



Review Article

Can arthropods produce *Paleodictyon*?

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ABSTRACT

Paleodictyon is a common structure documented in marine sediments from the Cambrian to the present times. Despite its pervasive distribution and distinctive hexagonal geometry, the tracemaker remains unidentified. This study investigates the hypothesis that a marine arthropod could be responsible for its production. We assess this hypothesis by reviewing six key characteristics of *Paleodictyon*: morphology, stratigraphic distribution, environmental distribution, taphonomy, tracemaker attributes, and inferred function. Arthropods are well-known for creating straight tunnel segments, a capability afforded by their jointed appendages and rigid exoskeletons, which also facilitate sharp directional changes. These attributes are consistent with the straight burrow segments of *Paleodictyon*, which converge at 120° angles. In contrast, worm-like organisms, characterised by their cylindrical body plan and hydrostatic skeletons, tend to create more tortuous burrows because burrowing proceeds preferentially along paths of least resistance. A review of published evidence suggests that the tracemaker was likely highly motile and, if solitary, an exceptionally rapid burrower. Morphometric analysis of 1314 landmarks shows that interior angles depart from 120° by only 8.5° and side lengths vary within each cell by 0.5 mm. Rather than propagating errors between cells, the tracemaker corrected them locally, indicating advanced capabilities in orientation and odometry. These cognitive skills are compatible (though not exclusive) with the sophisticated navigation skills of the arthropod brain. The first appearance of *Paleodictyon* in the early Cambrian coincides with the earliest fossil record of arthropods, further supporting the hypothesis. Although environmental distribution and inferred function provide less definitive evidence, they do not exclude arthropod tracemakers. Taken together, these observations suggest that arthropods are the most likely producers of *Paleodictyon*, challenging the hypotheses of a vermiform or protist producer. Isopods and amphipods emerge as the best potential candidates for producing *Paleodictyon*. However, only direct neoichnological observation of burrow construction, or the discovery of a tracemaker preserved within a fossil burrow, can definitively resolve the enduring mystery of its tracemaker.

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1. Introduction

Paleodictyon is one of the most iconic and common trace fossils, characterised by its distinctive horizontal network of hexagonal meshes and vertical outlets (Seilacher, 1977; Uchman, 1995; Miguez-Salas et al., 2023; Fig. 1). It is documented from the early Cambrian to the present seafloors with wide biogeographic and bathymetric distributions across time (Seilacher, 1977; Uchman, 1995; Fürsich et al., 2007; Rona et al., 2009; Kikuchi, 2018; Malekzadeh and Wetzel, 2020; Neto de Carvalho et al., 2020; Miguez-Salas et al., 2023). Despite its easily recognisable geometry and widespread occurrence, the identity of the organism responsible for producing these structures remains elusive.

This enduring enigma is particularly striking given the extensive historical research dedicated to *Paleodictyon* (Table 1). It is thought that Leonardo da Vinci might have been among the first to examine it, as evidenced by a drawing attributed to him that potentially illustrates *Paleodictyon* (Baucon, 2010a, 2010b). As a pioneering figure in ichnology, da Vinci introduced the idea of trace fossils as the product of the activities of worm-like organisms (Baucon et al., 2012). However, whether he specifically applied this interpretation to *Paleodictyon* remains uncertain. The hypothesis that *Paleodictyon* represents a fossil burrow produced by such worm-like organisms gained considerable support during the 1970s (Crimes, 1977) and remains a well-established hypothesis today (Miller, 2014).

In addition to the ichnological interpretation of *Paleodictyon*, the body-fossil hypothesis has garnered significant scholarly interest. When Meneghini first named it in the 19th century, *Paleodictyon* was interpreted as a body fossil based on comparisons to the freshwater green alga *Hydrodictyon pentagonum* and the marine alga *Halydictyon* (Meneghini, 1851). This perspective was echoed by Sacco (1886), Koriba and Miki (1939), and Kushlin (1982). Other body-fossil hypotheses considered *Paleodictyon* as the impression of glass sponges (De

Stefani, 1887) or a foraminifera, either astrophorids or xenophyophores (Swinbanks, 1982; Levin, 1991; Rona et al., 2009). These interpretations continue to fuel debate within the scientific community, reflecting the complex nature of this enigmatic structure (Honeycutt and Plotnick, 2005).

In addition to organic interpretations, a third category of hypotheses – those concerning inorganic processes – has been proposed. However, these are now largely absent from contemporary scientific discourse. In his comprehensive review of *Paleodictyon*, Silvestri (1911) provides an extensive overview of these inorganic hypotheses, which include mechanisms such as the filling of desiccation cracks, interference ripples, and raindrop imprints. Furthermore, Kushlin (1982) discusses alternative organic hypotheses encompassing tracks produced by the movement of tadpole tails, displaced bivalve shells, impressions from dinosaur dermal scales, tree-bark impressions, and the eggs or spawn of fish, frogs, or gastropods.

The persistence of this enigma is further underscored by the occurrence of *Paleodictyon* on the modern ocean floor, specifically within the Atlantic and Indian oceans. Paraphrasing Miller (2014), a pertinent question arises: if *Paleodictyon* is still being formed, why not directly observe the producer at work? Despite comprehensive neoichnological investigations (Ekdale, 1980; Rona et al., 2009; Przesławski et al., 2012; Durden et al., 2017; Miguez-Salas et al., 2023), the identity of the modern *Paleodictyon* producer remains unidentified. Research efforts have included the extraction of push cores from the seabed, which have successfully recovered modern *Paleodictyon* specimens. However, these cores consistently lack evidence of any residing organisms within the structures, leaving the scientific community without conclusive answers (Rona et al., 2009; Kikuchi and Naruse, 2022). Consequently, the true nature of the *Paleodictyon* producer remains central to what Miller (2014) has termed “the mystery of the graphoglyptids,” referring to the small, geometrically intricate group of trace fossils to which

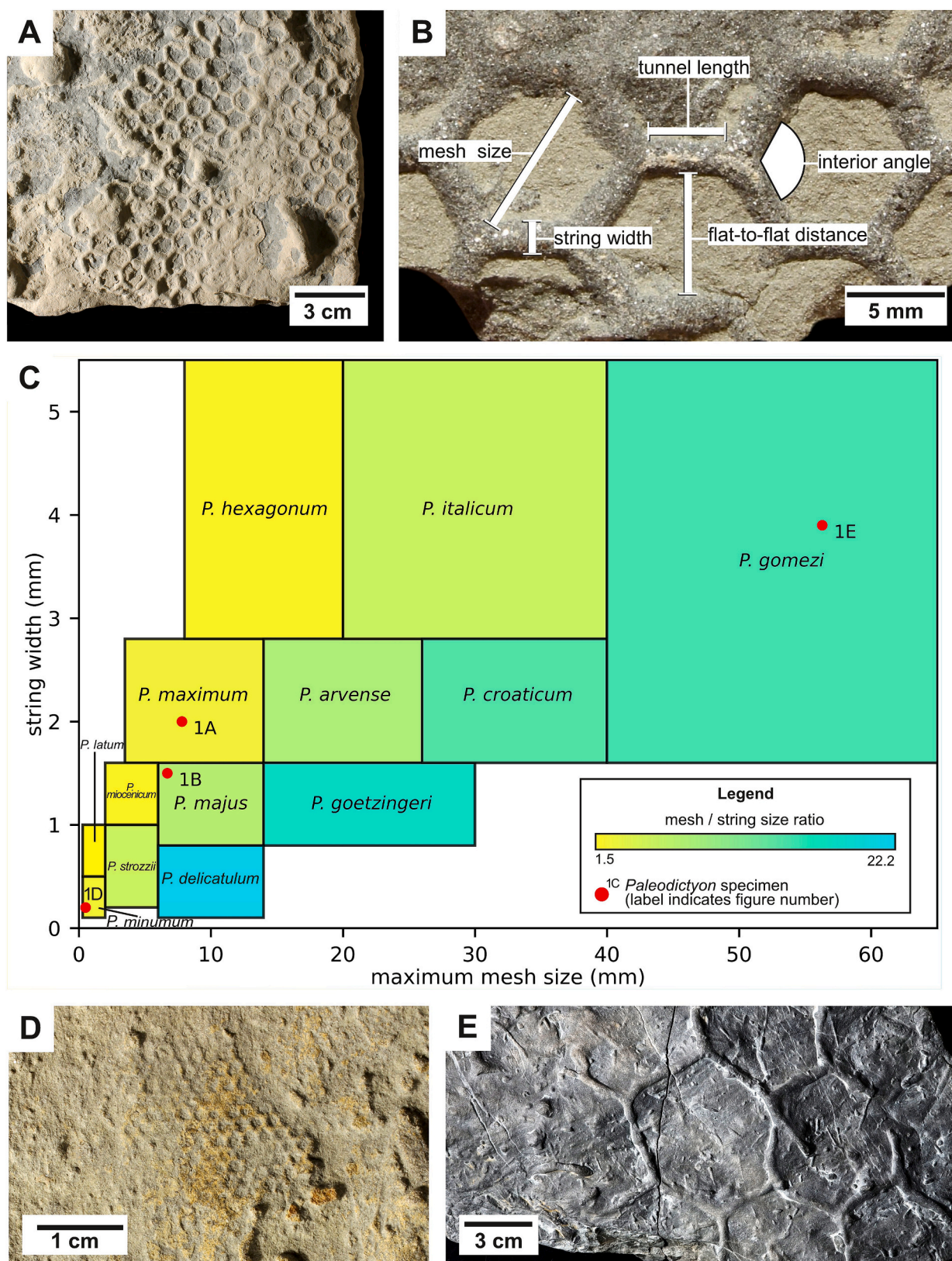


Fig. 1. *Paleodictyon* morphospace. A. *Paleodictyon maximum*. NHMP223. B. Terminology for *Paleodictyon* geometry illustrated on a *P. majus* specimen. NHMP257. C. Morphospace of *Paleodictyon*. Redrawn after Uchman (1995). D. *Paleodictyon minimum*. NHMP196. E. *Paleodictyon gomezi*. INGUJ144P98.

Table 1

Hypotheses for the producing agent of *Paleodictyon*. These hypotheses are divided into three categories, following the tripartite framework proposed by Antoniazzi (1966).

