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Jean-David Moreau, Emmanuel Fara, Georges Gand, Gérard Lafaurie, Louis Baret. Gigantism among Late Jurassic limulids: New ichnological evidence from the Causses Basin (Lozère, France) and comments on body-size evolution among horseshoe crabs. Geobios, 2014, 47 (4), pp.237-253. 10.1016/j.geobios.2014.06.005 . insu-01061091

HAL Id: insu-01061091
https://insu.hal.science/insu-01061091

Submitted on 5 Sep 2014

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Gigantism among Late Jurassic limulids: new ichnological evidence from the Causses Basin (Lozère, France) and comments on body-size evolution among horseshoe crabs ✡

Jean-David Moreau [a,*], Emmanuel Fara [b], Georges Gand [b], Gérard Lafaurie [c], Louis Baret [d]

[a] Laboratoire Géosciences, CNRS UMR 6118, Université de Rennes 1, Campus de Beaulieu bât. 15, 263 Avenue du Général Leclerc, 35042 Rennes, France.

[b] Laboratoire Biogéosciences, CNRS UMR 6282, Université de Bourgogne, 6 Boulevard Gabriel, 21000 Dijon, France.

[c] 10 rue Léon Baraillé, 46100 Figeac, France.

[d] Association Paléontologique des Hauts Plateaux du Languedoc, 14 Chemin des Ecureuils, 48000 Mende, France.

✡ Corresponding editor: Davide Olivero.

* Corresponding author; e-mail address: jean.david.moreau@gmail.com (J.-D. Moreau)

Abstract

An abundant ichnological material composed of xiphosuran trackways and isolated traces was discovered in Upper Jurassic limestones from the Causses Basin (Causse Méjean, Lozère, France). The morphology of the imprints supports their identification as *Kouphichnium* isp. In contrast to the most frequent case, the trackways are composed of omnipresent pusher imprints sometime associated with leg traces, but with no telson mark. We argue that this pattern reflects actual surface traces rather than an incomplete set of undertracks. The size distribution of the sampled ichnites is broadly bimodal. This is best explained by sexual dimorphism, a phenomenon frequently observed in modern xiphosurans. Analysis of the trace fossils further suggests that several growth stages are recorded and that the horseshoe crabs were walking in a protected and flat environment like a lagoon. This area,

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certainly close to a mating ground, was occasionally affected by a continental influence. The biometric study of the tracks suggests a gigantic size for the trackmakers whose body may have reached 84 cm in length. This discovery complements the few reports on other gigantic horseshoe crabs in the Jurassic of Western Europe, thus casting doubt on the postulated increase in body size from the Palaeozoic to the Recent. Furthermore, a literature review shows that there are still major gaps in the record of limulid body-fossils and tracks. Thus, neither of these archives can be taken at face value for quantifying the body-size evolution of horseshoe crabs.

Keywords:
Limulid traces
Xiphosura
Kouphichnium
Late Jurassic
Causses Basin
Body size

1. Introduction

Horseshoe crabs (Merostomata, Xiphosura) are known since the Palaeozoic (e.g., Rudkin et al., 2008) and are represented by four modern species (Sekigushi and Shuster, 2009; Obst et al., 2012). Their body fossils have a sporadic but broad geographical and stratigraphical distribution (Table 1). Their traces, most frequently assigned to the ichnogenus *Kouphichnium* (Nopsca, 1923), also occur sporadically on nearly all continents in rocks dated from the Late Devonian to the Oligocene (Table 1). Although Fernández and Pazos (2013) mentioned the relative scarcity of Mesozoic xiphosuran trace fossils, many occurrences of *Kouphichnium* are known from that time span (Table 1); recent discoveries further confirm the abundance of this ichnotaxon in the Mesozoic geological record (Pieńkowski and Niedźwiedzki, 2009; Gaillard, 2011; Diedrich, 2011; Fernández and Pazos, 2013; Peyre de Fabrègues and Allain, 2013). In this context, Late Jurassic occurrences of *Kouphichnium* are particularly significant for at least three reasons:

- Several of those occurrences are extremely well-documented in Fossil-Konservat-Lagerstätten, such as the famous mortichnial trackways associated with its trackmaker *Mesolimulus walchii* (Desmarest, 1817) from the Solnhofen

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Lithographic Limestones Formation (Desmarest, 1822; Maltz, 1964; Lomax and Racay, 2012);

- The Jurassic is the period during which the extant clade Limulinae von Zittel appeared in Europe, before being biogeographically isolated from its sister-group Trachypleinae Pocock at the dawn of the Cretaceous (Shishikura et al., 1982; Schuster, 1982);
- Gigantic trackways have been reported from Upper Jurassic Lagerstätten in Germany (Schweigert, 1998; Schweigert and Dietl, 2002) and France (Gaillard, 2011), thus questioning the supposed general increase in xiphosuran body size from the Palaeozoic to the Recent (Størmer, 1952; Diedrich, 2011).

Here we report on a new and abundant ichnological material composed of xiphosuran trackways and isolated traces that were discovered in upper Kimmeridgian/lower Tithonian strata from the Causses Basin (Lozère, France). This material is the first evidence of Late Jurassic xiphosurans in this region and it shows that some of these animals had a gigantic body size. The aims of this study are: (i) to characterize and to identify these traces, and (ii) to discuss their size and morphology based upon a quantitative analysis in order to better define the ecological features of Late Jurassic horseshoe crabs.

2. Geographical and geological setting

The ichnofossils were discovered in upper Kimmeridgian/lower Tithonian sediments of a quarry located 5 km east of Hures-la-Parade and that is not accessible anymore. It is located south of the Massif Central, in the Causses Basin (Causse Méjean, France; Fig. 1). In this area, the upper Kimmeridgian/lower Tithonian strata are divided in two units (Brouder et al., 1977; Gèze et al., 1980). The first one corresponds to white bioclastic limestones, locally and partially dolomitized, containing serpulids, bivalves and brachiopods (e.g., *Zeilleria humeralis* Roemer). The second one is composed of grey dolomites and rare coral limestones or local white-to-pink sublithographic limestones (Brouder et al., 1977). The ichnofossils described here were found in this latter lithological unit that is very homogenous and isopach. Fossils are rare as only some ammonites, belemnites, bivalves, echinids, fishes, crustaceans and terrestrial plants were reported and preserved as compressions. One continental vertebrate (the rhynchocephalian *Leptosaurus pulchellus* Zittel) was reported from these sublithographic limestones of the Causse Méjean (Bousquet and Vianey Liaud, 2001). Although Brouder et al. (1977) proposed a late Kimmeridgian age for these levels, we prefer to moderate their chronostratigraphic assignment for two reasons: (i) Brouder et al. (1977) could not justify

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their proposal with biostratigraphic evidence, and (ii) we noted the occurrence of rare ammonites assignable to cf. *Subplanites* Spath at the top of the quarry. In the absence of any firm biochronological evidence, we thus tentatively assign a late Kimmeridgian/early Tithonian age to the trace-bearing strata. In the Hures-la-Parade quarry, the section is only constituted by sublithographic limestones, and the limulid trackways occur recurrently along the stratigraphic column (Fig. 2).Three surfaces of unit 1 yielded most of the trace fossils. In this unit, thin sinusoidal traces ascribed to the ichnogenus *Cochlichnus* Hitchcock (whose trackmakers are either annelid worms, nematods or larvae of dipteran insects; Hasiotis, 2004) are frequently associated with the limulid trackways.

3. Material and Methods

Traces were successively observed by three of us: G.L. during 1994, then L.B. and J-D.M. in 2005. It was possible to localize the occurrence of imprints in the stratigraphical column but due to the activity of the quarry the samples available for study were mainly collected on isolated blocks. Thirteen trackways distributed in four large assemblages were discovered (Figs. 3-5). Assemblages are named "A" to "D" and are composed of trackways 1-6; 7; 8, 9 and 10-13, respectively. Each trace is designated by the letter of the assemblage followed by the step number. When possible, the letter "R" or "L" are used to indicate the side (right or left) of individual track. These ichnofossils are either preserved as convex epirelief (Assemblages A, B and D; Figs. 3, 5), or as concave hyporelief (Assemblage C; Fig. 4). Only Assemblage C was observed *in situ* (Unit 1; Fig. 2).

Typically, the concave ventral surface of limulid body possesses six pairs of cephalothoracic appendages (Hoeven, 1838; Seilacher, 2007; Fig. 6). The first pair corresponds to the chelicerae and the second to the pedipalps. Pairs III, IV and V are walking legs and are morphologically similar to the pedipalps. They are constituted of six segments: the coxa, trochanter, femur, patella, tibia and tarsus. The chelicerae are smaller and are composed of three articles only. The appendages I to V are chelate; the tibia and tarsus form a pincer (chela) at their distal extremity. The sixth pair forms the pusher limbs or "pushers" (Abel, 1935; Caster, 1938; Seilacher, 2007) that are used by the animal to propel its body during locomotion or for digging. This pair of appendages differs morphologically from the others (Fig. 6). In most fossil and living taxa, its tarsus has four large pusher "blades" which are extended when the limb is in contact with the sediment (Fig. 6(C)). The pretarsus of the pushers is elongated and has a structure like a short pincer or "tarsal spine" on its extremity. A complete trackway of limulids would typically be composed of traces of appendages II-VI

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together with the median impression of the telson (Caster, 1938, 1944). Ichnofossils from Hures-la-Parade do not show imprint of the prosoma and of the telson (Fig. 6(A)). In contrast, traces of the pusher limbs are abundant and well-marked on trackways or as isolated tracks. Trackways are mainly constituted by pusher imprints (Figs. 3-5, 7), and only one was made by walking legs (Fig. 8(M), unit 6). A total of 85 pusher traces belong to the trackway assemblages and 61 others are isolated traces found on various floating limestone slabs. Isolated pusher traces are named "I" followed by a number. Unfortunately, the active carrying activities could not allow us to save assemblages C and D for which only photographs are now available. All other specimens are housed in the public collections of the *Association Paléontologique des Hauts Plateaux du Languedoc* (A.P.H.P.L., Mende, Lozère, France).

The descriptive terminology used here follows Minter et al., (2007a), and biometric parameters measured on tracks and imprints are derived from Tyler (1988) and Gaillard (2011) (Fig. 7). We also measured the length of the anterior part of the pusher tracks because their posterior ends are sometime missing.

4. Systematic palaeontology

Ichnogenus ***Kouphichnium*** Nopsca, 1923

Type species: Ichnites lithographicus Oppel, 1862

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

Kouphichnium isp.

Description:

Trackways: Right and left pusher traces of a same step are opposite (Fig. 7). Pairs form generally a repetitive motif on each step (e.g., Trackway 1 of Assemblage A and Trackway 8 of Assemblage C; Figs. 3(A-C), 4). Traces of the pusher limb overlap in one case only (trace B9 in Assemblage B; Fig. 3(D)).The biometric characterization of the tracks is given in Tables 2-4. Extreme values of internal trackway width are 105 and 188 mm. Extreme values of external trackway width are 160 and 262 mm. Strides have a wide range of values (26-334 mm). The stride is often constant within the trackways (Assemblage A, Trackway 6;

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Fig. 3(A-C)), but it can be heterogenous in rare instances (Table 4; e.g., Assemblage D, Trackway 10; Fig. 5). For example, Trackway 10 shows a doubling of the second step on the left side (D2L and D2L').

Pusher and leg traces: The trackway only composed by leg imprints (Fig. 8(M)) shows that ichnites formed thin traces disposed perpendicularly to the trackway axis. The bifid extremities of the imprints are disposed externally to the track. On pusher trackways, leg traces are constituted by a thin line with an anterior bifid part forming an acute angle open toward the front of the track. This bifid part is the imprint of the pincer of walking legs. The association of leg and pusher traces is only and partially present on Assemblages A (Trackway3; Fig. 3).

Biometric values of pusher traces are synthesized in Tables 5 and 6. Although the width of these traces is rather constant within the trackways (Table 4), the imprints of pusher limbs are heterogeneously preserved along a same trackway (e.g., Trackway 10; Fig. 5). The anterior part of individual pusher imprints is constituted by the four triangular or digit-like marks of the pusher blades (Figs. 7, 8). In some traces, the two central digit-like marks are shorter and tend to be fainter than the external ones (Fig. 8(A-L)). This ichnological pattern is in agreement with the anatomy of the pusher limb (Fig. 6(C)). Blade imprints are sometime slightly curved and oriented inwardly (e.g., Trackways 7 and 9; Figs. 3, 4). The posterior part of the pusher trace is an elongated and thin furrow made by the tarsus. This posterior mark is absent in 26% (n = 146) of pusher traces (e.g., Assemblages A and C; Trackways 2 and 8; Figs. 3, 4). The extremity of the furrow is generally bifid as it corresponds to the imprint of the pretarsus.

