011; Chu et al., 2015b), as responses to rapid warming, high temperature, dramatically decreased solubility of oxygen, low productivity and allies in the aftermath of the PTME (Payne et al., 2004; Joachimski et al., 2012; Benton and Newell, 2014; Chu et al., 2015a, 2015b). Note that the observed sizes of *Kouphichnium* from the late Early Triassic are clearly smaller than in the Late Permian (Fig. 17), which suggests that the hostile environment did not diminish and life on land had not recovered to the pre-extinction condition, implying co-evolving continental-marine ecosystems in the Early Triassic.

6. Conclusions

Limuloid trackways are described systematically for the first time from the continental Upper Permian to Lower Triassic successions in North China. A new ichnotaxonomic system of *Kouphichnium* is

Table 4
Estimated sizes of trackmakers from Late Permian to Early Triassic.

Age	Horizons	No.	EW (mm)	I (mm)	L (mm)	
Early Triassic	4	STS-11	24.2	36.3	77.0	
		STS-9	29.8	44.7	94.8	
		STS-8	31.8	47.7	101.1	
		STS-3	33.0	49.5	104.9	
		STS-2	43.3	65.0	137.7	
	3	Average			48.6	103.1
		SLL-23	11.8	17.7	37.5	
		SLL-10	11.9	17.9	37.8	
		SLL-12	12.5	18.8	39.8	
		SLL-18-A	12.5	18.8	39.8	
		SLL-18-C	12.5	18.8	39.8	
		SLL-19	14.3	21.5	45.5	
		SLL-8	14.5	21.8	46.1	
		SLL-18-B	15.0	22.5	47.7	
		SLL-22	15.0	22.5	47.7	
		SLL-13	15.6	23.4	49.6	
		SLL-25	16.0	24.0	50.9	
		SLL-15	18.3	27.5	58.2	
		SLL-28	18.4	27.6	58.5	
		SLL-20	20.0	30.0	63.6	
	SLL-11	21.0	31.5	66.8		
	SLL-26	21.7	32.6	69.0		
	Average			23.6	49.9	
	2	SLL-1	8.4	12.6	26.7	
		SLL-2	10.3	15.5	32.8	
		SLL-5	11.4	17.1	36.3	
SLL-3		15.7	23.6	49.9		
SLL-4		16.7	25.1	53.1		
Average				18.8	39.8	
Late Permian		1	STS-1-Tr. 1	34.7	52.1	110.3
			Tr. 2	36.7	55.1	116.7
	Tr. 3		42.9	64.4	136.4	
	Tr. 5		42.9	64.4	136.4	
	Tr. 4		46.9	70.4	149.1	
	Average				61.3	129.8

Abbreviations: EW, external width of a trackway; I, width of trackmaker; L, length of trackmaker.

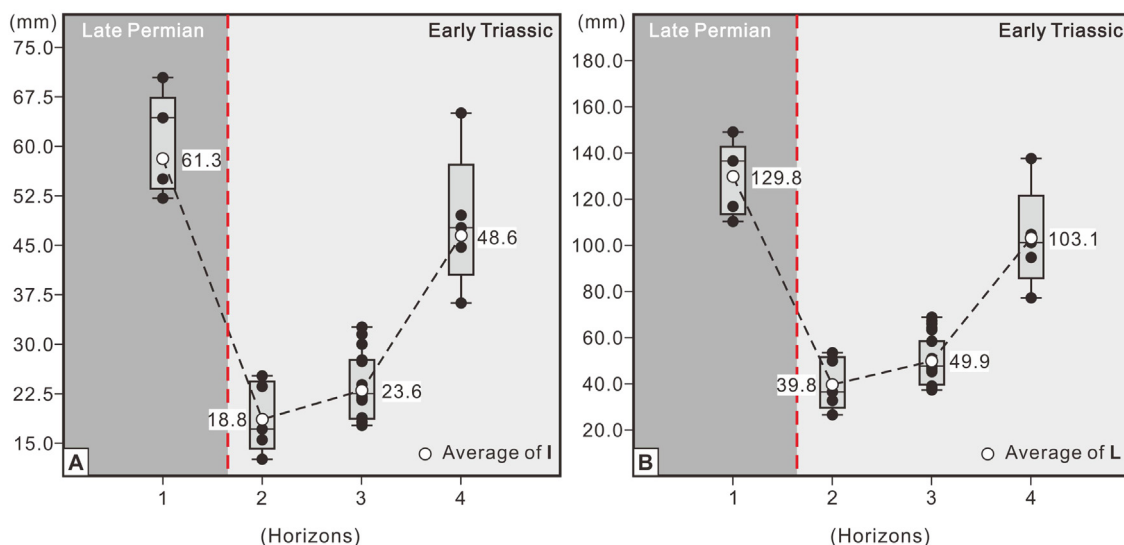


Fig. 17. Plots showing the variation of trackmaker sizes from the Late Permian to Early Triassic in the study sections of North China. A. Width of the trackmakers' prosoma; B. length of the trackmakers. White dots represent the average width of the trackmakers' prosoma (I in A) and length of trackmakers (L in B); Black dots represent all values of measurements; 1, fossil *Kouphichnium* from Horizon 1 in the upper Sunjiagou Formation; 2, fossil *Kouphichnium* from Horizon 2 in the upper Liujiagou Formation; 3, fossil *Kouphichnium* from Horizon 3 in the middle-upper Heshanggou Formation at the Liulin section; 4, fossil *Kouphichnium* from Horizon 4 in the upper Heshanggou Formation at the Shichuanhe section.

proposed, based on the ichnotaxobase of limuloids, including four elements, namely simple foot imprints (T), pusher imprints (P), median impressions (M), and genal spine impressions (GS). One ichnogenus and six ichnospecies are thus identified from the continental Upper Permian to Lower Triassic in North China according to the new ichnotaxobase, including a new ichnospecies, *Kouphichnium liulinensis* sp. nov. The diagnosis of ichnogenus *Kouphichnium* and two early ichnospecies, the type species *Kouphichnium lithographicum* Ooppel and *Kouphichnium didactylum* Willard, are revised. A general morphological-palaeoethological pattern is summarized based on the six ichnospecies of *Kouphichnium* from North China. Moreover, Index λ is introduced to express the relative locomotion rates of various *Kouphichnium* trackmakers in palaeoethology.

By estimating the sizes of limuloid trackmakers from the external widths of their trackways, it is concluded that the sizes of trackmakers declined drastically from the Late Permian to Early Triassic, followed by a gradual increase through the Early Triassic. This drastic drop of trackmaker size might be the response to the great Permian-Triassic transitional events and it also suggests that the hostile environments did not fade away and life not recover back to pre-extinction levels on land during the Early Triassic, probably implying co-evolving continental-marine ecosystems through the Permian-Triassic transition. In addition, the size differentiation of pusher imprints (P) from well-preserved specimens from Horizon 4 (an Early Triassic limuloid population) probably shows sexual dimorphism.

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