Category of hypotheses	Producing agent	Reference	Remarks
Trace fossil	Worm-like organism	Abel, 1935; Książkiewicz, 1977; Crimes, 1977	Abel (1935) proposed a worm tracemaker, whereas Książkiewicz (1977) suggested polychaetes
	Crustacean	Garlick and Miller, 1993; McMenamin, 2016	
	Tadpole	Hitchcock, 1858	Hitchcock (1858) describes <i>Paleodictyon</i> as “Batrachoides”, that is, “pertaining to frogs”
Body fossil	Alga	Meneghini, 1851; Silvestri, 1911	Impossible by (paleo) environmental reasons
	Sponge	Marck, 1863; Matyasowsky, 1878; Zeiller, 1887	Never found within the structures retrieved from the ocean floor
	Foraminifera	Swinbanks, 1982; Levin, 1991; Rona et al., 2009; Kikuchi and Naruse, 2022; Plotnick, 2003	Foraminifera-related hypotheses encompass astrophorids and xenophyophores
	Iterative modular growth of an unknown organism		
	Coral	Zeiller, 1887	Never found within the structures retrieved from the ocean floor
	Beehive, wasp nest	Scarabelli, 1880	Impossible by (paleo) environmental reasons
Inorganic structure	Gastropod eggs	Fuchs, 1895	
	Diagenesis	Hall, 1843	Interpreted as a concretion-like structure
	Desiccation	Mayer, 1877	Interpreted as mudcracks
	Wave interference on shallow-marine substrates	Sacco, 1888	The description seems to refer to interference ripples
	Rain	Capeder, 1905	Interpreted as raindrop prints
	Chemical processes	Craveri, 1909	
	Gas-escape structures	Karpinsky, 1932	

Paleodictyon belongs.

In this study, we explore the enduring question of the *Paleodictyon* producer by testing the hypothesis that a marine arthropod may have been responsible for its origin. Our investigation is motivated by the morphological resemblances between *Paleodictyon* and structures produced by terrestrial arthropods, including bees and wasps. Scarabelli (1880) even proposed that *Paleodictyon* might represent a fossilised beehive. While Scarabelli's theory can be dismissed on the basis of contemporary geological and ichnological knowledge, it highlights a significant morphological similarity. As noted by Honeycutt and Plotnick (2005), structures built by insects, shaped by geometric constraints such as the closest packing of elements, display symmetries similar to those observed in *Paleodictyon*.

Despite the apparent resemblance between arthropod-built structures and *Paleodictyon*, comprehensive investigations into a potential arthropod tracemaker remain scarce. Gage and Tyler (1991) suggested that a small, elongated crustacean likely produced *Paleodictyon*, considering the diverse life forms present on the modern deep-ocean floor. Similarly, Hantzpergue and Branger (1992) attributed *Paleodictyon* to an endobenthic arthropod, arguing that the discrete size

classes of their specimens reflect growth through successive moults. Later, Miller (2014) succinctly noted that graphoglyptid producers “probably include minute polychaete worms and small crustaceans.” This perspective gains support from Garlick and Miller (1993), who concluded that the precision needed to create *Paleodictyon* is improbable for protists or vermiform organisms, proposing instead that a small crustacean is responsible. The inference of a small-bodied tracemaker rests primarily on tunnel width, which in most ichnospecies of *Paleodictyon* does not exceed 3 mm (Table 2). McMenamin (2016) also suggested an arthropod tracemaker based on an interpretation of *Paleodictyon* as a brooding burrow. Further investigation into the arthropod hypothesis is needed, as deep-sea fauna encompasses not only crustaceans but also various worm-like burrowers; moreover, the navigational capabilities of worm-like invertebrates have yet to be fully assessed.

The objective of this study is to examine the hypothesis that a marine arthropod could have been responsible for producing *Paleodictyon*. We assess the arthropod hypothesis by evaluating its coherence with six key characteristics of *Paleodictyon*: (1) morphology, (2) taphonomy, (3) stratigraphic distribution, (4) environmental distribution, (5) trace-maker characteristics, and (6) inferred function.

2. Materials and methods

In this study, we examined the potential arthropod origin of *Paleodictyon* by testing this hypothesis through a review of existing literature, supplemented by new observations. New specimens were analysed from the Piacenza Apennines (Italy; Cenomanian–Rupelian; Fig. 2A; Table 3). Further new specimens were documented from Nozelos Quarry near Torre de Moncorvo (Portugal, early Cambrian; Fig. 2B) and Andreis (Italy, Triassic; Fig. 2A). These were sourced from the collections of the Natural History Museum of Piacenza and the University of Genoa. Further material was studied from the Eocene localities of Kamesznica, Zbludza, and Znamirówice (Poland; Fig. 2C), deposited at the Jagiellonian University. Neoichnological observations at the Tagliamento River in Italy and Tavira Island in Portugal also complemented our research. Additional neoichnological observations were conducted along the Erro Stream at the Lago dei Gulli locality (Italy).

The terminology employed for *Paleodictyon* follows Uchman (1995) and standard Euclidean geometric terms (Fig. 1B). Mesh size refers to the length of the principal diagonal, defined as the segment linking opposite vertices of a hexagonal cell. Notably, the mesh size exceeds the flat-to-flat distance, which is the separation between parallel sides. Tunnel dimensions are described by their length and width. The interior angle is defined as the angle formed at each hexagon vertex, measured between the meeting sides.

Outdoor photographs were captured using a Nikon W300 camera. Indoor images were taken with a Canon EOS 1100D DSLR camera, equipped with a Canon Zoom lens (18–55 mm f/3.5–5.6) and a Sigma Macro lens (105 mm f/2.8). The photographic arrangement included a Durst M301 stand with a micrometric slide, four 10 W LED lamps, and a cold light source (Starlight LED 3).

Photogrammetry was utilised to generate photo-textured digital elevation models of the specimens examined at the Natural History Museum of Piacenza.

Image processing was conducted in Agisoft Metashape Professional v.2.2.0 following a standard Structure-from-Motion (SfM) workflow. A total of 178 close-range images were aligned, generating 154,134 tie points with an average reprojection error of approximately 0.93 pixels, confirming stable camera calibration (Table 4). A dense point cloud was then computed at high quality with mild depth-map filtering and subsequently used to produce a textured 3D mesh and a preliminary Digital Elevation Model (DEM).

Because the photographs were not georeferenced, the reconstruction was performed in a local coordinate system. The model was scaled using a physical scale bar, based on a metric reference rod positioned adjacent

to the specimen during image acquisition, ensuring accurate relative dimensions. The DEM was generated from the dense point cloud, producing a metrically consistent, topographically accurate elevation model of the fossil trace surface.

A total of 9 specimens from the Museo di Storia Naturale di Piacenza collection were selected for quantitative analysis based on preservation quality (Table 5), each containing at least 7 cells with all 6 vertices preserved and all 6 sides measurable for thickness. Image analysis was performed using Fiji/ImageJ 1.54p. For each specimen, up to 10 cells were analysed: the 6 vertices were digitized, and the thickness of each of the six sides was measured from two points per side, yielding a total of 1314 digitized landmark points across the dataset. Vertex landmarks were digitised along the midline of the tunnels, while thickness landmarks were placed on tunnel margins. From these coordinates, we derived internal angles, side lengths, diagonal lengths, and side thickness for each cell. PAST 5.3 was used for visualizing cell metrics (Fig. 3).

A comprehensive database was constructed using Visual dBase to systematically catalogue the specimens housed at the Natural History Museum of Piacenza. At present, it includes data on approximately 500 specimens from the Piacenza Apennines. Each specimen is allocated a distinct identification number (e.g., NHMP357), which is consistently referenced throughout this article. The AI system GeologyOracle (Baucon and de Carvalho, 2024) was used for linguistic improvement of this paper.

3. Results

This section presents the results of the morphological analysis of *Paleodictyon*. We first describe the qualitative characters of the studied specimens (Section 3.1), then quantify cell regularity through morphometric analysis of selected specimens from the Natural History Museum of Piacenza (Section 3.2), and finally report the neoichnological observations used to test the arthropod origin of *Paleodictyon* (Section 3.3).

3.1. Qualitative analysis

The qualitative analysis of *Paleodictyon* focused on 5 morphological features, that are, the straightness of tunnel segments (Fig. 4), the angles of the hexagonal cells (Fig. 5), the consistency of interior angles and

tunnel dimensions (Figs. 5, 6), the horizontality of the hexagonal network relative to the bedding plane (Fig. 8), vertical shafts (Fig. 9), and mid-cell features (Fig. 10).

Most of the specimens of the Natural History Museum of Piacenza (Table 5) show a substantially uniform network, with tunnel segments of approximately constant length and width. All examined specimens show distinctly straight tunnels, lacking appreciable curvature changes along their course. At one vertex of specimen NHMP348 we measured the transition length—the distance along the tunnel centreline over which a change in direction is completed. Here the transition length between converging segments was effectively zero, indicating an abrupt directional change. Qualitative examination of the entire collection revealed no specimen with appreciable angular transitions, so quantitative estimation of curvature was unnecessary.

Vertical shafts were documented as nodose elements superimposed on the horizontal network. Well-defined vertical shafts occur in specimen NHMP218, while photogrammetric analysis of NHMP153 confirms the horizontality of the hexagonal network relative to the bedding plane. None of the examined specimens shows evident scratch marks on the tunnel walls. Among the accessory features of *Paleodictyon*, single (NHMP154) and paired (NHMP153) mid-cell structures are observed.

Beyond the Piacenza collection, the Polish and Portuguese material confirm the same general morphological picture. The specimen of *P. gomezi* from Nozelos Quarry (Cambrian, Portugal) shows sharp, well-defined pointy corners. Vertical shafts are well documented, as shown by the nodose pattern of specimen UJ TF 101 (*P. strozzii*, Znamierowice, Poland), analogous to that of the Piacenza specimen NHMP218. Specimen INGUJ144P98 (*P. gomezi*, Zbludza) instead shows localised swellings and small lateral tunnels branching from the sides of the hexagonal cells (Fig. 7E–F), a character not observed in the Piacenza specimens. Neither the Portuguese material nor the Polish specimens display scratch marks on the tunnel walls, consistent with the specimens of the Piacenza collection.

3.2. Morphometric analysis of cell regularity

Morphometric analysis of 438 tunnel segments corroborates the qualitative observations. Cell regularity was assessed through three complementary aspects: (1) equilaterality—how much the 6 sides of a

Table 2
Size ranges of the valid ichnospecies of *Paleodictyon*.