5. Discussion

5.1. Taxonomic assignment

The morphology of the tracks from the Causses Basin shares many similarities with the xiphosuran locomotion traces firstly named *Ichnites lithographicus* by Oppel (1862) and later named *Kouphichnium lithographicum* by Nopsa (1923). In France, beside some rare reported occurrences in the Carboniferous (Racheboeuf et al., 2002; Crônier and Courville, 2005) and the Triassic (Gall, 1971), xiphosurans are only documented in the Cerin Lagerstätte (southern Jura Mountains, late Kimmeridgian/early Tithonian) by a few body fossils and one limulid trackway (Gall et al., 1996; Gaillard, 2011), as well as by a Tithonian trackway from Canjuers, southeastern France (Peyre de Fabrègues and Allain, 2013). All these late Jurassic traces were assigned to *Kouphichnium*. This ichnogenus was also reported from the

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contemporaneous sites of Nusplingen, Germany (Schweigert, 1998; Schweigert and Dietl, 2002) and from the Morrison Formation, USA (Hasiotis, 2004).

Kouphichnium is characterized by strongly heteropodous tracks that might show a large variety of shapes (Oppel, 1862; Nopsca, 1923; Caster, 1938; Malz, 1964). In contrast, the repichnia from the Causses Basin have a rather homogeneous morphology. The trackways and traces from Hures-la-Parade are morphologically similar to the *Kouphichnium* trackways from Cerin and Canjuers, France (Gaillard, 2011; Peyre de Fabrègues and Allain, 2013). The material from Cerin corresponds to a single trackway with leg and pusher imprints assigned to *Kouphichnium lithographicum*. The biometric characteristics of the pusher traces from Cerin are close to those described here. However, pending a comprehensive taxonomic revision of limulid traces and of the numerous species of *Kouphichnium*, we refrain ourselves from assigning our material to an ichnospecies and refer it to *Kouphichnium* isp. We agree with many other authors who suggested a whole revision of this ichnogenus and its ichnospecies (e.g., Buatois et al., 1998; Romano and Whyte, 2003; Lucas et al., 2006; Lucas and Lerner, 2005; Gaillard, 2011; Fernández and Pazos, 2013).

5.2. Size of the trackmakers

Fig. 9 shows the broad range of size for the pusher traces whose total length varies from 11 to 69 mm (Tables 5, 6). This distribution is coarsely bimodal, as observed in several fossil and recent limulid trackways or populations (Caster, 1938; Tyler, 1988; Penn and Brockmann, 1995; Smith et al., 2009). Except one small trace 11 mm long, the first cluster forms a rather continuous distribution of pusher lengths comprised between 17 mm and *ca.* 50 mm. After a gap between 50 mm and 60-65 mm, there is second, more contracted cluster of pusher tracks whose lengths are essentially comprised between 65 mm and 70 mm (Fig. 9). The large extent of the first cluster may be interpreted as representative of various growth stages. The presence of two clusters certainly reflects the sexual dimorphism in body size frequently observed among modern horseshoe crabs, females being about one third larger than males (Caster, 1938; Shuster, 1982; Smith et al., 2009). Consequently, the first cluster was probably made by individuals of both sexes at various growth stages and by adult males, whereas the second cluster probably represents adult females.

According to Malz (1964), the size of the trackmaker can be deduced from the external width (= Ex.W) of a limulid trackway (Fig. 7). For the extant *Limulus polyphemus* Linnaeus, the width of the prosoma and the total length of the body are respectively 1.50 and 2.12 times longer than Ex.W (Malz, 1964); these ratios are similar for other modern limulids

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(Sekiguchi, 1988). Such a simple calculation yields an estimated prosomal width of 24.0 to 39.3 cm and a body length of 50.9 to 83.3 cm for the trackmakers of the Hures-la-Parade quarry. These large values are close to those reported by Gaillard (2011) for the trackway of Cerin (estimated body length: 77.4 to 85.1 cm) and higher than those of most modern limulids. If the report by Goldring and Seilacher (1971) on Early Jurassic traces (Lias of Plochingen, Germany) made by 40 cm-wide limulids can be confirmed, it would be, to our knowledge, the oldest occurrence of very large limulid traces. It seems that the epicontinental seas of Western Europe were locally favorable to gigantic limulids during the Late Jurassic (Schweigert, 1998; Schweigert and Dietl, 2002; Gaillard, 2011; this study). In turn, these very large tracks contradict the idea of a progressive size increase for limulids over geological times (Størmer, 1952; Diedrich, 2011). In order to explore this issue further, we synthetized 90 published papers in which the width of prosoma and/or trackways were reported for Phanerozoic horseshoe crabs (Table 1; Fig. 10). Direct measures of prosomal width (black bars and dots in Fig. 10) suggest that the maximal size has increased through time. However, this pattern cannot be interpreted as a genuine evolutionary trend for several reasons. First because the values include different ontogenetic stages, males and females, as well as freshwater *vs*. marine taxa (the formers, which were smaller than the latters, became extinct in the Jurassic; Hauschke and Wilde, 1991). Second because most extant horseshoe crabs have a prosomal width comprised between 10 and 30 cm, and they rarely reach 35 cm or more. Third because the limulid track record is at odd with the data provided by body fossils (Fig. 10). The gigantic Jurassic trackways are nearly twice as large as the largest limulid body-fossils known for this geological period, and the corresponding estimated prosomal width is close to 50 cm (dotted line in Fig. 10). The absence of recorded trackways for the entire Neogene is also noteworthy. Overall, these data show that there are major gaps in the record of limulid body-fossils and tracks, and that neither of these archives can be taken at face value for quantifying the body-size evolution in this clade. The tracks from Hures-la-Parade support the view that a gigantic size may have been frequent among some Tethyan horseshoe crabs in the Late Jurassic.

5.3. Taphonomic and palaeoethological implications

The variability of trace fossils arises from the complex combination of taphonomic and palaeoethological factors, and the highly variable *Kouphichnium* is no exception (Caster, 1938; Goldring and Seilacher, 1971; Häntzschel, 1975; Buatois and Mángano, 2011). The limulid trace fossils from the Hures-la-Parade quarry are characterized by the systematic

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presence of pusher imprints, the rarity of leg imprints, and the absence of prosoma and telson mark. How to explain such a pattern? Goldring and Seilacher (1971) warned that the best preserved arthropod tracks may represent undertracks rather than true tracks for taphonomic reasons. Indeed, traces left at the water-sediment surface may be instable and easily erased by water movements. In contrast, undertracks may be better preserved but they usually record only a part of the original trackway due to undertrack fallout, that is, the appendices having the shallowest contact with the substratum are not preserved in deeper laminae (Goldring and Seilacher, 1971). This taphonomic scenario is consistent with the preservational features of the imprints described here and that could therefore be interpreted as a repichnia made of an incomplete set of undertracks. However, two main arguments can be put forward to moderate this interpretation. First, it does not consider the probable presence of microbial mats developed at the sediment surface and that plays a crucial role in the preservation of many types of original trackways. Although such a microbially-induced preservation of true tracks still needs to be confirmed for the lithographic limestone of the Hures-la-Parade quarry, it has already been reported for the analogous site of Cerin (Gaillard, 2011) and for sedimentologically distinct *Kouphichnium*-bearing sites (e.g., Fernández and Pazos, 2013). Second, genuine pusher-only trackways are known to be produced by extant horseshoe crabs as a direct consequence of behavioral rather than taphonomical factors. For example, Caster (1938) and Gaillard (2011) observed that modern horseshoe crabs produce such trackways while speeding up their demersal swimming or walking. During propulsion, the anterior appendages are retracted, the body weight is supported by the pusher limbs whose imprints are generally sharp and can even be made by the four anterior blades only (Lessertisseur, 1955; Tyler, 1988; Romano and Whyte, 2003). Such a pattern is consistent with the trackways and isolated tracks from the Hures-la-Parade quarry: pusher imprints predominate, their posterior part is not recorded in 26% of cases, and they are rarely associated with imprints of other walking legs. This is very similar to the trackway from Cerin described by Gaillard (2011). This author attributed these surface or sub-surface traces to a limulid walking vigorously on the sea-floor. We concur with his interpretation and we argue that it also applies to the ichnites described here. Fig. 11 shows that for strides of comparable dimensions, the widths of pusher tracks recorded in the Causses Basin and in Cerin are similar. The great heterogeneity of strides observed between the different trackways from Hures-la-Parade may be explained by a large range of body size (Table 4). However, Fig. 11 shows that the relation between the strides and the pusher dimensions is not linear. The long strides are associated with pushers having a medium size (width between 32 and 43 mm).

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This suggests that medium-sized horseshoe crabs may have been more vigorous or faster than larger ones.

5.4. Palaeoenvironmental implications

Living horseshoe crabs are ecological generalists that can live in diverse habitats mostly located on the continental shelf and up to the tidal zone (Sekigushi and Shuster, 2009). In the fossil record, limulids and their traces have been reported from a broad range of palaeoenvironments. The ichnogenus *Kouphichnium* was reported both from non-marine and freshwater palaeoenvironments (Hardy, 1970; Hasiotis and Dubiel, 1993; Hasiotis, 2004; Pieńkowski and Niedźwiedzki, 2009), ephemeral freshwater lakes (Pollard and Hardy, 1991; Zhang et al., 1998; Lucas et al., 2006), lagoons (Gaillard, 2011; Peyre de Fabrègues and Allain, 2013), estuaries (Lucas and Lerner, 2005), tidal flat areas (Gastaldo et al., 1989; Harris and Lacovara, 2004; Diedrich, 2011; Fernández and Pazos, 2013), and coastal plains (Romano and Whyte, 2003).

The ichnological association of horizontal traces such as *Kouphichnium* and *Cochlichnus* has been reported in tidal flat environments (Gastaldo et al., 1989).The coral facies known in the upper Kimmeridgian/lower Tithonian of the Causse Méjean (Brouder et al., 1977) and the presence of some echinoderms, ammonites and belemnites all argue in favor of a marine palaeoenvironment. However, the rare terrestrial fossil plants and vertebrates suppose that the area was occasionally open to continental influences. Jarzembowski (1989) noted that xiphosurid traces are often present in poorly fossiliferous strata, and this is the case in the Hures-la-Parade quarry too. The lithographic nature of the limestones supports the hypothesis of a protected environment like a lagoon or a bay. The numerous occurrences of traces along the stratigraphic column suggest that this area was close to a regular mating ground, as was probably the case for many other *Kouphichnium* assemblages (Caster, 1938; Diedrich, 2011; Fernández and Pazos, 2013).

6. Conclusion

The Upper Jurassic fossil traces from the Hures-la-Parade quarry can be confidently assigned to *Kouphichnium* isp. This is the first evidence of this heteropodous ichnotaxon in the Causses Basin. Although *Kouphichnium* is fundamentally characterized by a great variability, the reported tracks and trackways have a homogenous morphology as most of them show omnipresent and well-preserved pusher imprints. We suggest that this pattern reflects the actual surface or sub-surface traces rather than an incomplete set of deep

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undertracks. The biometric study of these traces suggests a gigantic size for the trackmakers whose body length may have reached 84 cm. This discovery complements a few other reports of contemporaneous gigantic horseshoe crabs in Western Europe, thus casting doubt on their postulated increase in body size from the Palaeozoic to the Recent. These traces likely represent various growth stages as well as sexually dimorphic adult limulids. Analysis of the trace fossils suggests that the horseshoe crabs vigorously walked in a protected and flat environment like a lagoon, probably close to a mating ground.

Acknowledgements

We thank Sylvain Charbonnier and Günter Schweigert for their constructive reviews on the manuscript, as well as Gilles Escarguel for his rigorous editorial suggestions. We address our sincere thanks to Jacques Fages, the owner of the quarry and André Baret, the mayor of the municipality who gave their agreements for palaeontological sampling in the area under their care. We thank Norbert Hauschke, Dean Lomax, Ruth Carmichael, James Lamsdell, Günter Schweigert and Ronan Allain who kindly shared bibliographic references and data with us.

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Table and Figure captions

Table 1. Synthesis of widths measured on xiphosurid bodies and trackways from the Palaeozoic to the Recent (in cm). *: Dimension estimated from published illustrations.

Table 2. Measurements of internal and external widths of trackways (in mm).

Table 3. Measurements of the strides (in mm).

Table 4. Mean and standard deviation (SD) values of stride length and width of pushers for each trackway (in mm).

Table 5. Measurements of width, total length and length of the anterior part of the pusher imprints preserved on trackways (in mm).