Taxon	Minimum string width (mm)	Maximum string width (mm)	Minimum mesh size (mm)	Maximum mesh size (mm)	Mesh/string size ratio	Remarks
<i>P. majus</i>	0.8	1.6	6	14	8.3	The original diagnosis (Uchman, 1995) specifies only maximum mesh size ("maximum mesh size up to 14 mm"); the minimum value has been set arbitrarily for graphical representation in Fig. 1C.
<i>P. strozzii</i>	0.2	1	2	6	6.7	
<i>P. maximum</i>	1.6	2.8	3.5	14	4	
<i>P. hexagonum</i>	2.8	6	8	20	3.2	The original diagnosis specifies only minimum string diameter ("string diameter more than 2.8 mm"); the maximum value has been arbitrarily set.
<i>P. miocenicum</i>	1	1.6	2	6	3.1	The original diagnosis specifies only maximum values ("mesh size up to 2 mm, string width up to 0.5 mm"); the minimum values have been arbitrarily set.
<i>P. minimum</i>	0.1	0.5	0.3	2	3.8	
<i>P. arvense</i>	1.6	2.8	14	26	9.1	The original diagnosis specifies only maximum mesh size ("mesh size up to 2 mm"); the minimum value has been arbitrarily set.
<i>P. latum</i>	0.5	1	0.3	2	1.5	
<i>P. goetzingeri</i>	0.8	1.6	14	30	18.3	The original diagnosis specifies only the minimum mesh size ("string diameter more than 2.8 mm"); the maximum value has been arbitrarily set.
<i>P. italicum</i>	2.8	6	20	40	6.8	
<i>P. croaticum</i>	1.6	2.8	26	40	15	The original diagnosis specifies only minimum values ("mesh size more than 40 mm, string diameter more than 1.6 mm"); the maximum values have been arbitrarily set.
<i>P. delicatulum</i>	0.1	0.8	6	14	22.2	
<i>P. gomezi</i>	1.6	6	40	80	15.8	

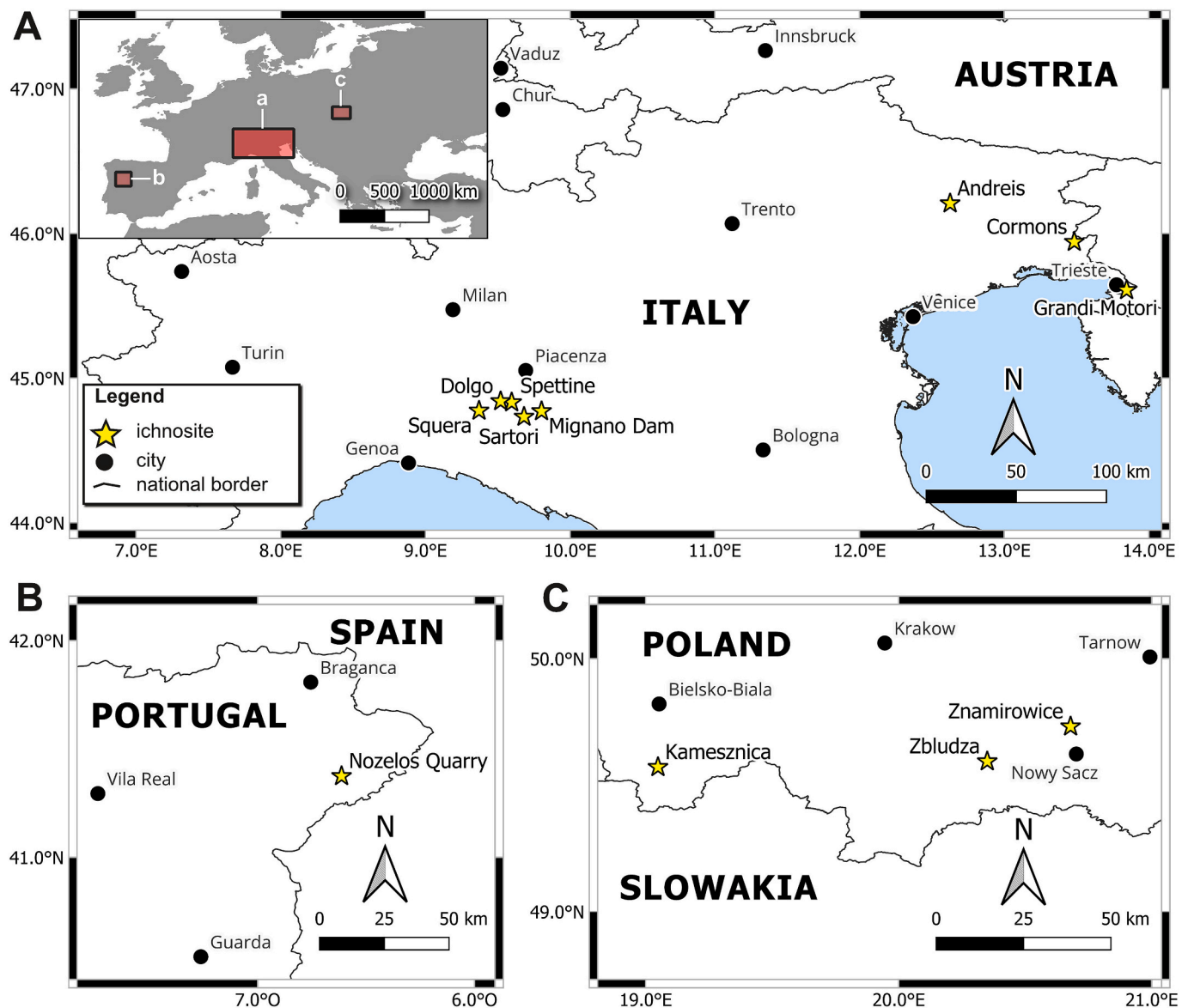


Fig. 2. Geographical setting. Stratigraphical information for each site is given in Table 3. A. Ichnosites in Italy. The inset shows the position of the plates of the figure. B. Ichnosites in Portugal. C. Ichnosites in Poland.

cell differ from one another; (2) equiangularity—how much its 6 interior angles differ from one another; and (3) equidimensionality—the extent to which a given cell has equal extension in all directions. The first two describe local regularity (the geometry of the individual sides and angles of each cell), whereas the third describes global distortion (the overall shape of the cell).

3.2.1. Equilaterality

Equilaterality was quantified through the within-cell standard deviation of side length (length deviation, σ_l ; Fig. 3A). In other words, the value of σ_l quantifies in millimetres how much the sides of a given cell depart from the mean side length of that cell. Most cells of the Piacenza dataset approach equilaterality (Fig. 3A); appreciable departures occur, notably in some cells of specimens NHMP153 and NHMP209.

The mean σ_l across the 73 measured cells is 0.5 mm, implying that the sides of a typical cell deviate by only 0.5 mm from the mean side length of the same cell.

While σ_l describes the regularity of an individual cell, its within-specimen (between-cell) counterpart σ_e describes whether the cells of a specimen resemble one another in size. It is the standard deviation of

the mean side lengths of the cells within the same specimen. The values of σ_e range from 0.05 to 0.31 mm (mean 0.19 mm), showing that the cells of a given *Paleodictyon* specimen are highly uniform in size, with the network maintaining a nearly constant mesh throughout.

3.2.2. Equiangularity

Interior-angle values range from 89.4° to 165.4° (Fig. 3B). The mean interior angle (120°) is uninformative, as it is a geometric artefact: the interior angles of a hexagon sum to 720°, so the mean of six angles is necessarily 120° in every cell and every specimen, however irregular the hexagon. The biological signal therefore resides not in the mean but in the dispersion around 120°. We accordingly quantified, for each cell, the standard deviation of its 6 interior angles (angular deviation, σ_a), which measures the departure of the interior angles from the ideal 120° of a regular hexagon (Fig. 3C). The values of σ_a range from a minimum of 3.3° to a maximum of 25.1°, with a mean of 8.5°.

3.2.3. Equidimensionality

Each hexagon has three major diagonals, joining opposite vertices through the centre; in a regular hexagon these are equal, and their

Table 3
Study sites.

Site	Area	Coordinates	Period	Epoch/Age	Unit
Spettine	Ponte dell'Olio, Italy	N 44.833547 E 9.594144	Paleogene	Eocene-Oligocene (Priabonian-Rupelian)	Ranzano Fm.
Zbludza	Gmina Kamienica	N 49.593939, E 20.349405	Paleogene	Eocene	Beloveža Formation
Grandi Motori	Muggia, Italy	N 45.607773 E 13.847483	Paleogene	Eocene (Lutetian)	Trieste Flysch Fm.
Kamesnica	Żywiec, Poland	N 49.573197 E 19.060566	Paleogene	Eocene	Hieroglyphic Beds
Dolgo	Travo, Italy	N 44.839504 E 9.521192	Paleogene	Eocene (Ypresian)	Val Luretta Fm.
Znamirówice	Tarnów, Poland	N 49.736241 E 20.681720	Paleogene	Eocene (Ypresian)	Ciężkowice Sandstone
Squera	Bobbio, Italy	N 44.772889 E 9.37512	Paleogene	Paleocene (Thanetian)	M. Penice Flysch
Diga di Mignano	Morfasso, Italy	N 44.772315 E 9.797981	Cretaceous	Maastrichtian	M. Cassio Flysch
Sartori	Morfasso, Italy	N 44.735218 E 9.687570	Cretaceous	Cenomanian	Guselli Argillite
Andreis	Andreis, Italy	N 46.207759 E 12.626773	Triassic	Norian	Dolomia Principale
Nozelos Quarry	Torre de Moncorvo, Portugal	N41.298622, W7.039122	Cambrian	Stage 2 or 3	Desejosa Fm.

Table 4
Photogrammetry parameters.

Parameter	Value / Setting	Notes
Software	Agisoft Metashape Professional v.2.2.0	SfM + MVS workflow
Camera	Canon IXUS 145	4608 × 3456 px; 5 mm focal length
Number of images	178	Close-range, rotating platform
Image acquisition	Rotating platform	Uniform coverage, high overlap
Working distance	~13.7 cm	Very close-range
Ground sampling distance (GSD)	0.0359 mm/pix	Extremely high spatial resolution
Tie points (sparse cloud)	154,135	Total projections: 577,561
Reprojection error	~0.93 px	Stable camera self-calibration
Alignment settings	High quality	Generic preselection: enabled
Dense cloud	19,077,746 points	High quality; Mild depth filtering
Surface model	Textured 3D mesh (tiled model)	Resolution ~3.09 mm/pix
Reference system	Local coordinates (m)	No global georeferencing
Scaling method	Scale bar (6 mm metric rod)	Residual error ~ 0
Re-orientation	CloudCompare (best-fit plane)	Corrects unconstrained local axes
DEM generation	From re-oriented dense cloud	Micro-topographic visualisation
Primary outputs	Textured mesh + DEM	Used for ichnological quantification

disparity is a further measure of irregularity. We expressed this as the regularity ratio R_r , the ratio of the shortest to the longest diagonal (Fig. 3D). $R_r = 1$ for a perfectly equidimensional hexagon and decreases towards 0 as the cell becomes elongate. In the Piacenza material, the most distorted cell (in NHMP153) has $R_r = 0.59$, its short diagonal about two-fifths of the long one. Most cells, however, approach regularity, and six specimens (NHMP153, NHMP154, NHMP168, NHMP257, NHMP348, NHMP459) include nearly equidimensional cells ($R_r > 0.95$). The mean R_r of 0.90 indicates that in the typical cell the short diagonal is about 90% of the long one—cells are thus slightly elongate in one direction.

3.2.4. Width uniformity

The distribution of tunnel width at the single-cell level shows low,

though not always negligible, local variability. For each of the 73 cells we computed the standard deviation of tunnel width (width deviation, σ_w), a measure of how much thickness varies relative to the mean width of the 6 tunnels of that cell (Fig. 3E). Averaged over the 73 cells, σ_w shows that per-cell tunnel thickness varies on average by only 0.21 mm from the mean thickness.

3.3. Neoichnological observations

Palaeoichnological results were complemented by localised neo-ichnological examples. The mole cricket burrow from Tavira Island comprises straight tunnel segments—the longest reaching 25.8 times the burrow width—and a looping section of irregular polygonal outline; segment length normalised by burrow width is high ($l/w > 5$), approaching the elevated ratios of *Paleodictyon* (e.g. NHMP223, $l/w > 2$). Mole cricket burrows from the Tagliamento River, Italy, similarly show abrupt directional changes and vertical shafts penetrating only ~1 mm into the sediment, meeting the horizontal tunnel system at a sharp ~90° branching angle, whereas the ?staphylinid burrows are predominantly horizontal. Both these insect burrows and insect leaf mines from Plessiva, Italy, display pointed and smooth corners.

4. Discussion

In this section, we test the hypothesis that marine arthropods can produce *Paleodictyon*. The hypothesis is evaluated through six principal characteristics of *Paleodictyon*: morphology, taphonomy, stratigraphic distribution, environmental distribution, tracemaker characteristics, and inferred function. Each characteristic is analysed in relation to the known traits and behaviours of arthropods.

4.1. Morphology

4.1.1. Hexagonal meshes with straight segments

The hexagonal mesh of *Paleodictyon* is probably its most visually striking feature. Each cell of the mesh comprises a nearly regular hexagon with six straight tunnels (Fig. 4A), indicating that the trace-maker maintained predominantly linear trajectories during its burrowing. We suggest that the ability to create straight burrow segments is a characteristic trait of arthropod tracemakers, highlighting their potential to produce *Paleodictyon*.

Arthropods exhibit a notable tendency to generate linear tunnel segments, primarily due to their unique bauplan, which includes jointed appendages and a rigid exoskeleton - defining traits of their phylum.

Table 5

Studied specimens. The prefix in the specimen codes refer to the museum in which the specimens are stored (NHMP: Natural History Museum of Piacenza; UJ: Jagiellonian University).

Taxon	Site	Specimen code	Remarks
Insect leaf mine	Plessiva	Not applicable (modern trace)	
Mole cricket burrow	Tagliamento	Not applicable (modern trace)	
Mole cricket burrow	Tavira	Not applicable (modern trace)	Straight segments with looping section
<i>Paleodictyon gomezi</i>	Zbludza	INGUJ144P98	
<i>Paleodictyon?</i> isp.	Dolgo	NHMP218	
<i>Paleodictyon</i> isp.	Spettine	NHMP192_B	
<i>Paleodictyon</i> isp.	Spettine	NHMP193_B	associated with <i>Desmograption</i>
<i>Megagraption</i> isp.	Diga di Mignano	NHMP274	
<i>Paleodictyon</i> isp.	Spettine	NHMP376	
<i>Paleodictyon</i> isp.	Spettine	NHMP380	
<i>Paleodictyon</i> isp.	Spettine	NHMP383	
<i>Paleodictyon</i> isp.	Spettine	NHMP388_A	
<i>Paleodictyon</i> isp.	Spettine	NHMP416	
<i>Paleodictyon</i> isp.	Spettine	NHMP418_A	
<i>Paleodictyon</i> isp.	Dolgo	NHMP455	
<i>Paleodictyon</i> isp.	Dolgo	NHMP456	
<i>Paleodictyon</i> isp.	Spettine	NHMP458	
<i>Paleodictyon</i> isp.	Spettine	NHMP459	Morphometric analysis was performed on the specimen.
<i>Paleodictyon</i> isp.	Squera	NHMP99_A	
<i>Paleodictyon gomezi</i>	Nozelos Quarry		
<i>Paleodictyon minimum</i>	Spettine	NHMP195	
<i>Paleodictyon minimum</i>	Spettine	NHMP196	
<i>Paleodictyon minimum</i>	Spettine	NHMP281	
<i>Paleodictyon minimum</i>	Spettine	NHMP282	
<i>Paleodictyon minimum</i>	Sartori	NHMP354	
<i>Paleodictyon minimum</i>	Spettine	NHMP377	
<i>Paleodictyon minimum</i>	Spettine	NHMP382	
<i>Paleodictyon minimum</i>	Spettine	NHMP417	
<i>Paleodictyon minimum</i>	Spettine	NHMP418_B	
<i>Paleodictyon minimum</i>	Spettine	NHMP453	
<i>Paleodictyon strozzii</i>	Spettine	NHMP133	
<i>Paleodictyon strozzii</i>	Spettine	NHMP153	mid-cell tunnels. Morphometric analysis was performed on the specimen.
<i>Paleodictyon strozzii</i>	Spettine	NHMP154	mid-cell tunnels. Morphometric analysis was performed on the specimen.
<i>Paleodictyon strozzii</i>	Spettine	NHMP158_A	associated with <i>Halopoa</i> . Morphometric analysis was performed on the specimen.
<i>Paleodictyon strozzii</i>	Spettine	NHMP160	
<i>Paleodictyon strozzii</i>	Spettine	NHMP209	Morphometric analysis was performed on the specimen.
<i>Paleodictyon strozzii</i>	Spettine	NHMP223	Morphometric analysis was performed on the specimen.
<i>Paleodictyon strozzii</i>	Spettine	NHMP257_A	mid-cell tunnels? Morphometric analysis was performed on the specimen.

Table 5 (continued)

Taxon	Site	Specimen code	Remarks
<i>Paleodictyon strozzii</i>	Spettine	NHMP257_A	Morphometric analysis was performed on the specimen.
<i>Paleodictyon strozzii</i>	Spettine	NHMP267	
<i>Paleodictyon strozzii</i>	Squera	NHMP2_A	mid-cell tunnels; associated with <i>Spirophycus</i>
<i>Paleodictyon strozzii</i>	Spettine	NHMP348	Morphometric analysis was performed on the specimen. Two-tier network?
<i>Paleodictyon strozzii</i>	Spettine	NHMP371	
<i>Paleodictyon strozzii</i>	Spettine	NHMP372	preserved at the base of a flute
<i>Paleodictyon strozzii</i>	Spettine	NHMP452	mid-cell tunnels?
<i>Paleodictyon strozzii</i>	Znamirówice	UJ TF 101	
<i>Protopaleodictyon incompositum</i>	Spettine	NHMP375	
<i>Protopaleodictyon</i> isp.	Sartori	NHMP340	
<i>Thalassinoides</i> isp. cf. <i>Paleodictyon</i>	Andreis Grandi Motori		
<i>Paleodictyon miocenicum</i>	Kamesznica	UJ TF 1827	

These appendages, comprising legs, claws, and mandibles, are crucial for employing the burrowing technique known as excavation (sensu Bromley, 1996). This burrowing technique involves scraping the anterior burrow wall and conveying the resulting spoils elsewhere (Bromley, 1996; Dorgan and Daltorio, 2023), as demonstrated by the deep-sea isopod *Bathynomus doederleini*. This isopod uses its thoracic legs to loosen sediment ahead and employs water currents generated by its swimmerets to remove the resulting debris (Matsui et al., 2011).

The excavation technique facilitates precise, straight-line burrowing by removing sediment instead of following paths of least resistance. This method is used by mole crickets to produce straight, horizontal burrows, which are found in locations such as the dunes of Tavira Island (Fig. 4B).

These burrows feature straight tunnel segments approximately 5 to 10 cm in length (Fig. 4C, D). This segment length (l) refers specifically to the unbranched, linear sections of a burrow between two consecutive directional changes. When normalised by burrow width (w), it yields a dimensionless metric of the burrow geometry. This metric distinguishes tightly winding patterns ($l/w \approx 0-1$) from those with extended straight sections ($l/w \gg 1$). Both *Paleodictyon* ($l/w > 2$) and mole cricket burrows ($l/w > 5$) exhibit high ratios, suggesting that their tracemakers may employ similar burrowing techniques. During burrowing, mole crickets use their specialised forelimbs to excavate efficiently. These limbs function as shovels, enabling the insect to displace sediment sideways and backwards (Sedorko et al., 2024a). Wolf spiders are another example of excavation burrowers, producing straight, vertical burrows by scraping and dislodging soil with their scraping fangs (Belmontes et al., 2018; Dorgan and Daltorio, 2023; Suter et al., 2011; Uchman et al., 2018).

It should be noted that the arthropod bauplan allows them to create both straight and curved traces, exemplified by the curved borings of the Southern pine beetle, *Dendroctonus frontalis*.