Table 6. Measurements of width, total length and length of the anterior part of the isolated pusher imprints (in mm).

Figure 1. Location and geological context of the Causses Basin. The star indicates the Hures-la-Parade quarry (late Kimmeridgian/early Tithonian). Modified after Grigniac and Taugourdeau-Lantz (1982).

Figure 2. Stratigraphic occurrences of the trace-bearing surfaces. **A**: stratigraphic log of the Hures-la-Parade quarry. **B**: detail of the top of the section (lithological unit 6). L. Un., lithological units (1 to 6); L. S. Un., lithological sub-units (S1 to S21); Lith., lithology. Scale bars: 1 m (A), 20 cm (B).

Figure 3. Two assemblages bearing limulid trackways. **A-C**: Assemblage A, photograph and interpretation; T1-T6 = Pusher trackways 1 to 6, A1-A26 = step number. **D**: Assemblage B; T7 = Pusher trackway 7, B1-B26 = step number. R = right, L = left. The arrows indicate the direction of movement. Scale bars: 20 cm (A-C), 10 cm (D).

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Figure 4. One assemblage bearing limulid trackways. **A, B**: Assemblage C, photograph and interpretation; T8, T9 = Pusher trackways 8 and 9, C1-C6 = step number. R = right, L = left. Scale bar: 20 cm.

Figure 5. One assemblage bearing limulid trackways. **A-C**: Assemblage D, photograph and interpretation; T10-T13 = Pusher trackways 10 to 13, D1-D16 = step number. R = right, L = left. The arrows indicate the direction of movement. Scale bar: 20 cm.

Figure 6. Anatomy of limulid appendages. **A**: simplified ventral view of a limulid showing the six pairs of appendages I-VI. **B**: left sixth appendage or "pusher limb" with blades regrouped in resting position. **C**: distal part of the sixth appendage showing the spread of pusher blades during propulsion. I, chelicerae; II, pedipalps; III, IV and V, walking legs; VI, pusher limbs. 1, coxa; 2, trochanter; 3, femur; 4, patella; 5, tibia; 6, tarsus; Pb., pusher blades; Ts., tarsal spines.

Figure 7. Biometric characters measured on trackways and pusher traces. W, width; TL, total length; Lap, length of the anterior part; St, stride; In.W, inner width; Ex.W, external width.

Figure 8. Illustration of some traces of the sixth cephalothoracic appendage. **A-L**: APHPL_I2, APHPL_I8B, APHPL_I11, APHPL_I12, APHPL_I25, APHPL_I36, APHPL_I37A, APHPL_D8, APHPL_I39B, APHPL_I48, APHPL_I45, and APHPL_I49, respectively. **M**: APHPL_L1, trackway composed of legs only. Scale bar: 1 cm.

Figure 9. Bivariate diagram (width *vs*. total length) of limulid traces from the Hures-la-Parade quarry and from Cerin (Gaillard, 2011).

Figure 10. Variation in width as measured on limulid bodies (black dots and bars) and trackways (white dots and bars) from the Palaeozoic to the Recent. The dotted line represents the maximal prosomal width inferred from the external width of trackways based on the 1.5 ratio given by Malz (1964). The measured width of the trackway from Hures-la-Parade, as well as the corresponding estimated prosomal width, are indicated by a white square and a white star, respectively. Data from the references listed in Table 1. Є, Cambrian; O, Ordovician; S, Silurian; D, Devonian; C, Carboniferous; P, Permian; T, Triassic; J, Jurassic; K, Cretaceous; Pg, Palaeogene; N, Neogene; Q, Quaternary.

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Figure 11. Bivariate diagram showing the average values of pusher widths and strides for each trackway from the Hures-la-Parade quarry and Cerin (Gaillard, 2011). Dashed contour line: 95 % confidence interval.

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Table 1.

Age	Locality	Body	Trace	Body width	Trackway width	Reference
Ordovician	Manitoba, Canada	1	0	2.6	-	Rudkin et al. (2008)
Devonian	Parkes, Australia	1	0	6	-	Pickett (1993)
Devonian	Pennsylvania, USA	1	1	5*	about 2.2*	Babcock et al. (1995)
Carboniferous	Graissessac, France	1	0	2.5	-	Crônier and Courville (2005)
Carboniferous	Montceau-les-Mines, France	1	0	0.8*	-	Anderson (1997)
Carboniferous	Montceau-les-Mines, France	1	0	0.84–1.08	-	Racheboeuf et al. (2002)
Carboniferous	Piesberg, Germany	1	0	0.7–6	-	Haug et al. (2012)
Carboniferous	Sosnowiec Basin, Poland	1	0	2.0–4.8	-	Filipiac and Krawczyński (1996)
Carboniferous	Bude Formation, south-west UK	0	1	-	0.03–0.20	Tyler (1988)
Carboniferous	Central Pennine Basin, UK	0	1	-	2.8	Eagar et al. (1985)
Carboniferous	Country Durham, UK	1	0	1.5	-	Siveter and Selden (1987)
Carboniferous	Cornwall, UK	0	1	-	?	Goldring and Seilacher (1971)
Carboniferous	Lancashire, UK	0	1	-	0.16–0.17	Hardy (1970)
Carboniferous	Lancashire, UK	0	1	-	3	Chisholm (1983)
Carboniferous	Lancashire, UK	1	0	about 3.3*	-	Anderson et al. (1999)
Carboniferous	Lancashire, UK	1	0	about 3.7*	-	Anderson and Selden (1997)
Carboniferous	Pantyffynon, UK	1	0	up to 1*	-	Anderson and Horrock (1995)
Carboniferous	Writhlington, UK	1	1	less than 3*	?	Jarzembowski 1989)
Carboniferous	Writhlington, UK	0	1	-	2.5–5.0	Pollard and Hardy (1991)
Carboniferous	Alabama, USA	0	1	-	3–4	Lucas and Lerner (2005)
Carboniferous	Alabama, USA	0	1	-	2.5–7.5	Buta et al. (2005)
Carboniferous	Alabama, USA	0	1	-	up to 2*	Gastaldo et al. (1989)
Carboniferous	Illinois, USA	1	0	up to 7*	-	Anderson (1994)
Carboniferous	Kansas, USA	0	1	-	1.96–5.11	Buatois et al. (1998)
Carboniferous	Kansas, USA	0	1	-	1.3–5.5	Bandel (1967)
Carboniferous	Kansas, USA	1	0	up to 7*	-	Babcock and Merriam (2000)
Carboniferous	Montana, USA	1	0	2.1–2.2	-	Moore et al. (2007)
Carboniferous	Pennsylvania, USA	0	1	-	?	Fillmore et al. (2010)
Carboniferous	Tennessee, USA	0	1	-	up to 11	Miller (1982)
Uppermost Carboniferous/Permian	Kansas, USA	1	0	up to 9*	-	Babcock et al. (2000)
Permian	Great Karoo Basin, Africa	0	1	-	about 8*	Anderson (1975)
Permian (?)	Western Argentina	0	1	-	?	Zang et al. (1998)
Permian	Hessen, Germany	1	0	about 15	-	Hauschke and Wilde (1989)
Permian	India	0	1	-	up to 9*	Chakraborty and Bhattacharya (2012)
Permian	Kansas, USA	1	0	?	-	Beecher (1904)
Permian	New Mexico, USA	0	1	-	up to 5	Minter and Braddy (2009)
Permian	Texas, USA	0	1	-	?	Minter et al. (2007b)
Permian	Texas, USA	1	0	up to 1.348	-	Allen and Feldmann (2005)
Permian	Texas, USA	1	0	2.4	-	Dunbar (1923)
Triassic	Australia	1	0	2.78	-	Pickett (1984)
Triassic	Vosges, France	0	1	-	5–12	Gall (1971)
Triassic	Bernburg, Germany	0	1	-	6–10	Diedrich (2011)
Triassic	Northwestern, Germany	1	1	up to 1.47	about 2.5	Hauschke and Wilde (1987)
Triassic	Rüdersdorf, Germany	1	0	10	-	Hauschke et al. (1992)
Triassic	Southern Germany	1	0	0.8–2.9	-	Hauschke and Wilde (2008)
Triassic	East Greenland	0	1	-	3.5–7.5	Nielsen (1949)
Triassic	Ankitokazo Basin, Madagascar	1	0	about 5 and 7	-	Hauschke et al. (2004)
Triassic	Tarragona Province, Spain	1	0	3.1–5.3	-	Vía Boada 1987; Roméro and Vía Boada (1977)
Triassic	Spain	1	0	less than 20	-	Vía Boada and Villalta (1966)
Triassic	Staffordshire, UK	0	1	-	1.5–2.0	Wright and Benton (1987)
Triassic	Westbury Formation, UK	0	1	-	7–8	Wang (1993)
Triassic	Arizona, USA	0	1	-	8–10	Hunt et al. (1993)
Triassic	Arizona, USA	0	1	-	?	Hasiotis and Dubiel (1993)
Triassic	Arizona, USA	0	1	-	6.5	Caster (1944)
Triassic	Pinceton (New Jercey), USA	0	1	-	?	Goldring and Seilacher (1971)
Triassic	Utah, USA	0	1	-	less than 8*	Hamblin and Foster (2000)
Jurassic	Canjuers, France	0	1	-	17.2–17.5	Peyre de Fabrèges and Allain (2013)
Jurassic	Causses Basin, France	0	1	-	10.0–26.2	This study
Jurassic	Cerin, France	1	0	9–16	-	Gall et al. (1996)
Jurassic	Cerin, France	0	1	-	25.7–26.0	Gaillard (2011)
Jurassic	Nusplingen, Germany	1	1	23.5	26	Schweigert (1998)
Jurassic	Nusplingen, Germany	1	1	less than 12*	?	Schweigert and Dietl (2002)
Jurassic	Solhofen, Germany	0	1	-	6.1	Caster (1941)
Jurassic	Solhofen, Germany	1	1	?	?	Goldring and Seilacher (1971)
Jurassic	Solhofen, Germany	1	1	about 10	about 10	Groiss (1975)
Jurassic	Solhofen, Germany	1	1	9.2	about 9	Barthel et al. (1994)
Jurassic	Solhofen, Germany	1	1	23	33	Frickhinger (1994)
Jurassic	Solhofen, Germany	0	1	-	22.5	Kolb (1963)
Jurassic	Solnhofen, Germany	1	0	? (53 for the length)	-	Frickhinger (1999)
Jurassic	Southern Germany	0	1	-	40 (?)	Goldring and Seilacher (1971)
Jurassic	Wintershof, Germany	1	1	6.9 (immature)	4.25	Lomax and Racay (2012)
Jurassic	Holy Cross Mountain, Poland	0	1	-	?	Pieńkowski and Niedźwiedzki 2009)
Jurassic	Rocky Montain, USA	0	1	-	?	Hasiotis (2004)
Jurassic	Utah, USA	0	1	-	up to 4	Lucas et al. (2006)
Jurassic	Wyoming, USA	0	1	-	up to 10*	Harris and Lacovara (2004)
Jurassic	Cleveland Basin, Yorkshire	0	1	-	16–17	Romano and Whyte (2003)
Cretaceous	Patagonia, Argentina	0	1	-	2.5	Pazos et al. (2012); Fernández and Pazos (2013)
Cretaceous	Australia	1	0	8.5	-	Riek and Gill (1971)
Cretaceous	Dakota, USA	1	0	10.6	-	Holland et al. (1975)
Cretaceous	Texas, USA	1	0	17.5	-	Feldmann et al. (2011)
Eocene	Weißelster Basin, Germany	1	0	17.5–29.5	-	Hauschke and Wilde (2008)
Oligocene	Takeo, Japan	1	0	24.6	-	Oishi et al. (1993); Lockley and Matsukawa (2009)
Palaeogene	Yunnan Province, China	0	1	-	2.67	Xing et al. (2012)
Recent	?	1	0	16.6–22.0	-	Shuster (1982)
Recent	East coast of North America	1	0	3.7–5.0 (immatures)	-	Eldredge (1970)
Recent	Hong Kong, China	1	0	1.71–9.11	-	Lee and Morton (2005)
Recent	Seehorse Key, Florida, USA	1	0	up to 31.1*	-	Cohen and Brockmann (1983)
Recent	Pleasant Bay, Massachusetts, USA	1	0	18.5–30.0	-	Leschen et al. (2006)
Recent	Delaware Bay, New Jersey, USA	1	0	27–38	-	Smith et al. (2009)
Recent	Delaware Bay, New Jersey, USA	1	0	about 13–33	-	Loveland and Botton (1992)

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Table 2.