The worm bauplan, with its cylindrical form and hydrostatic skeleton, facilitates efficient burrowing by exploiting paths of least resistance rather than by excavation, thereby generally producing tortuous burrows. In muddy sediments, for example, worms burrow by fracture, in which an alternating anchor system serves as a wedge to extend a crack-shaped burrow (Dorgan et al., 2005, 2007). The resulting burrows are unlikely to be straight, as cracks propagate along paths of least resistance, whose direction varies even within small sediment volumes. While worms commonly use crack propagation for burrowing, there are notable exceptions to this rule. Arenicolid polychaetes, despite lacking

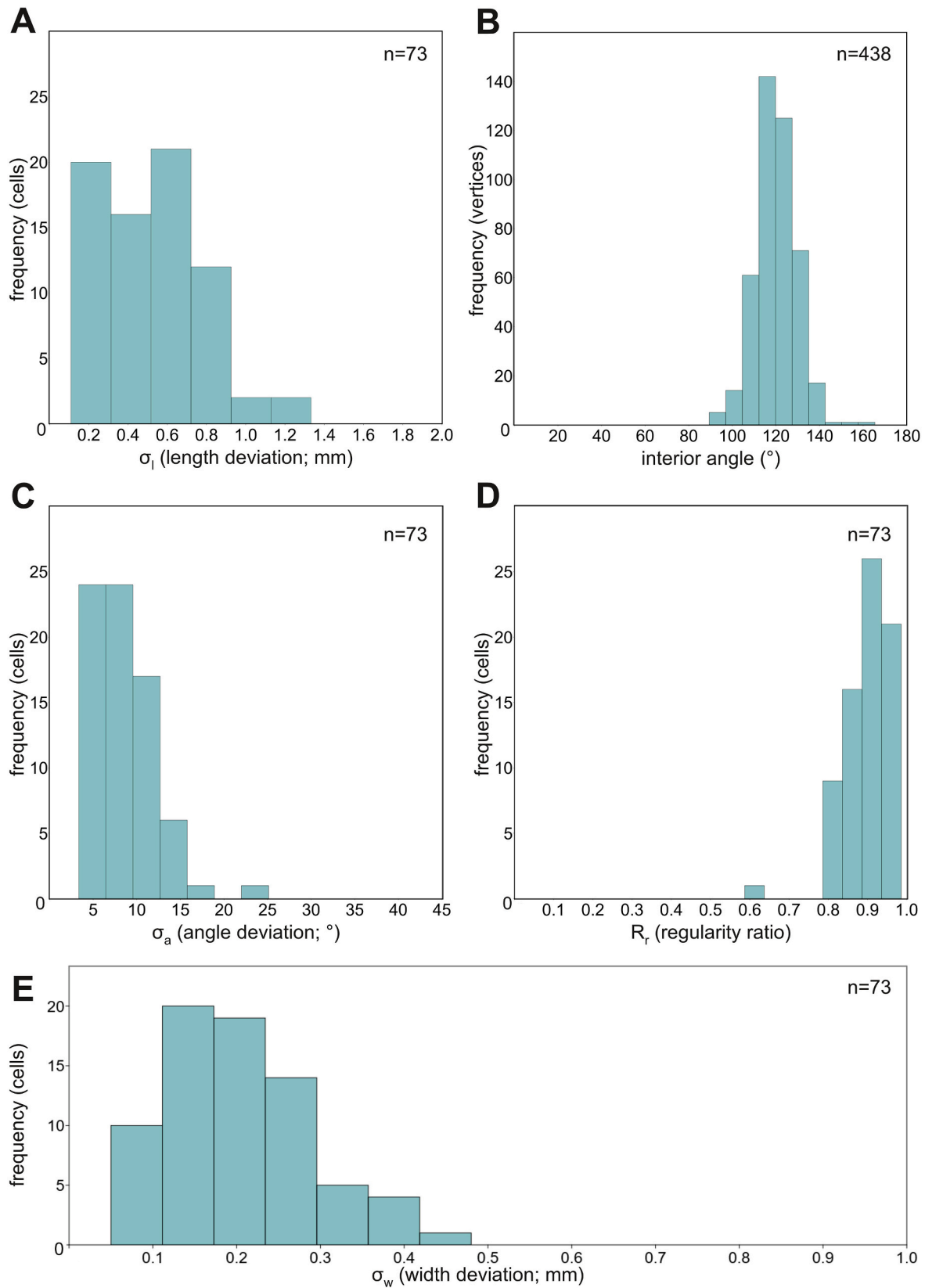


Fig. 3. Results of the morphometric analysis. A. Distribution of length deviation (σ_l). Length deviation measures the within-cell standard deviation of side length. B. Distribution of interior angles. Values cluster symmetrically around the ideal 120° characterizing regular hexagons. C. Distribution of angle deviation (σ_a). Angle deviation represents the within-cell standard deviation of interior angles. D. Distribution of regularity ratio (R_r). Regularity ratio measures the ratio between the shortest and the longest diagonal. E. Distribution of width deviation (σ_w). Width deviation quantifies the within-cell standard deviation of tunnel width.

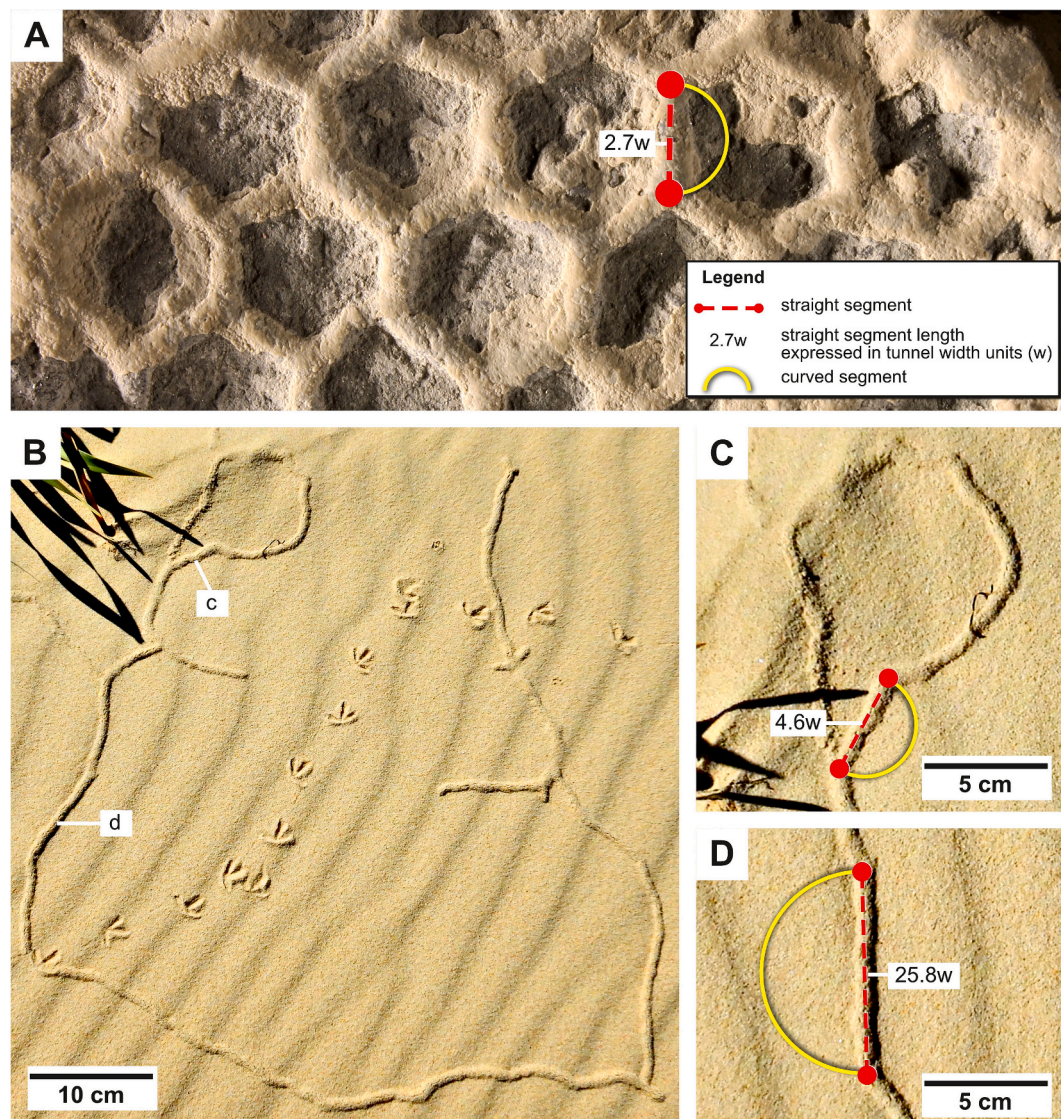


Fig. 4. Straight tunnels in *Paleodictyon* and mole cricket burrows. A. *P. strozii* showing characteristically straight tunnels. The highlighted tunnel is 2.7 times as long as its width. A curved segment is shown for comparison. Detail of the specimen in Fig. 1A (NHMP223). B. Mole cricket burrow displaying multiple straight segments. Labels 'c' and 'd' indicate details shown in Fig. 4C and D. Tavira Island, Portugal. C. Detail from B showing a looping section with an irregular polygonal shape. D. Straight segment in the burrow, measuring 25.8 times the burrow width; detail from B.

rigid structures for scraping, excavate by ingesting sediment at depth and egesting it at the surface (Dorgan and Daltorio, 2023). The straight, *Skolithos*-like burrows of certain polychaetes, such as *Lanice* and *Megalomma* represent another exception (Baucon and Felletti, 2013).

Peristaltic movement significantly influences the creation of tortuous burrows by vermiform organisms. Worm-like organisms often employ peristalsis – waves of muscle contraction moving anteriorly or posteriorly along the body - to facilitate forward motion (Dorgan, 2015, 2018). The movement of a worm in a perfectly straight line requires each peristaltic wave to be symmetrical around the central axis of its body. However, achieving perfect symmetry is challenging in multi-segmented, soft-bodied animals navigating a non-uniform medium. Each segment requires precise coordination of circular and longitudinal muscles to maintain straight locomotion. Even minor asymmetries in muscle activation can be amplified along their length, complicating straight movement. Moreover, the substrate is non-homogeneous, with varying resistance areas. Consequently, maintaining a straight line is difficult because worm bodies are flexible and compressible, lacking structures to constrain body alignment.

Finally, tortuous burrows may confer significant advantages to

vermiform organisms. Curved paths enable anchoring thrust for space-making penetration to be supported by normal forces, rather than by shear alone (Dorgan and Daltorio, 2023).

In sum, our observations demonstrate that arthropods can create straight burrow segments, similar to those found in *Paleodictyon*. No current arthropod species forms exact hexagonal networks of tunnels, although mole crickets can form looping burrow sections with irregular polygonal shapes (Fig. 4C). The prevalence of hexagonal patterns in arthropod structures, such as those found in hymenopteran nests, typically results from the arrangement of wax cell margins rather than the presence of tunnels. Assassin bugs (Reduviidae) also exhibit hexagonal arrangements in their egg masses. These instances neither confirm nor refute the arthropod hypothesis, yet they indicate a propensity among arthropods for hexagonal tiling. In contrast, such configurations are not observed in worm-like phyla. It should be noted that these observations are ancillary; the case for an arthropod tracemaker rests primarily on the biomechanical evidence discussed above. Overall, the evidence suggests that arthropods are more likely producers of *Paleodictyon* than worm-like animals, although a vermiform tracemaker cannot be entirely excluded.