Assemblage	Trackway	Trace	Internal width	External width
A	1	A1R-A1L	140	214
A	1	A2R-A2L	148	227
A	2	A5R-A5L	105	160
B	7	B5R-B5L	147	-
C	8	C1R-C1L	188	262
C	8	C2R-C2L	178	248
C	9	C4R-C4L	186	256
D	10	D1R-D1L	148	227
D	10	D2R-D2L	164	248
D	10	D3R-D3L	149	237
D	10	D4R-D4L	130	217

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Table 3.

Assemblage	Trackway	Trace	Stride
A	1	A1L-A2L	152
A	1	A2L-A3L	185
A	1	A3L-A4L	215
A	1	A1R-A2R	195
A	3	A6-A7	147
A	3	A7-A8	180
A	3	A8-A9	190
A	4	A10-A11	334
A	4	A11-A12	330
A	5	A13-A14	-
A	5	A14-A15	-
A	6	A16-A17	52
A	6	A17-A18	47
A	6	A18-A19	59
A	6	A19-A20	47
A	6	A20-A21	47
A	6	A21-A22	-
A	6	A22-A23	-
A	6	A23-A24	48
A	6	A24-A25	48
A	6	A25-A26	50
B	7	B1R-B2R	189
C	8	C1L-C2L	264
C	8	C1R-CR2	317
C	9	C3L-C4L	317
D	10	D1L-D2L	90
D	10	D2L-D2L'	26
D	10	D2L'-D3L	124
D	10	D3L-D4L	131
D	10	D4L-D5L	100
D	10	D1R-DR2	135
D	10	D2R-D3R	177
D	10	D3R-D4R	144
D	11	D8-D9	229
D	12	D10-D11	163
D	12	D11-D12	160

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Table 4.

	Stride		Width	
Trackway	**Mean**	**SD**	**Mean**	**SD**
T1	186.7	26.31	47.0	2.54
T2	-	-	25.0	-
T3	172.3	22.50	28.5	6.36
T4	332.0	2.82	43.3	2.56
T5	-	-	40.6	2.56
T6	49.7	4.13	22.7	3.40
T7	189.0	-	31.0	0
T8	290.5	37.47	34.2	1.70
T9	317.0	-	32.0	-
T10	115.8	45.01	48.5	4.44
T11	229.0	-	44.0	2.82
T12	161.5	2.12	43.3	6.65
T13	-	-	22.5	3.53

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Table 5.

Assemblage	N° of Trackway	Trace	Width	Total lenght	Lenght of the anterior part
A	1	A1R	51	47	27
A	1	A1L	-	-	-
A	1	A2R	50	45	27
A	1	A2L	-	43	-
A	1	A3L	41	49	29
A	1	A4L	46	-	-
A	2	A5R	25	-	-
A	2	A5L	-	-	-
A	3	A6	-	-	-
A	3	A7	-	-	-
A	3	A8	24	-	-
A	3	A9	33	50	30
A	4	A10	41	47	26
A	4	A11	43	48	26
A	4	A12	46	-	-
A	5	A13	43	45	28
A	5	A14	41	-	-
A	5	A15	38	42	26
A	6	A16	25	-	-
A	6	A17	29	-	-
A	6	A18	nc	-	-
A	6	A19	21	-	-
A	6	A20	-	-	-
A	6	A21	-	-	-
A	6	A22	-	-	-
A	6	A23	19	-	-
A	6	A24	23	-	-
A	6	A25	20	-	-
A	6	A26	22	-	-
B	7	B1R	31	39	16
B	7	B2R	-	-	-
B	7	B2L	31	42	20
B	7	B3L	-	39	-
B	-	B4	27	28	10
B	-	B5	30	33	14
B	-	B6	27	-	12
B	-	B7	21	-	-
B	-	B8	22	17	8
B	-	B9	-	-	-
B	-	B10	18	32	12
B	-	B11	-	26	12
B	-	B12	-	-	-
B	-	B13	-	-	-

Assemblage	N° of Trackway	Trace	Width	Total lenght	Lenght of the anterior part
B	-	B14	24	30	10
B	-	B15	30	28	12
B	-	B16	33	-	14
B	-	B17	29	-	14
B	-	B19	-	-	-
B	-	B18	28	30	15
B	-	B20	32	30	13
B	-	B21	24	34	16
B	-	B22	25	30	9
B	-	B23	28	34	14
B	-	B24	25	34	11
B	-	B25	27	19	14
B	-	B26	22	38	17
C	8	C1L	36	-	12
C	8	C1R	35	-	12
C	8	C2L	32	-	9
C	8	C2R	34	-	10
C	9	C3L	-	58	25
C	9	C4R	32	53	22
C	9	C4L	-	60	26
C	-	C5	38	65	27
C	-	C6	-	35	15
D	10	D1R	45	-	-
D	10	D1L	43	41	22
D	10	D2R	42	-	26
D	10	D2L'	50	-	25
D	10	D2L'	49	-	25
D	10	D3R	48	-	-
D	10	D3L	53	52	27
D	10	D4R	-	-	-
D	10	D4L	53	-	-
D	10	D5L	54	61	33
D	13	D6	25	36	17
D	13	D7	20	-	17
D	11	D8	46	63	24
D	11	D9	42	45	20
D	12	D10	39	-	15
D	12	D11	51	-	21
D	12	D12	40	-	16
D	-	D13	59	-	32
D	-	D14	35	-	20
D	-	D15	40	-	19
D	-	D16	-	-	-

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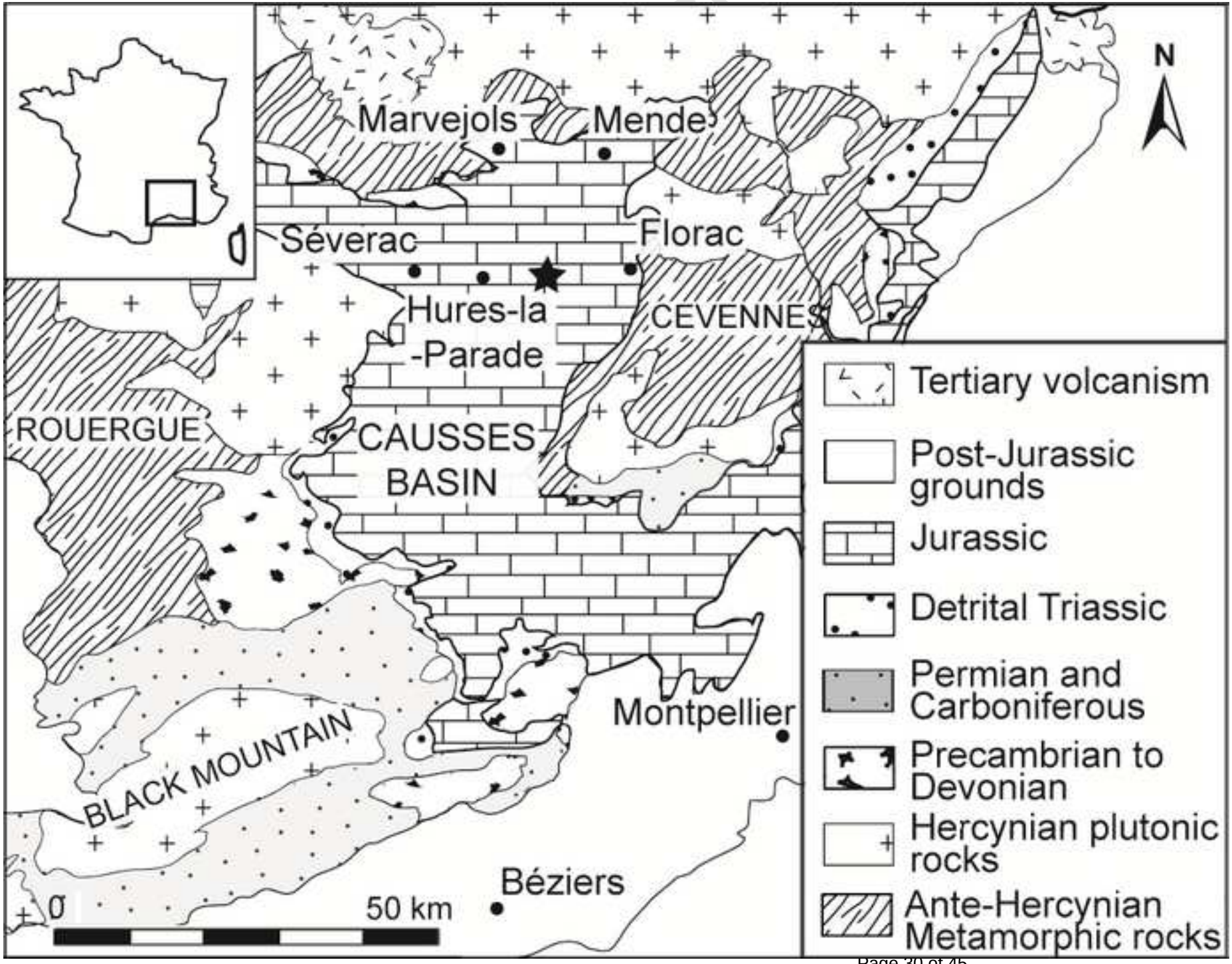
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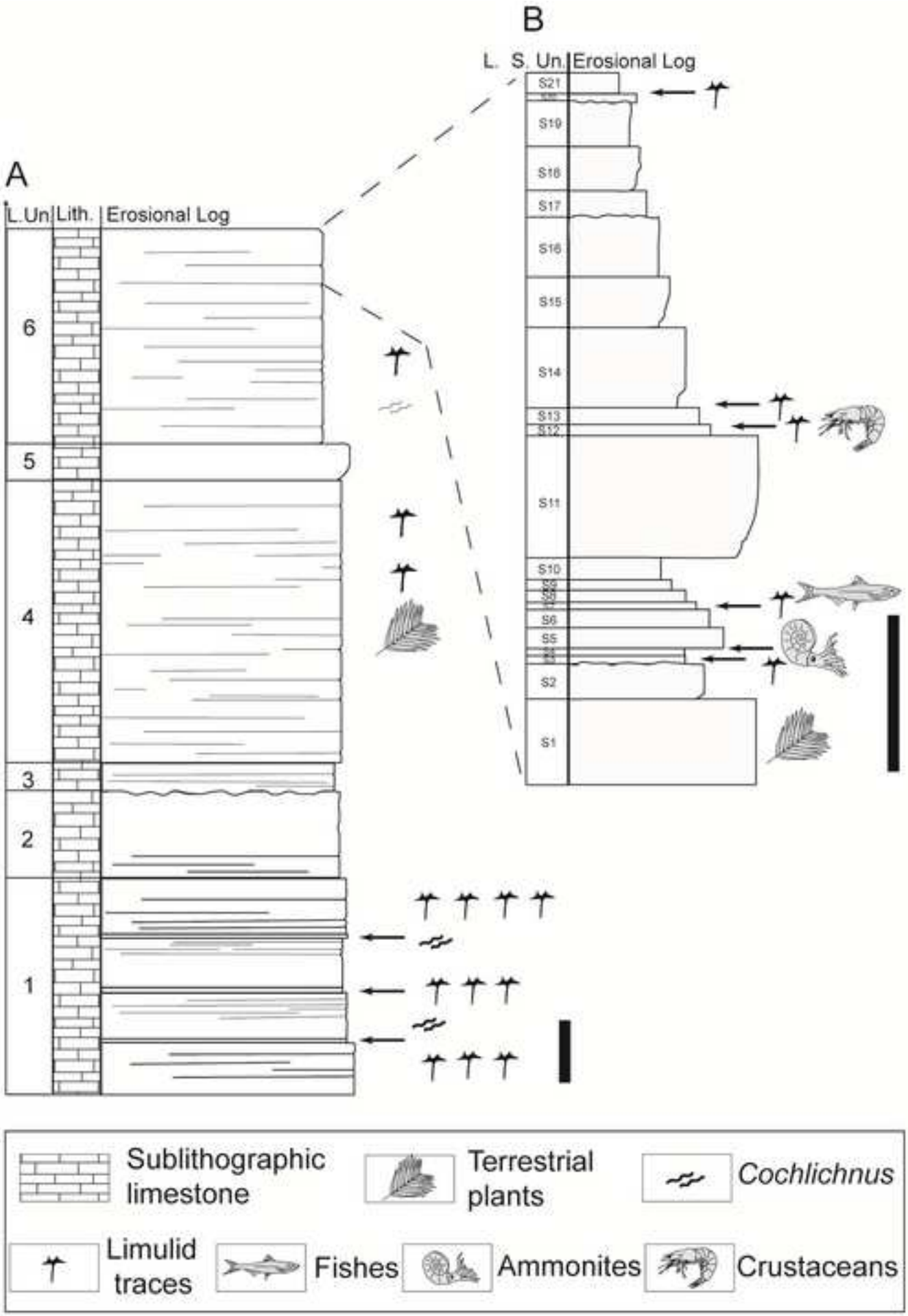
Isolated trace	Width	Total lenght	Lenght of the anterior part
I1A	-	-	35
I1B	53	-	31
I1C	-	-	-
I1D	52	66	32
I2	58	68	32
I3	57	-	29
I4	39	-	18
I5	37	-	14
I6	-	-	-
I7	51	58	22
I8A	42	-	28
I8B	53	67	28
I8C	47	66	29
I9A	31	49	19
I9B	29	-	12
I10	38	65	25
I11	37	64	28
I12	42	69	29
I13	-	-	-
I14	39	45	11
I15	21	34	13
I16	36	49	23
I17	56	68	30
I18	25	37	12
I19	22	20	10
I20	41	-	19
I21	31	42	17
I22	32	-	18
I23	-	-	-
I24A	39	41	16
I24B	27	42	14
I25	29	36	13
I26	45	-	17
I27	37	41	21
I29	44	46	20
I30	30	-	15
I31	-	-	-
I36A	33	46	22
I36B	33	41	17
I37A	50	57	30
I37B	52	68	27
I38A	29	41	18
I38B	30	42	20
I39A	21	-	10
I39B	21	24	9
I40	31	38	14
I41	19	23	9
I42	27	39	15
I43	20	25	12
I44	19	20	7
I45	22	24	8
I46A	11	11	6
I46B	11	-	5
I46C	24	25	10
I47	21	19	8
I48	34	32	14
I49	50	69	28
I50	20	23	8
I51	30	31	12
I52A	16	-	5
I52B	16	-	5