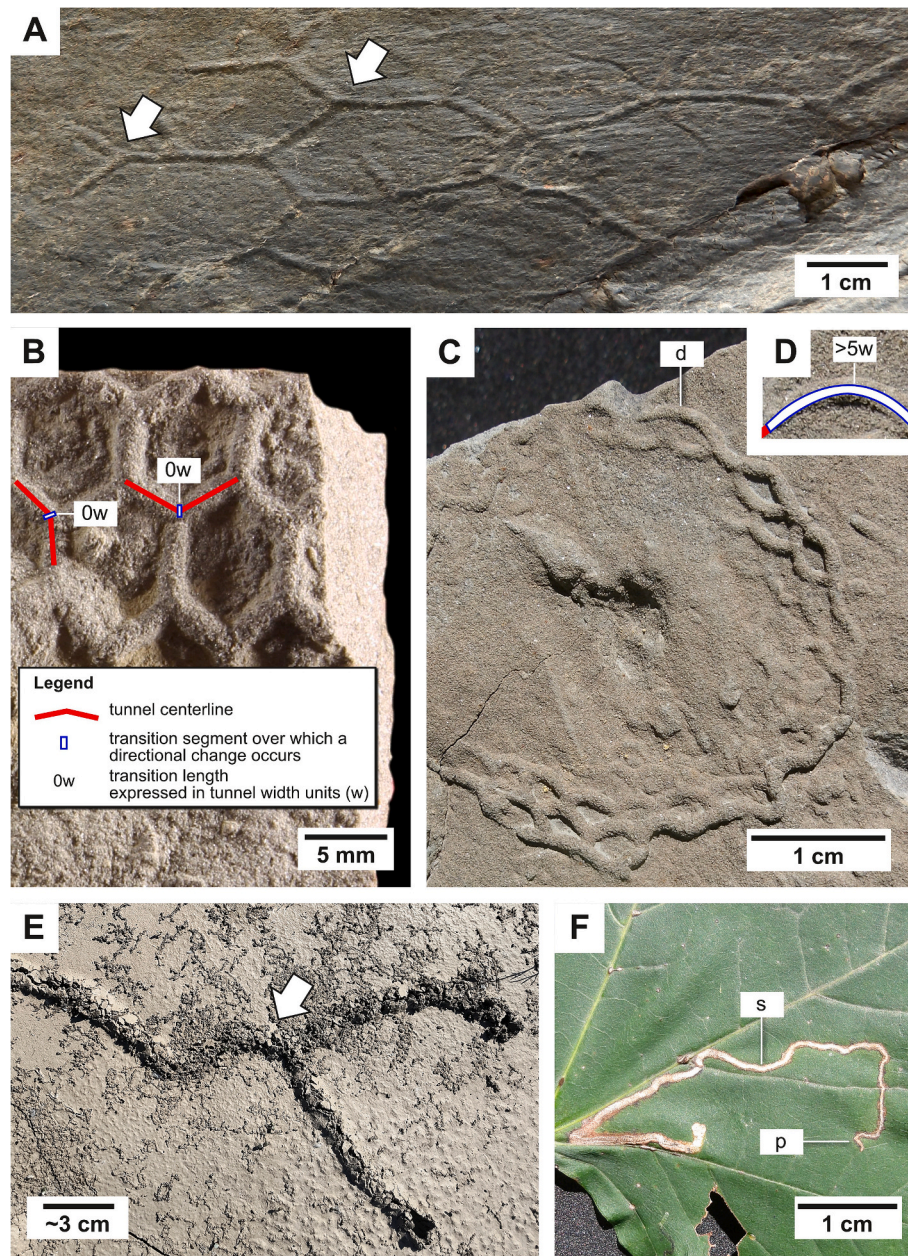


Fig. 5. Pointy corners. A. Pointy corners (indicated by arrows) in *Paleodictyon gomezi* from Nozelos Quarry, Cambrian. B. Short transition length ($t = 0w$) observed in *Paleodictyon* specimen NHMP348. C. Mesh-forming graphoglyptid (*Squamodictyon* cf. *petaloideum*) from Grandi Motori exhibiting smooth, gradual changes in direction. The arrow indicates the detail shown in D. D. Detailed view of a long transition length ($t > 5w$) in the mesh-forming graphoglyptid from C. E. Abrupt directional change identified in a mole cricket burrow from the Tagliamento River. F. Leaf mine produced by an insect displaying both pointed (p) and smooth (s) curves.

4.1.2. Pointy corners

Paleodictyon cell meshes are characterised by six tunnels that converge at $\sim 120^\circ$ angles, often forming distinct, pointed corners (Fig. 5A). These pointed corners reflect a very short transition length (t), defined as the distance along the burrow centreline where a change in direction occurs. This is calculated from the point at which the burrow starts deviating from its initial trajectory to the point at which it stabilizes in its new path. When the transition length is normalised by the burrow width (w), it reveals the sharpness of the turns made by the tracemaker. *Paleodictyon* shows a transition length approaching zero (Fig. 5B), indicating abrupt directional changes over distances much smaller than the burrow diameter. Conversely, burrows with a transition length greater than 3 reflect smooth, gradual curves extending over several burrow diameters (Fig. 5C).

The short transition length of *Paleodictyon* suggests that its producer could execute sharp 120° directional junctions (or equivalently 60° turns), aligning with the abrupt directional changes typical of arthropod tracemakers (Fig. 5E, F). Arthropods exhibit remarkable maneuverability, primarily due to the jointed legs characteristic of their bauplan. By adjusting the position of their legs, arthropods can achieve precise, abrupt turning angles. In addition, the rigid exoskeletons of infaunal arthropods allow for direct force in specific directions, facilitating the development of burrows with pointed corners.

In contrast, worm-like burrowers, characterised by their flexible, soft and elongated bodies, typically form rounded corners in burrows, as also noted by McIlroy (2022). Worm bodies are mechanically challenging to turn (Dorgan and Daltorio, 2023), therefore, sharp turns with pointy corners are not typical of worm burrows. In addition, the elongate body

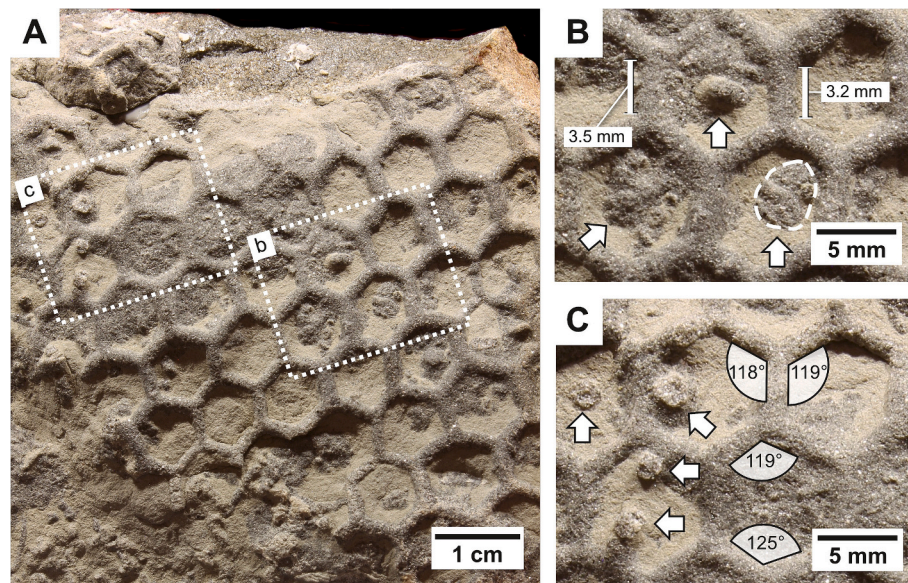


Fig. 6. Angles and tunnel dimensions in *Paleodictyon*. A. *Paleodictyon* displaying a nearly uniform geometry throughout the burrow system, with details highlighted in B and C. NHMP257. B. Consistent segment lengths in *Paleodictyon* cells. Arrows mark mid-cell shafts, with one shaft highlighted by a dashed line. C. Minor, yet notable variation in angles. Arrows indicate mid-cell shafts. Detail of A.

plan of worms tends to smooth any sharp angles in their burrows. The worm head initiates directional changes, and the forward movement of the body presses against the tunnel walls, progressively smoothing any sharp angles created during the initial turn. This action rounds off corners as the worm advances.

In summary, our observations indicate that the arthropod bauplan can produce the characteristic pointed angles observed in *Paleodictyon*. By contrast, it seems improbable that a worm-like organism with an elongate body could have formed these geometries. However, this does not entirely rule out alternative hypotheses, such as the body fossil hypothesis. For instance, [McIlroy \(2022\)](#) suggests that the absence of rounded corners indicates a branched growth pattern that preserves the external moulds of an organism rather than a continuously patrolled burrow.

4.1.3. Consistency of interior angles and tunnel dimensions

A single *Paleodictyon* network is characterised by cells of nearly uniform geometry ([Fig. 6A](#)), consistent with an arthropod tracemaker. The arthropod bauplan, defined by jointed appendages and a rigid exoskeleton, allows the precise motor control required to form such geometrically consistent structures.

The geometry of *Paleodictyon* shows remarkable consistency across three primary parameters: (1) tunnel width, (2) tunnel length, and (3) the angles between tunnels. Specifically, each cell of a *Paleodictyon* network typically comprises segments of roughly equal width and length ([Fig. 3A](#), [Fig. 3E](#), [Fig. 6B](#)), intersecting at angles close to 120° ([Fig. 6C](#)). This configuration closely mirrors a monohedral tessellation, a tiling pattern composed of congruent prototiles (tiles of the same size and shape). The tessellation pattern of *Paleodictyon* reflects significant precision in the burrowing process, as evidenced by the consistent reproduction of near-identical hexagons throughout the network.

Significant burrowing precision is indicated by the distribution of length deviation σ_l ([Fig. 3A](#)). The distribution is unimodal, with mean and median almost coinciding (0.520 and 0.524 mm), and its central half (interquartile range) falls between 0.31 and 0.68 mm. The tracemaker therefore controlled tunnel length with sub-millimetric precision. It should be noted that σ_l scales with cell size, so that the right-hand tail of the distribution reflects large cells rather than anomalously irregular ones.

At the level of individual cell vertices, precise positioning of the

tracemaker body is crucial for forming *Paleodictyon*. The angles between tunnel segments must closely approximate 120° , the ideal angle for seamless tessellation with equilateral hexagons. Deviations from this ideal angle would produce geometric irregularities, such as gaps or overlaps, thereby compromising the integrity of the tessellation ([Garlick and Miller, 1993](#); [Plotnick, 2003](#)).

Quantitative analysis of the Piacenza collection confirms that the tracemaker was capable of precise positioning of its body. The 438 measured interior angles ([Fig. 3B](#)) are distributed unimodally and symmetrically (median: 119.8° ; mean: 120°). Whereas the mean of 120° is a geometric artefact—the six deviations within each cell necessarily sum to zero—the symmetry is not. A symmetric distribution indicates that the tracemaker aimed at the 120° angle, with random deviations in both directions. The mean absolute departure from 120° is only 7.1° . The interquartile range—the central half of the distribution—spans 114.3° to 125.6° , so that half of all measured angles lie within about 6° of the ideal 120° angle. This suggests that the tracemaker could estimate and reproduce a 120° angle to within about 6° , or better, since the measured scatter also includes digitisation error.

It should be noted that, based on the Piacenza dataset, the tracemaker was not flawless, since occasional cells depart markedly from the ideal regular hexagon. This is shown by the distribution of angular deviation σ_a ([Fig. 3C](#)), which is unimodal and strongly right-skewed. Most cells cluster around a mode of about 6° , indicating frequently precise execution, while fewer than 3% of the cells exceed an angular deviation of 15° . Large departures from the ideal hexagon are therefore concentrated in a few isolated cells rather than evenly distributed across the network—the pattern expected from precise motor control punctuated by occasional errors.

The arthropod bauplan, with its jointed appendages and exoskeleton, is compatible with the significant motor control required to produce *Paleodictyon*. Jointed legs and rigid skeleton enable precise positioning at specific angles, allowing for precision in burrowing behaviour. In contrast, worm-like tracemakers, with their soft bodies and reliance on peristaltic movement, lack the structural framework needed to maintain consistent angles throughout the burrow network. In addition, vermiform tracemakers often exploit paths of least resistance when burrowing ([Dorgan et al., 2005](#); [Dorgan and Daltorio, 2023](#)); therefore, they are unlikely to replicate angles over vast areas consistently. Furthermore, the precision required to produce *Paleodictyon* has been cited as a

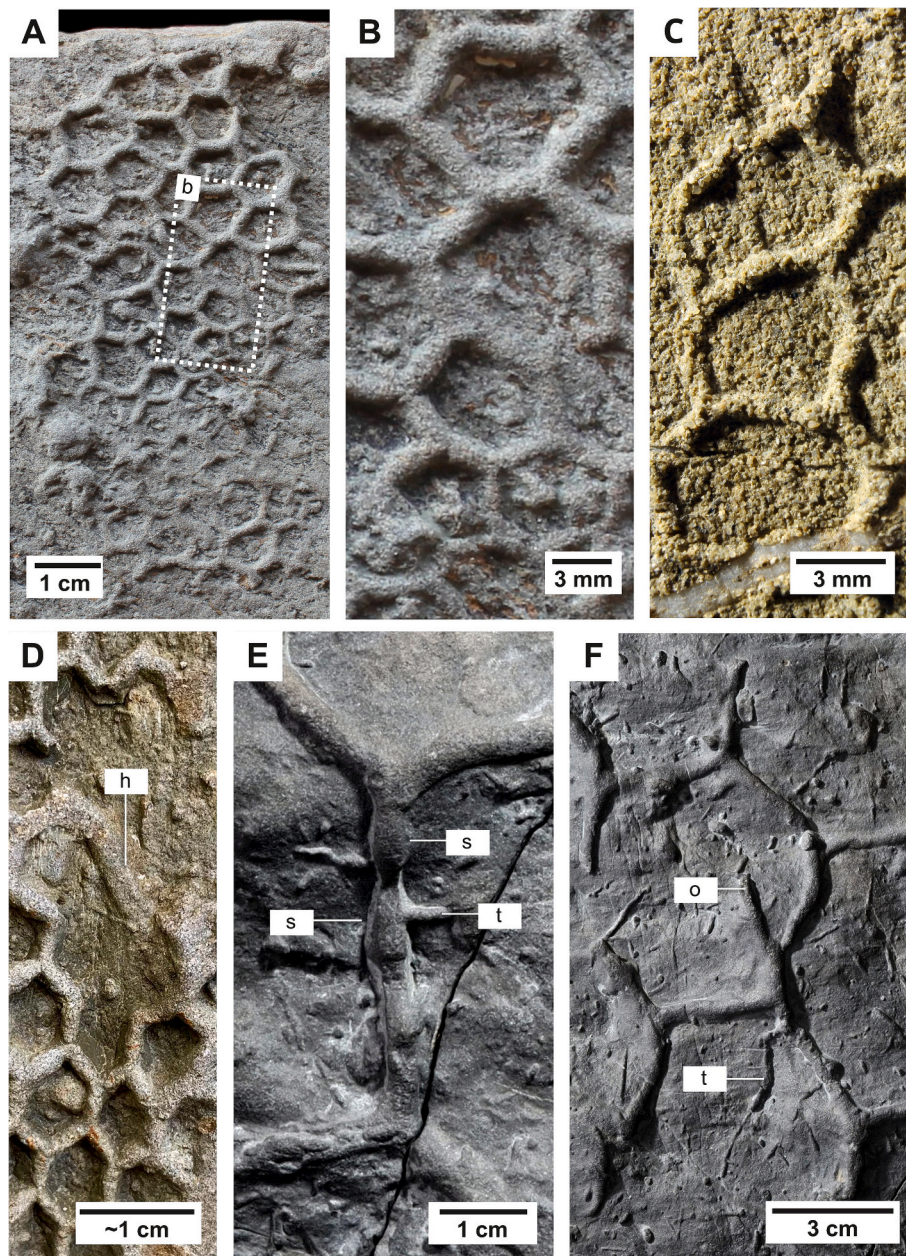


Fig. 7. Variations in angles and tunnel dimensions. A. *Megagraption aequale* displaying irregular hexagons with notable cell size variation. The dashed inset highlights the area detailed in B. NHMP458. B. Detail of A, illustrating pronounced variation in cell size, shape and tunnel width. C. *Megagraption* showing significant variations in cell shape. NHMP274. D. Shortcut (h) between two areas of the same burrow system. E. *Paleodictyon gomezi* featuring localised swellings (s) and smaller side tunnels (t). F. Branched side tunnel in *Paleodictyon gomezi* (l).

counterpoint to the xenophyophore hypothesis, noting that modern xenophyophores lack the near-perfect hexagonal geometry of *Paleodictyon* itself (Levin, 1994; Antcliffe et al., 2011).

The consistency of burrow width represents another significant geometric feature. Tunnel width is indeed highly uniform in the measured specimens, with σ_w averaging 0.21 mm against a mean width of 1.59 mm (Fig. 3E).

While consistency in tunnel length and angle provides insights into motion control abilities, uniform width primarily reflects the tracemaker size. Consistent tunnel width suggests two possibilities according to Vallon et al. (2016): (1) the burrow may represent a fraction of the tracemaker lifespan or (2) it might have been continuously modified through time. Accordingly, *Paleodictyon* may have been produced during a time range when the tracemaker maintained a constant body size, or older sections have been expanded to accommodate the growth of the

tracemaker. The consistent tunnel width of *Paleodictyon* may also be attributed to a colonial origin. Such a colony could achieve uniform tunnel dimensions if a specific caste or size class of individuals is responsible for excavation. Furthermore, consistent tunnel dimensions could be maintained through repeated passage and reshaping by multiple individuals, employing social coordination to uphold a standard width.

Examples of *Paleodictyon* that deviate from its characteristic geometric constancy provide additional insights into the tracemaker behaviour and identity. Minor deviations from the ideal 120° angle occasionally occur (Fig. 6C). Strongly aberrant vertices are rare: only 0.7% of the measured angles (3 of 438) depart from 120° by more than 30° (Fig. 3B). Despite such irregularities, *Paleodictyon* tends to cover the available space without gaps or overlaps between cells. Since we observe angular irregularities without corresponding tessellation gaps, the

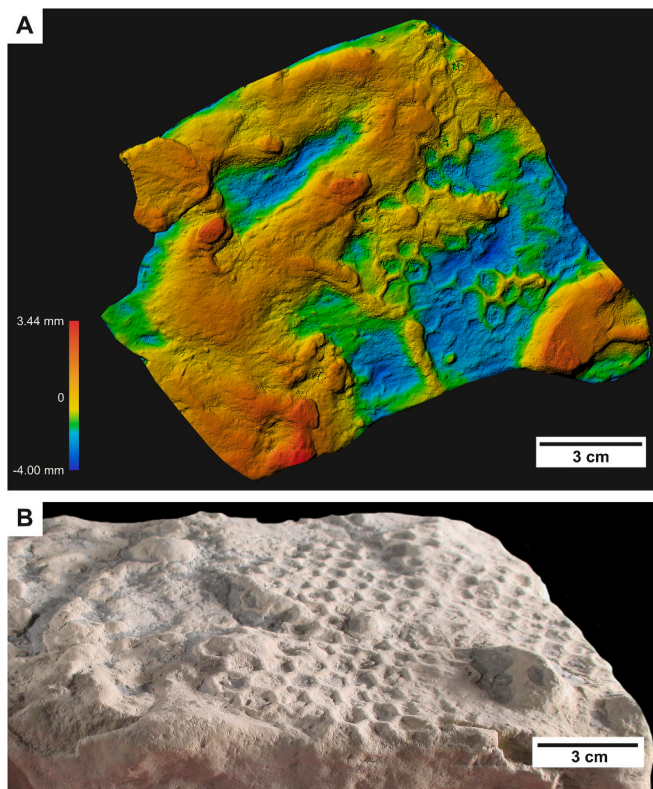


Fig. 8. Horizontal tunnel system in *Paleodictyon*. A. Photogrammetry of *Paleodictyon* showing the horizontality of the hexagonal mesh. NHMP153. B. Oblique view of NHMP223 demonstrating the parallel orientation of the hexagonal mesh with respect to the bedding plane.

tracemaker possessed the ability to detect and correct errors during burrow construction. If the tracemaker relied solely on a rigid behavioural programme to direct its movements, any minor deviations from the ideal 120° angle would have resulted in observable gaps within the cells (see Garlick and Miller, 1993; Plotnick, 2003). This is confirmed by the morphometric analysis, as the mean within-specimen variation in mesh size (σ_c) is smaller (0.19 mm) than the mean within-cell variation in side length (mean $\sigma_1 = 0.5$ mm), indicating that deviations were compensated rather than propagated. This is the signature of active error correction rather than of a rigid behavioural programme.

This is even more evident in *Megagraption*, a graphoglyptid often mistaken for *Paleodictyon* because it also forms polygonal nets, though irregular (Fig. 7A–C). There is the possibility that *Megagraption* and *Paleodictyon* share the same tracemaker, based on a specimen of *Megagraption aequale* that is connected with *Paleodictyon* (Uchman et al., 2022; fig. 8E). However, further evidence is needed to demonstrate this hypothesis. The absence of tessellation gaps in *Megagraption* indicates continuous sensory feedback to actively correct errors, as also demonstrated by the gradual changes in cell shape observed in Fig. 7C.