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Figure 1

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A
L.Un
Lith.
Erosional Log
6
5
4
3
2
1
B
L. S. Un.
Erosional Log
S21
S19
S18
S17
S16
S15
S14
S13
S12
S11
S10
S6
S5
S2
S1
Sublithographic limestone
Terrestrial plants
Cochlichnus
Limulid traces
Fishes
Ammonites
Crustaceans

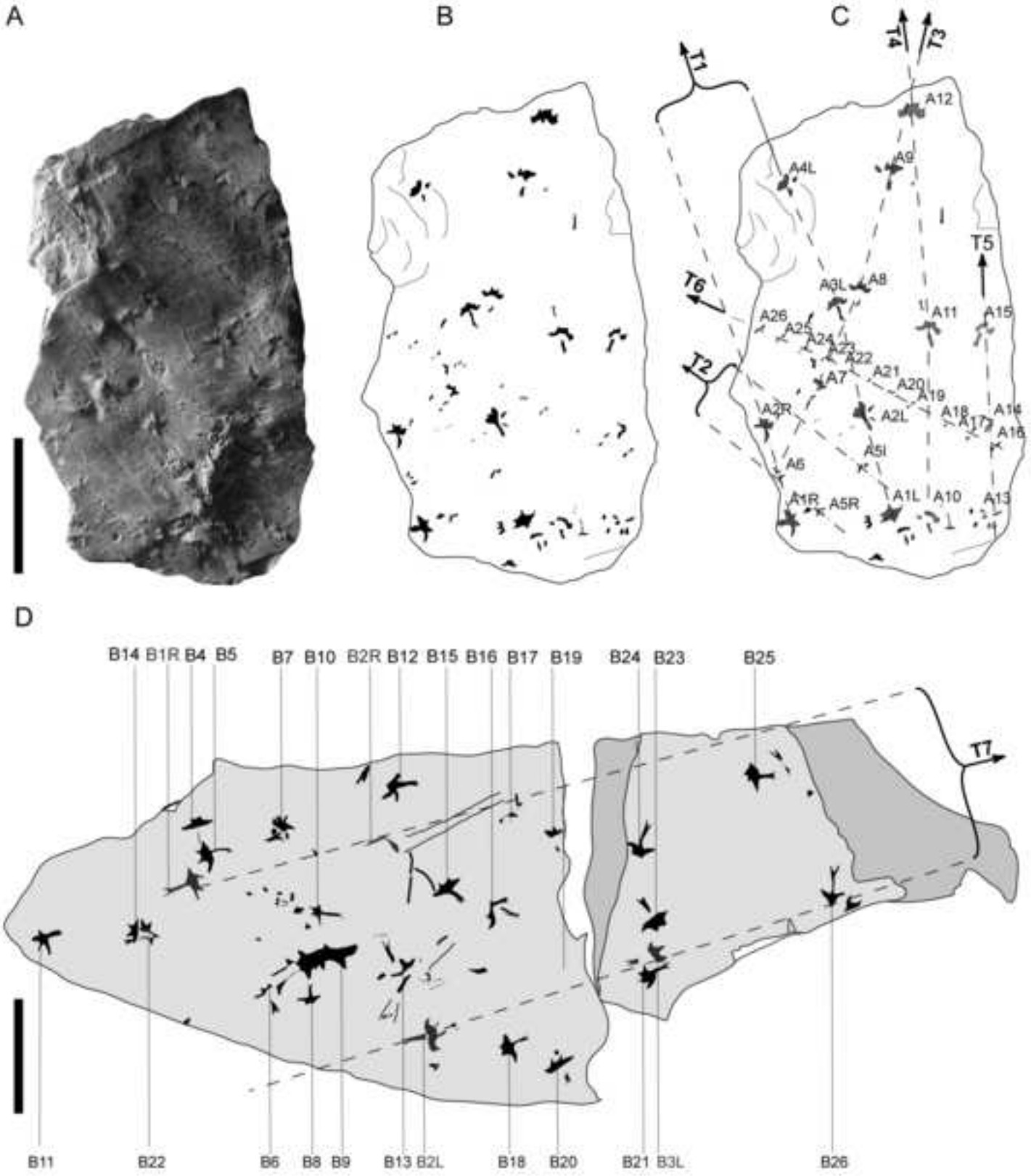
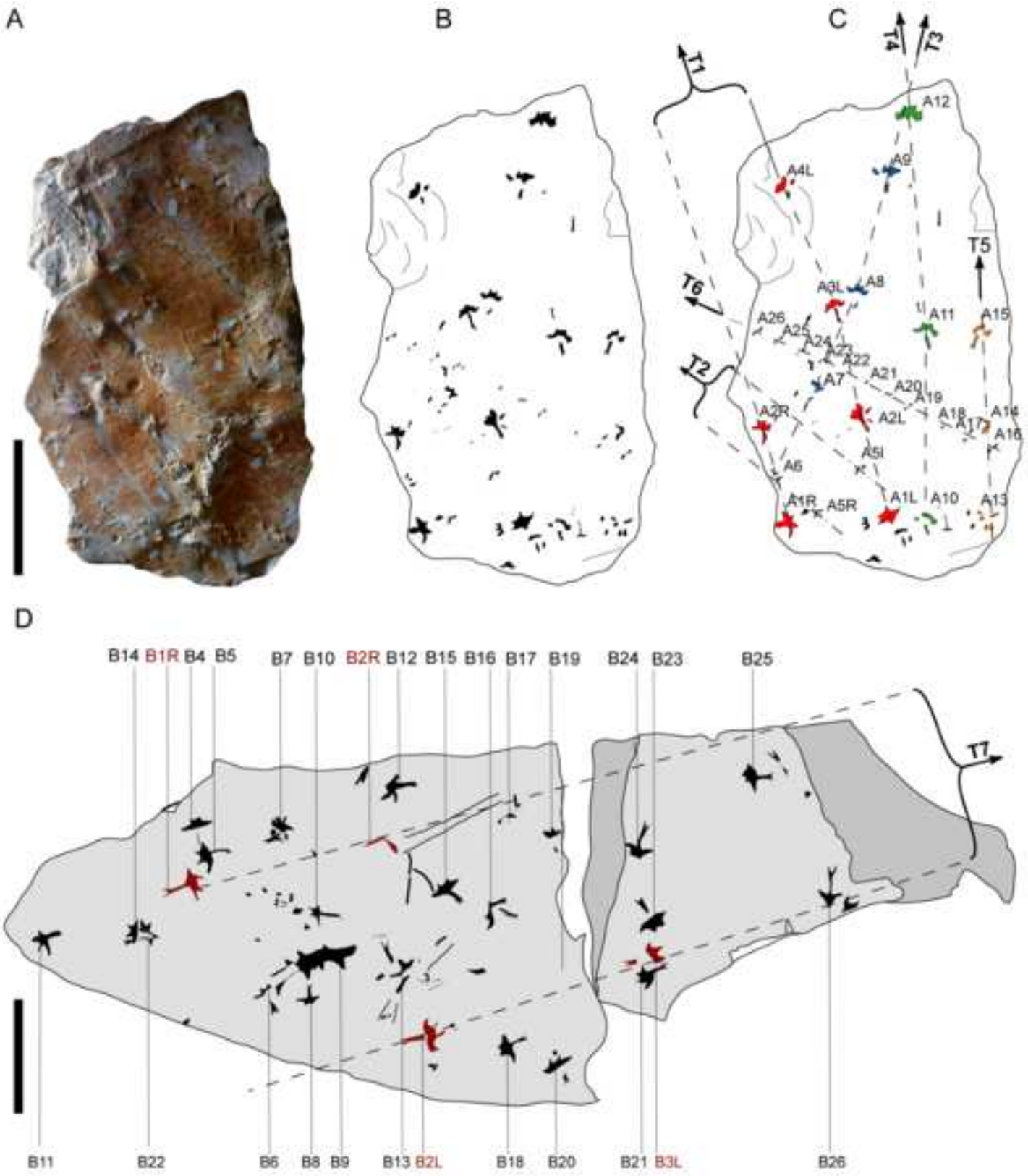

A
B
C
T1
T2
T3
T4
T5
T6
A12
A4L
A9
A3L
A8
A11
A15
A26
A25
A24
A23
A22
A21
A7
A20
A19
A2R
A2L
A18
A17
A16
A5I
A6
A1R
A5R
A1L
A10
A13
D
T7
B14 B1R B4 B5
B7 B10 B2R B12 B15 B16 B17 B19
B24 B23
B25
B11
B22
B6 B8 B9
B13 B2L
B18 B20
B21 B3L
B26

Figure 3 color
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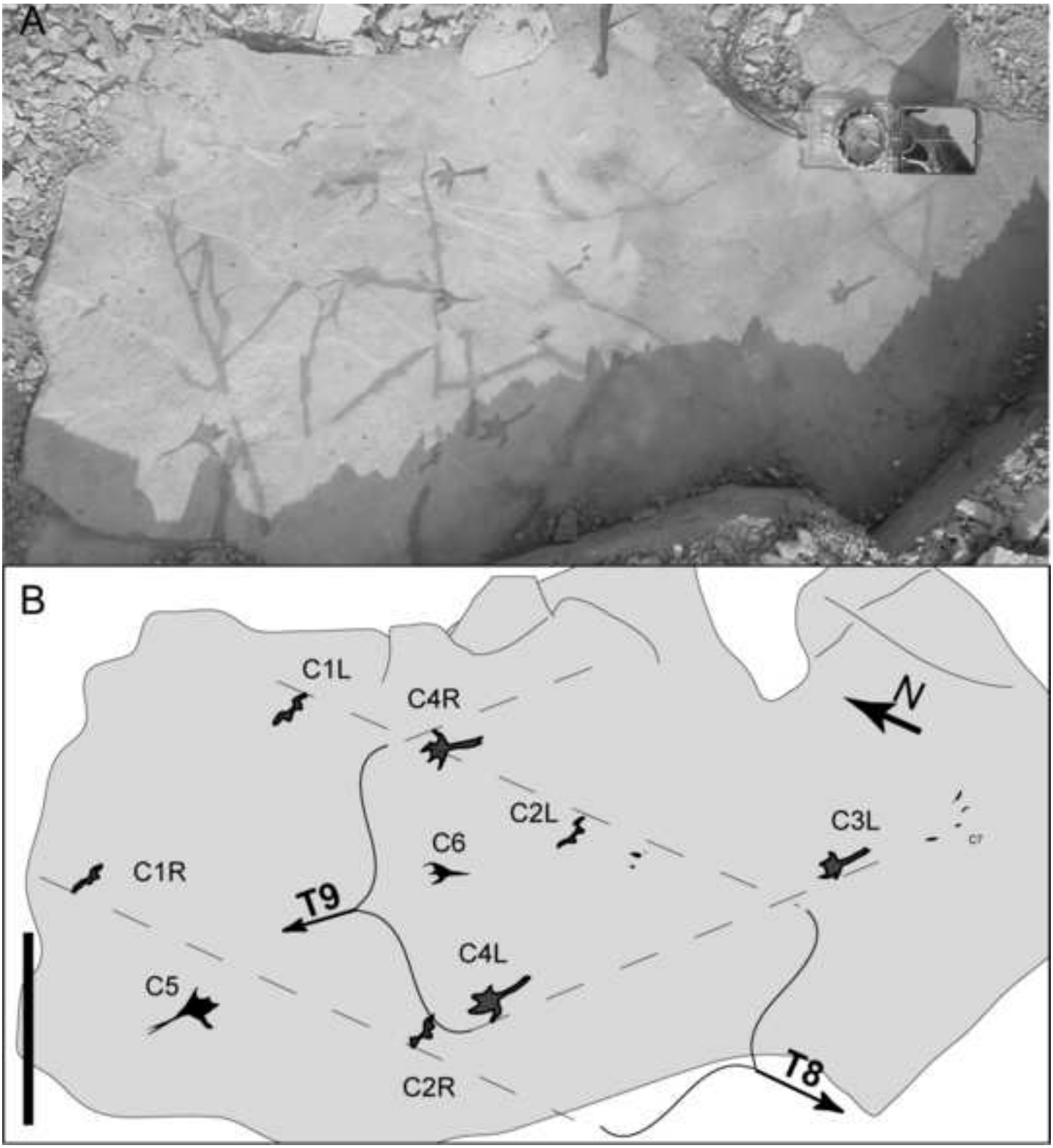

A
B
C1L
C4R
N
C2L
C3L
C6
C1R
T9
C4L
C5
C2R
T8

Figure 4 color
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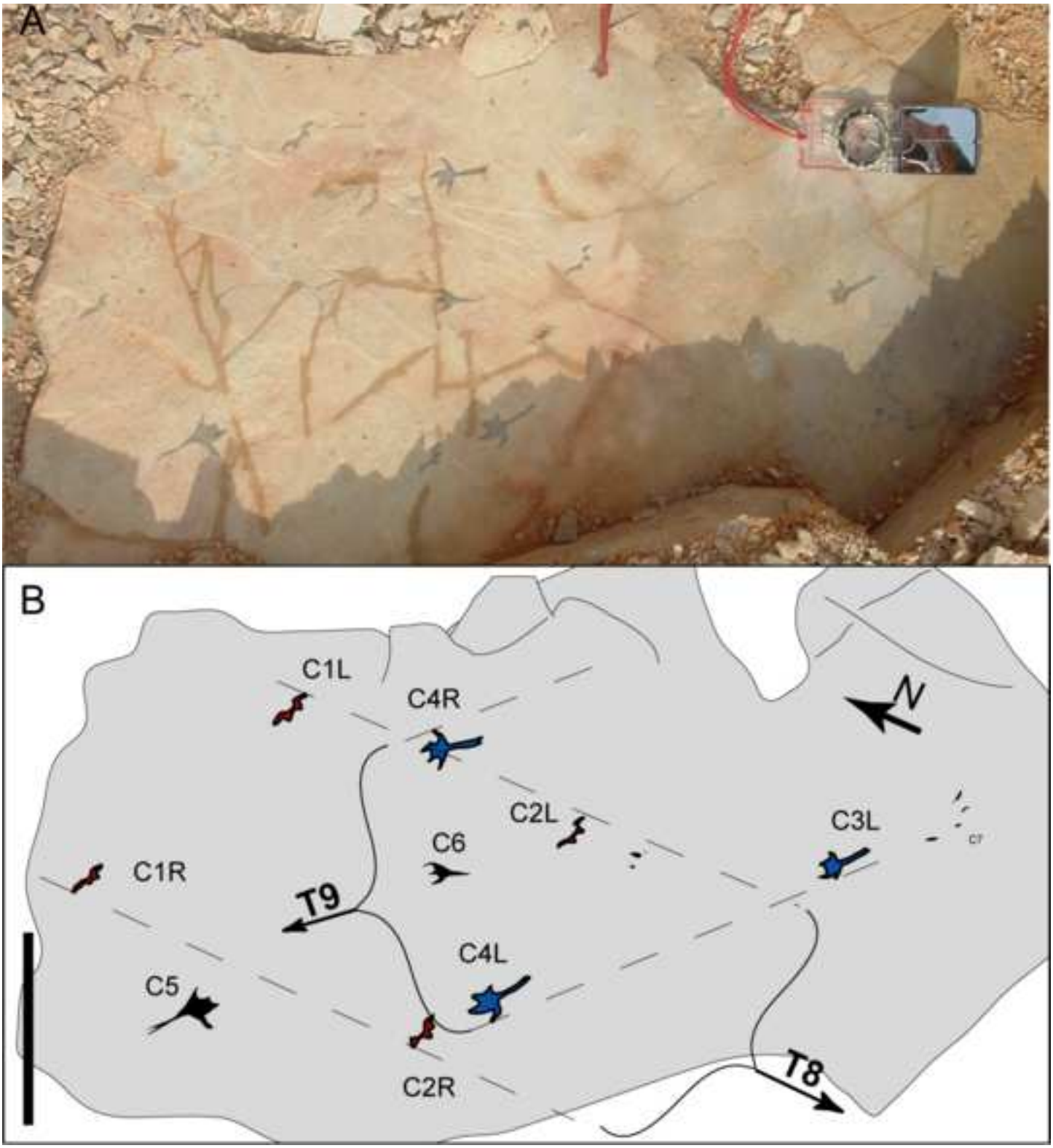


Figure 5 B&W
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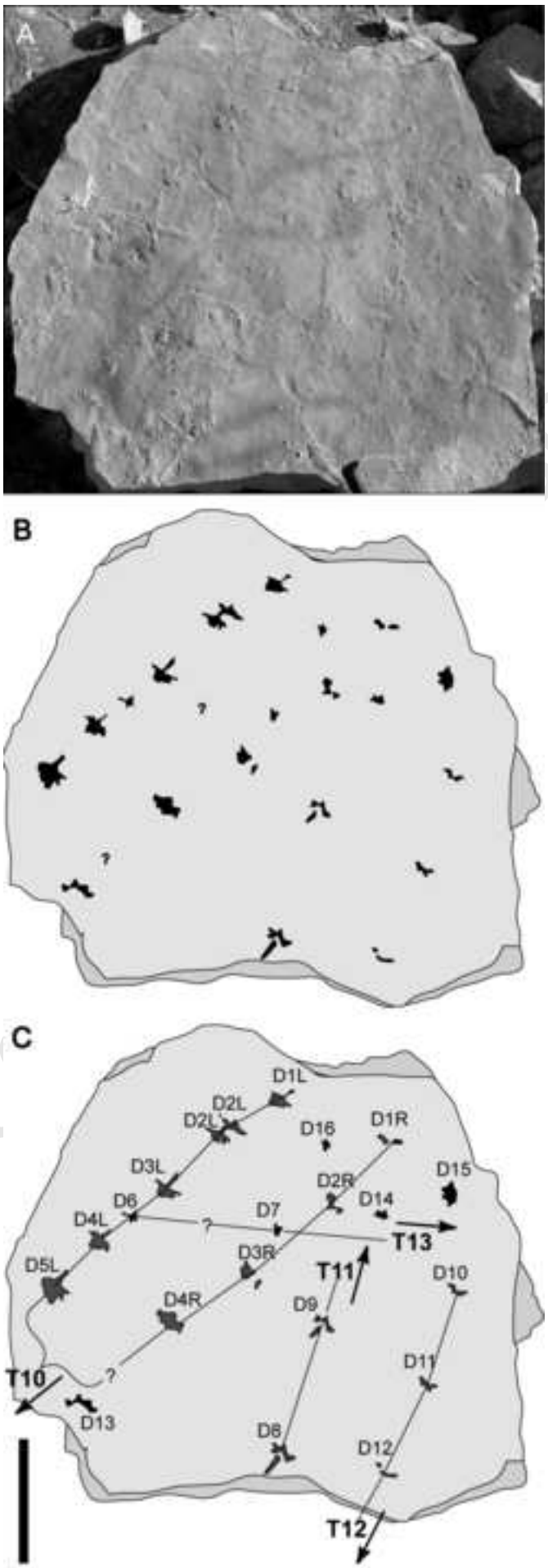
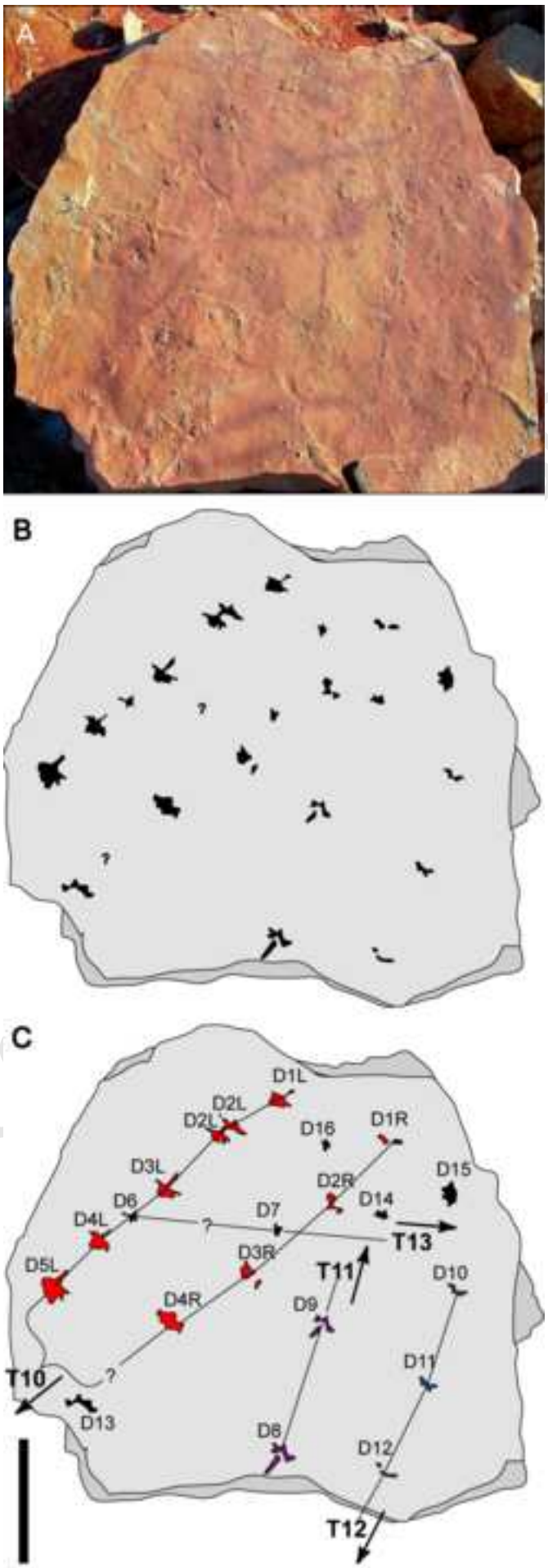
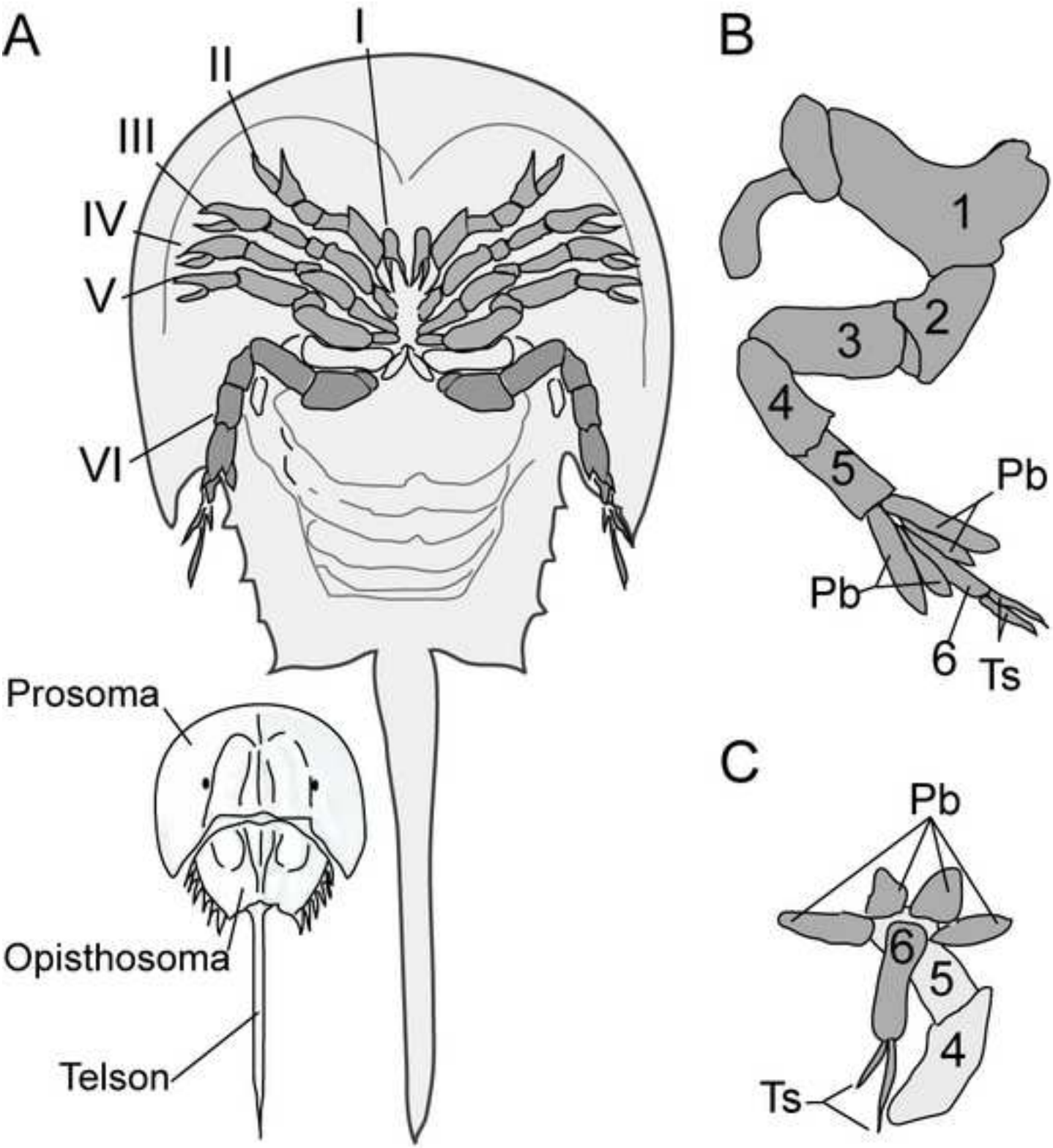
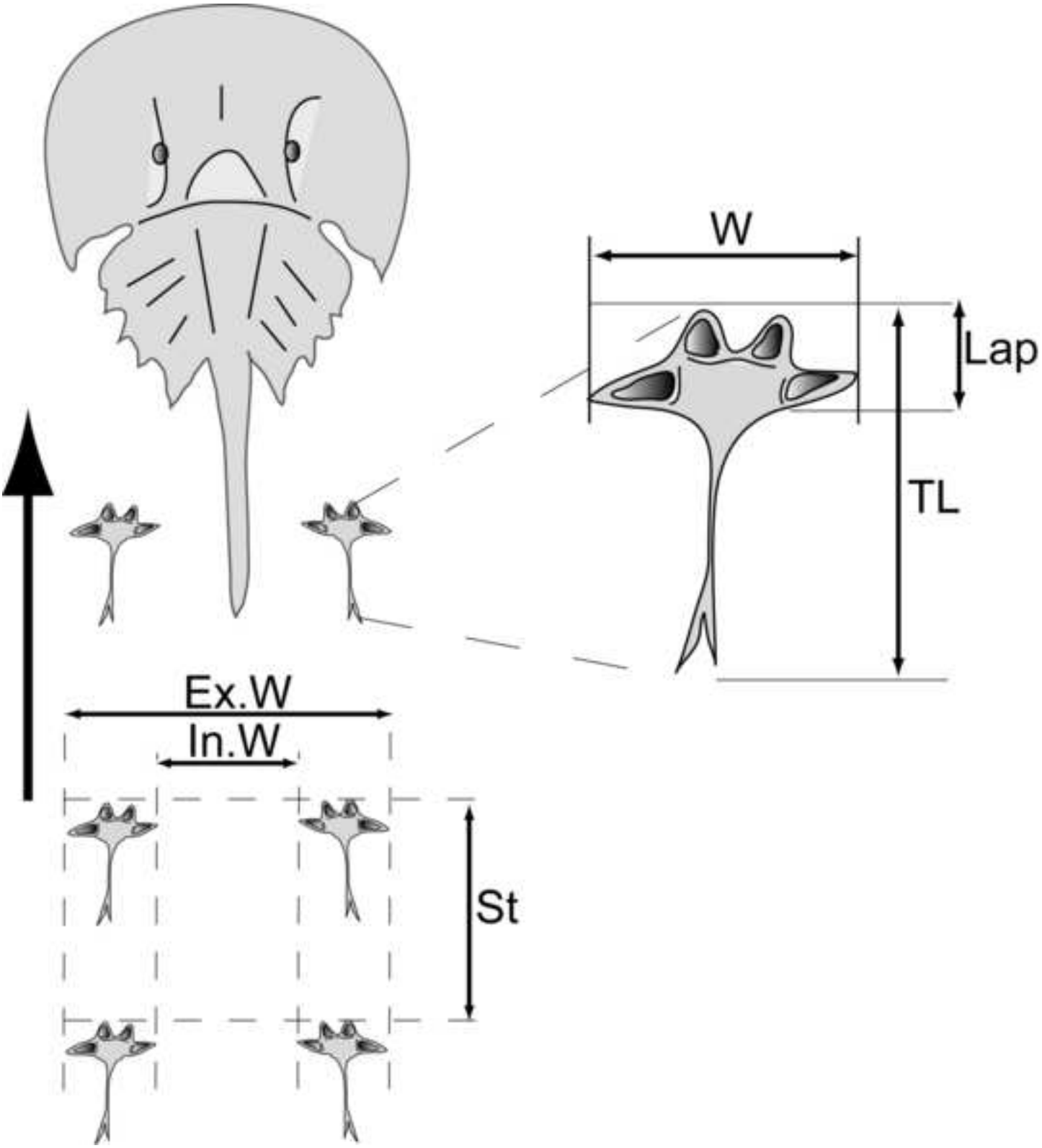


Figure 5 color
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A
I
II
III
IV
V
VI
Prosoma
Opisthosoma
Telson
B
1
2
3
4
5
Pb
Pb
6
Ts
C
Pb
6
5
4
Ts


W
Lap
TL
Ex.W
In.W
St

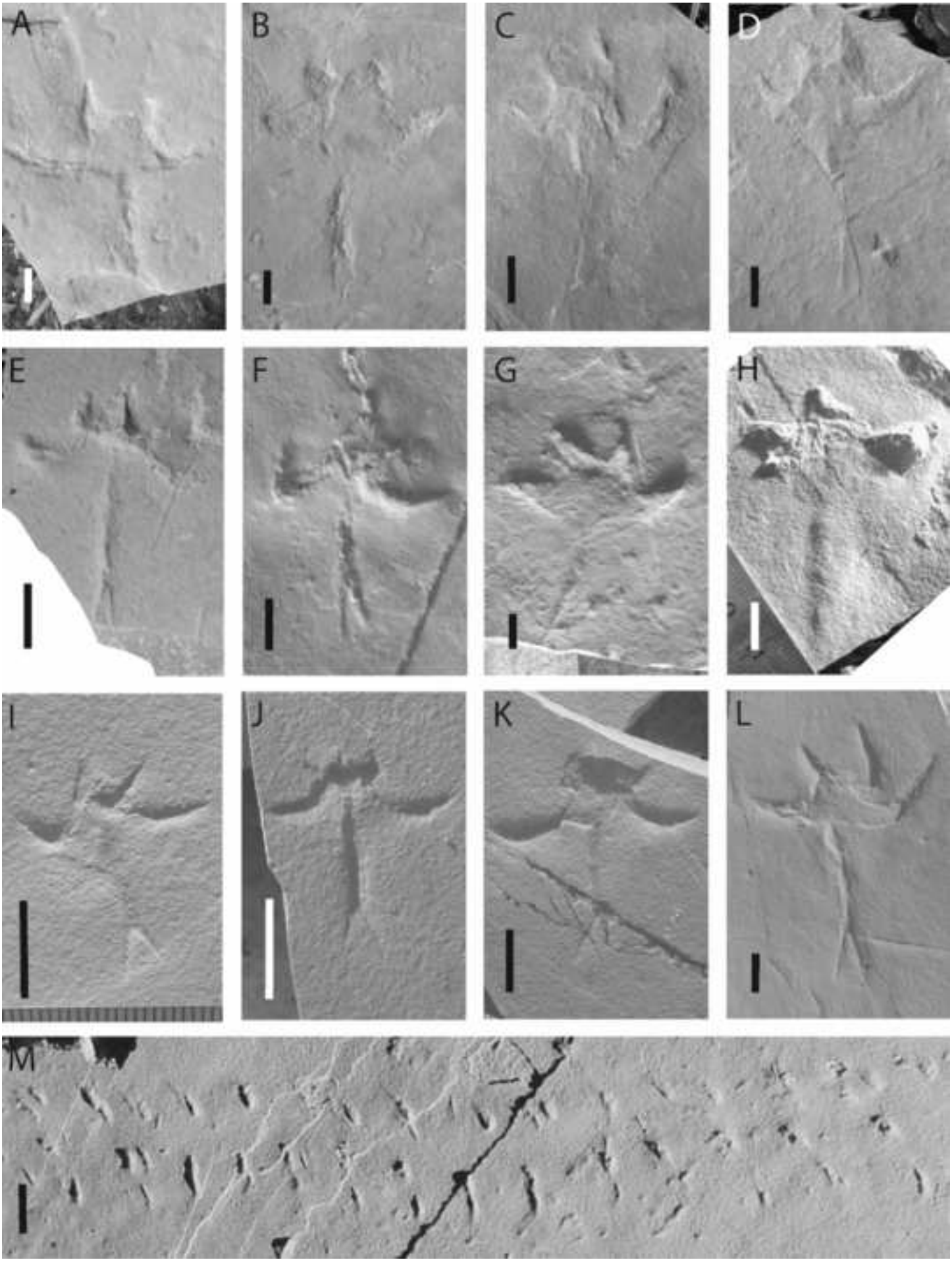

A
B
C
D
E
F
G
H
I
J
K
L
M

Figure 8 color
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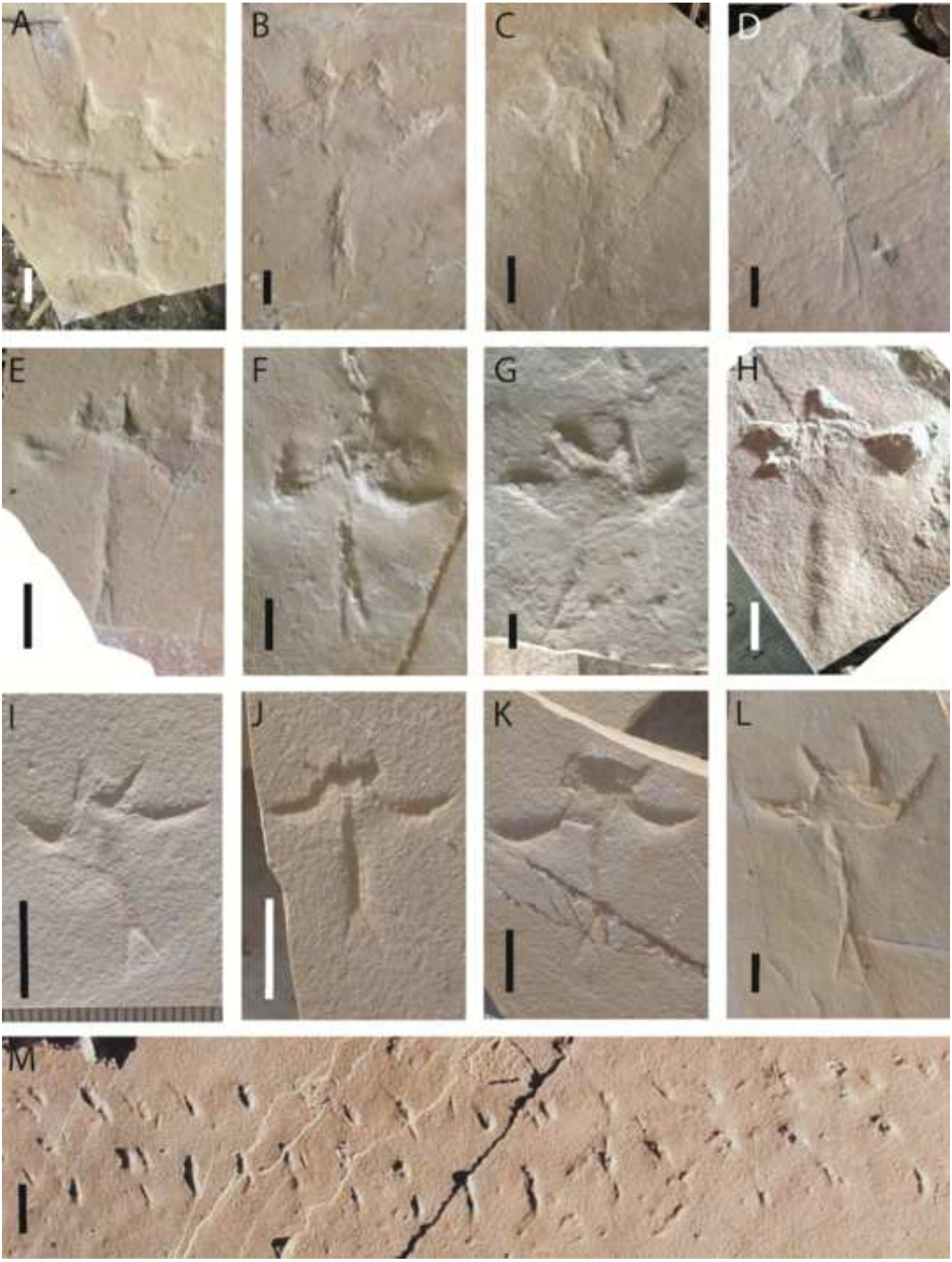


Figure 9

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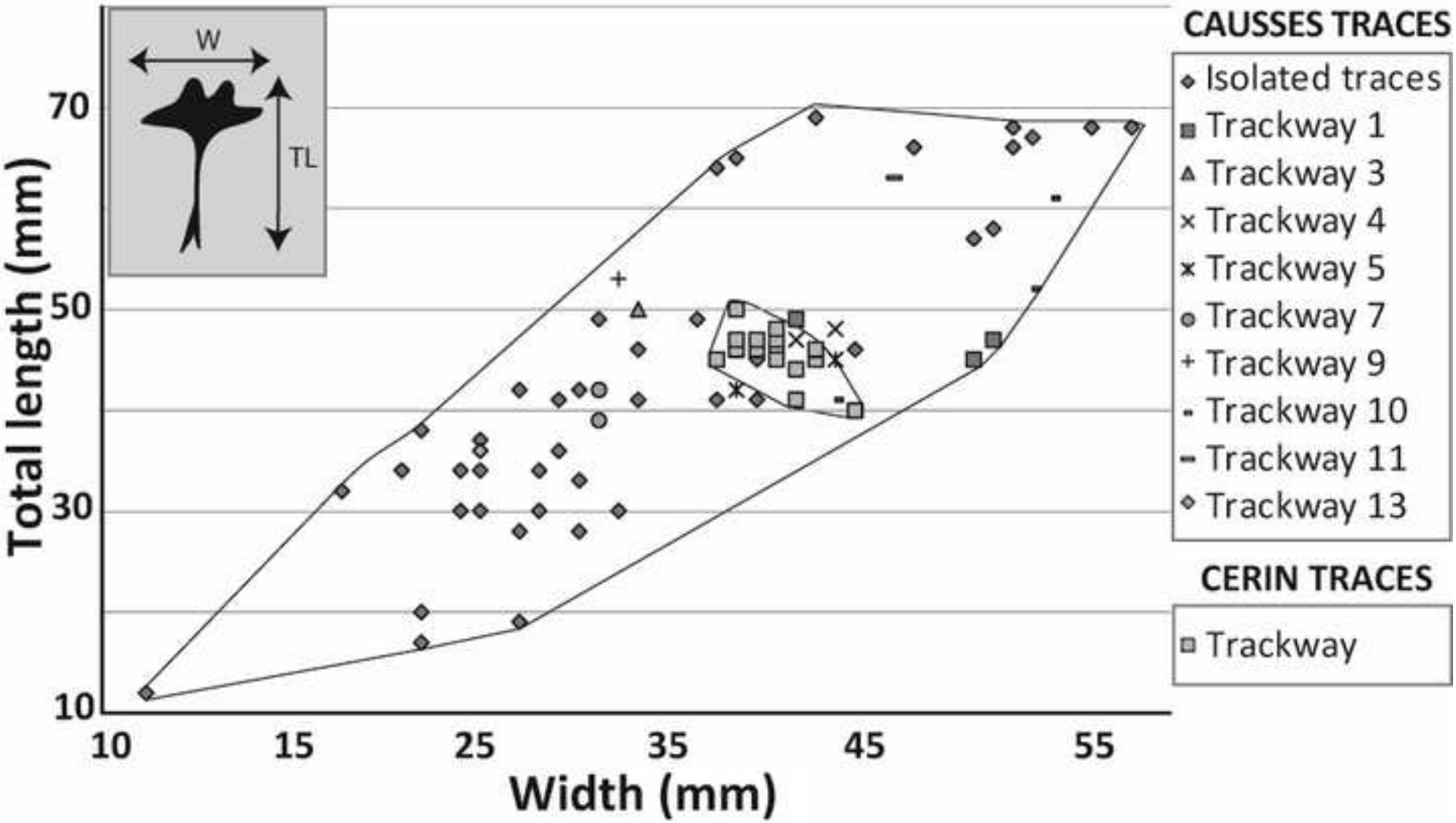


Figure 10 B&W

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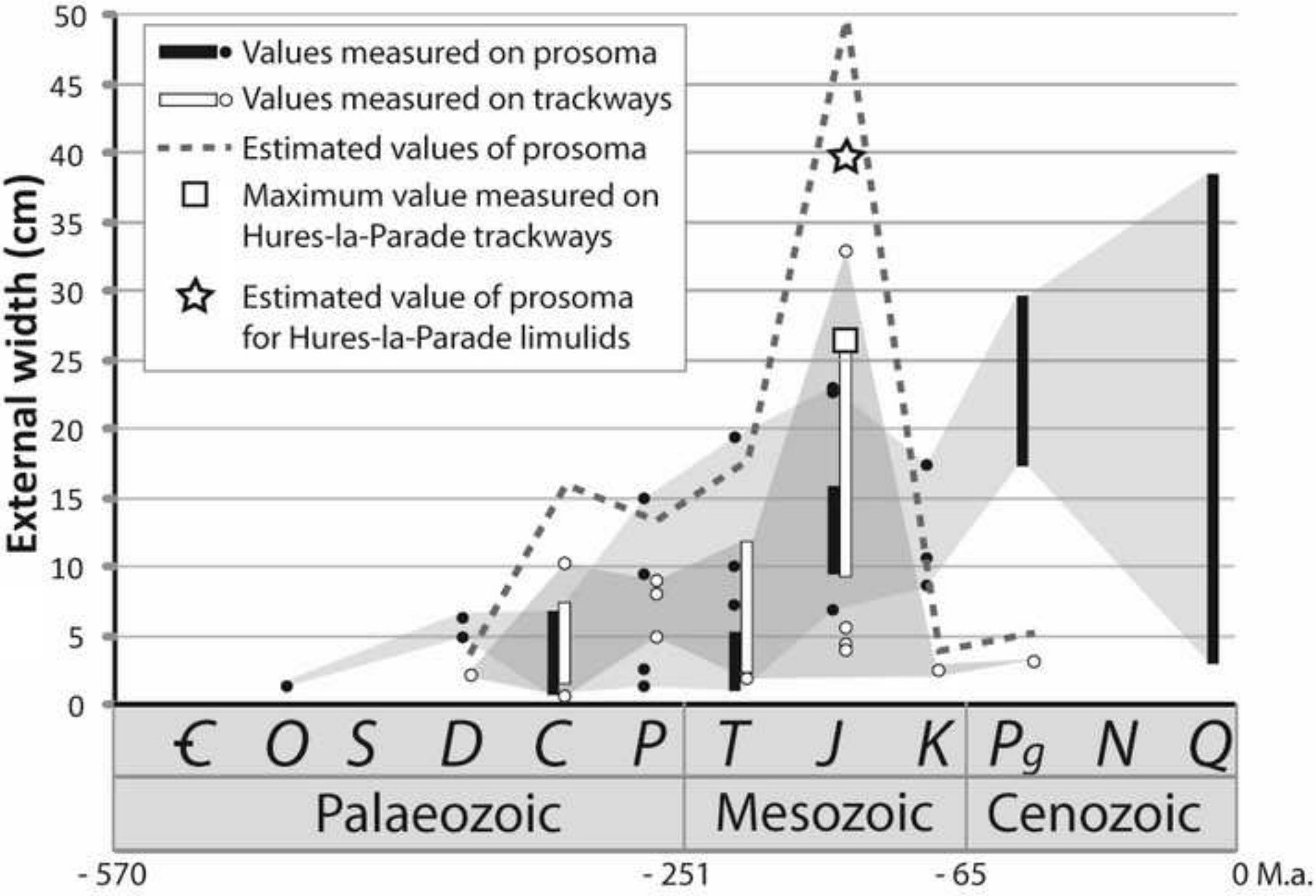


Figure 10 color

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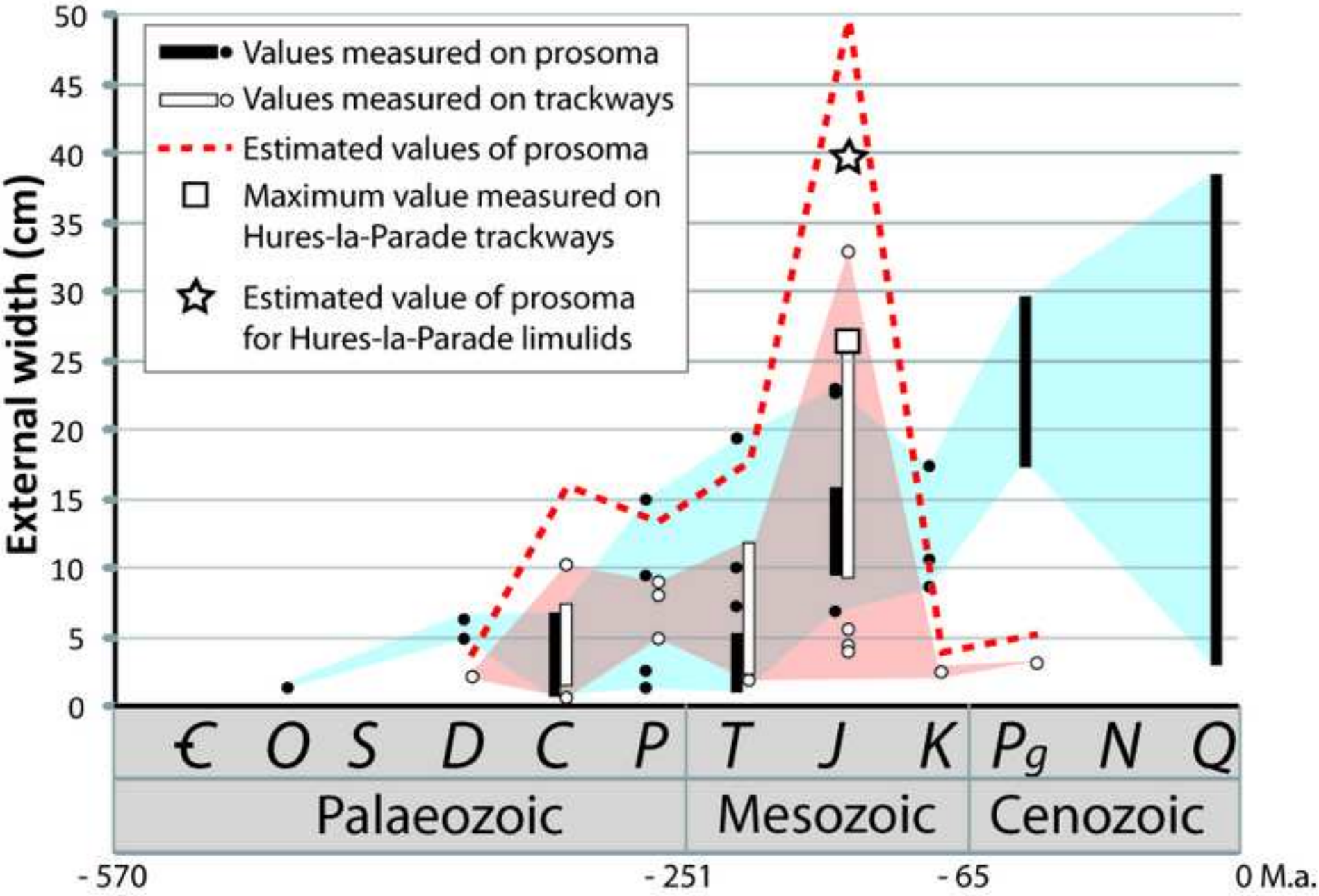


Figure 11

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