It should be noted that the constraints imposed by existing tunnels contributed to minimising mesh irregularities in *Paleodictyon* and other net-forming graphoglyptids. The formation of branches requires back-tracking, forcing the tracemaker to stop burrowing and return to the branching point using pre-existing tunnels. In these cases, pre-established tunnel walls likely directed burrowing, reducing random deviations and maintaining adherence to the regular hexagon geometry, even with imperfect body orientation. Active burrow maintenance is further evidenced by shortcuts that connect otherwise poorly connected areas of the tunnel network (Fig. 7D). These shortcuts were plausibly formed to reconnect areas divided by damage within the burrow system, thus evidencing burrow repair. Variations in burrow width within *Paleodictyon* are seldom documented, yet they hold potential to suggest

an arthropod interpretation of the tracemaker. Certain specimens of *Paleodictyon* reveal localised swellings in their tunnels (Fig. 7E), akin to turning chambers in both modern and fossil crustacean burrows, such as those made by upogebiid shrimps and their Pleistocene counterpart (*Parmaichnus*; Pervesler and Uchman, 2009). These structures likely facilitated the tracemaker in reversing direction within the burrow system.

Width variations are also evident at the burrow scale, with rare specimens showing considerable variation in tunnel width across cells. For instance, the burrow system depicted in Fig. 6B shows smaller cells having narrower tunnels and larger cells having wider tunnels. This pattern may suggest contributions from individuals of different sizes, pointing to a possible colonial origin or to the expansion of older tunnel sections to accommodate the tracemaker growth. It could also reflect vertical variation in the burrow system, which may not have been perfectly horizontal. However, as this feature is observed in only a few specimens, further evidence is essential to support this hypothesis.

Small side tunnels could also indicate contributions from individuals of different sizes to the production of *Paleodictyon*. Specifically, a *P. gomezi* specimen displays small lateral tunnels branching from the sides of hexagonal cells (Fig. 7E–F). This pattern resembles certain wood borings, with a central tunnel formed by adult insects and smaller ones by larvae. Nevertheless, the pattern observed in *Paleodictyon* might also be due to commensal organisms inhabiting the same tunnels but unrelated to its producer. Consequently, this does not conclusively prove a colonial origin for *Paleodictyon*.

4.1.4. Vertical shafts connected with a horizontal tunnel system

The three-dimensional architecture of *Paleodictyon* comprises a horizontal hexagonal network (Fig. 8) connected to the seafloor by vertical shafts (Fig. 9). The transition between these vertical shafts and the horizontal network is notably sharp, consistent with the abrupt directional changes typical of arthropod tracemakers.

The evidence that the lower level is horizontal is primarily based on its spatial relationship with the bedding plane; that is, the structure runs parallel to bedding (Fig. 8). Photogrammetric analysis further supports this observation by showing that the hexagonal cells of *Paleodictyon* maintain a consistent elevation relative to a reference level parallel to the bedding plane (Fig. 8A).

The existence of vertical shafts is primarily indicated by specimens with a nodose pattern (Fig. 9A–D), often superimposed upon the horizontal hexagonal mesh. This suggests the presence of vertical shafts that open to the seafloor, referred to as ‘outlets’ by Uchman (1999) (see also Kikuchi and Naruse, 2022; Seilacher, 1977, 2007; Uchman and Wetzel, 2025). Intriguingly, features interpreted as bases of short vertical shafts have been observed in *P. ramidictyon tripartens* and *P. ramidictyon nodosum* (Honeycutt and Plotnick, 2005; Kikuchi and Naruse, 2022). These shafts are located either at the vertices of the mesh or at the midpoints of tunnels (Seilacher, 1977; Honeycutt and Plotnick, 2005). Vertical shafts have also been proposed for incipient *Paleodictyon* (Rona et al., 2009; Boehringer et al., 2021). In these modern examples, each opening aligns with shafts penetrating 2–3 mm into the sediment, connecting to the horizontal hexagonal network (Boehringer et al., 2021; Rona et al., 2009).

Analysis of the trace fossil specimens indicates that the angle between the horizontal network and the vertical shafts was likely close to 90° , with a very short transition between the vertical and horizontal parts. The geometry of the nodose pattern supports this. Notably, the nodose elements retain a circular cross-section even at submillimetric distances above the horizontal plane (Fig. 9B). Had the transition been longer—with extended curved segments linking the vertical and horizontal portions—the nodose elements would appear predominantly elliptical rather than circular. The short transition suggests that the *Paleodictyon* producer could execute sharp turns, consistent with the abrupt directional changes typical of arthropod tracemakers. This interpretation is supported by observations of several modern

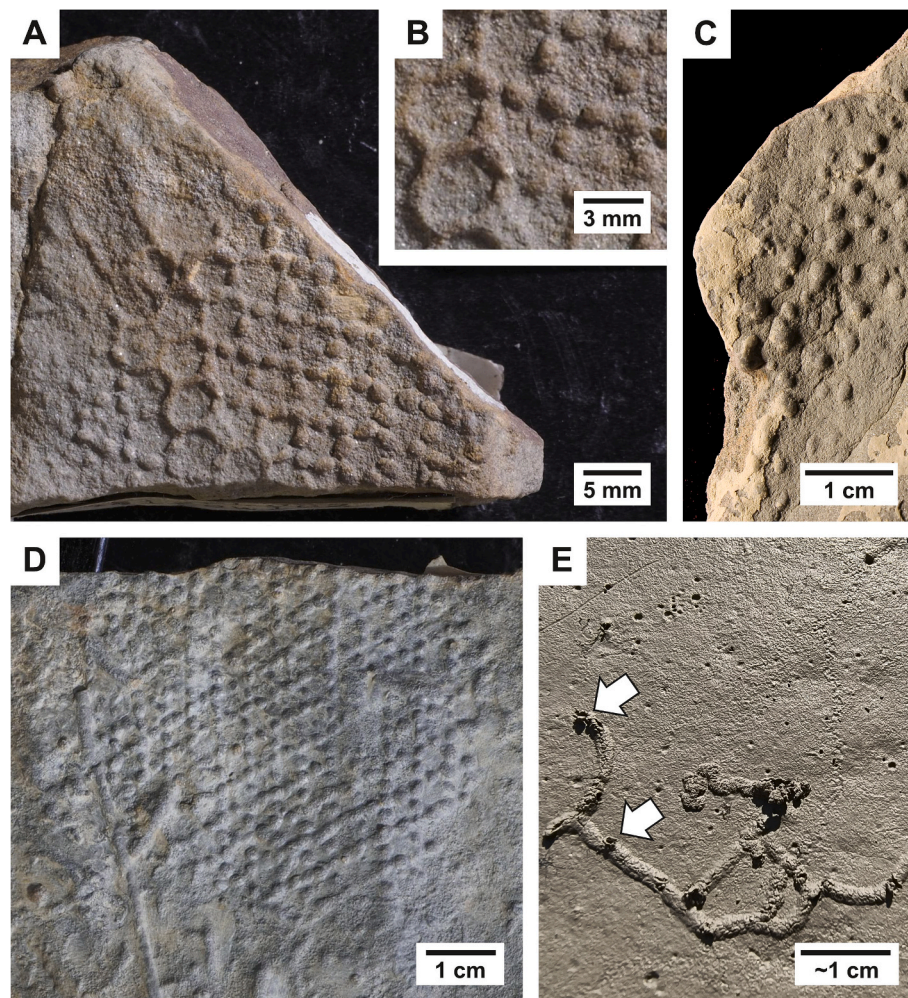


Fig. 9. Vertical shafts in *Paleodictyon*. A. Nodose pattern in *Paleodictyon strozzii* (UJ TF 101). B. Close-up of A, highlighting the nodose pattern at a close vertical distance above the horizontal hexagonal network. C. Vertical shafts (NHMP218). D. Nodose pattern in *P. miocenicum* (UJ TF 1827). E. Vertical chimneys connecting to the horizontal section of a modern insect burrow. Tagliamento River, Italy.

arthropods, both marine and terrestrial, which often construct burrows with vertical shafts linked to underlying horizontal tunnel networks. For instance, insect burrows along the Tagliamento River include vertical shafts that penetrate only 1 mm into the sediment, forming a sharp 90° branching angle with the underlying horizontal tunnel system (Fig. 9E). Shallow-marine decapods, such as *Callinassa subterranea*, produce long vertical shafts that connect to a complex network of tunnels at depth. This tunnel system exhibits both subhorizontal and subvertical segments; therefore, it differs from the burrows of staphylinids and possibly *Paleodictyon*, which present a predominantly horizontal development. In the deep sea, at depths of up to 3500 m, amphipods may construct intricate sublinear burrows with subvertical shafts (Brandt et al., 2023).

It is essential to consider that certain worm-like organisms, such as *Eunice aphroditois* and *Lanice conchilega*, produce subvertical tunnels in their burrows.

Nonetheless, no extant worm-like animal is known to form burrow systems with a short transition length between the vertical shafts and the underlying horizontal parts of their burrows. The closest possible exception is the Devonian polychaete *Annulitubus*, reported in association with *Bifungites* (Sedorko et al., 2024b). This distinction again points to arthropods, rather than annelids, as the more likely producers of *Paleodictyon*.

4.1.5. Unornamented walls

One potential argument against attributing the tracemaker of *Paleodictyon* to arthropods is the lack of scratch marks. Typically, one would expect an arthropod with biomineralized or sclerotized appendages to leave such marks on the walls of its burrows. However, it is crucial to consider that the presence of scratch marks is significantly influenced by the nature of the substrate (Buatois and Mángano, 2011; Veenma et al., 2025). Even crustacean tracemakers may not leave bioglyphs on substrates that are not sufficiently cohesive. The substrate hosting *Paleodictyon* was such a softground, as indicated by its very shallow-tier position. This interpretation is consistent with the wider record of crustacean burrows on comparable substrates. For example, the crustacean burrow *Thalassinoides* rarely shows scratch marks. Similarly, many modern crustacean burrows, such as those created by ghost shrimps, display smooth, unornamented walls. In addition, *Paleodictyon* is commonly preserved as a hyporelief at the base of sandy turbidites, and sand is poorly suited to cast fine scratch marks. The absence of scratch marks, therefore, does not need to reflect a lack of sclerotised appendages.

4.1.6. Accessory features: mid-cell tunnels and shield mounds

Some specimens of *Paleodictyon* are associated with seafloor elevations (shield mounds) and vertical shafts within the hexagonal cell boundaries (mid-cell structures). The inconsistent occurrence of these

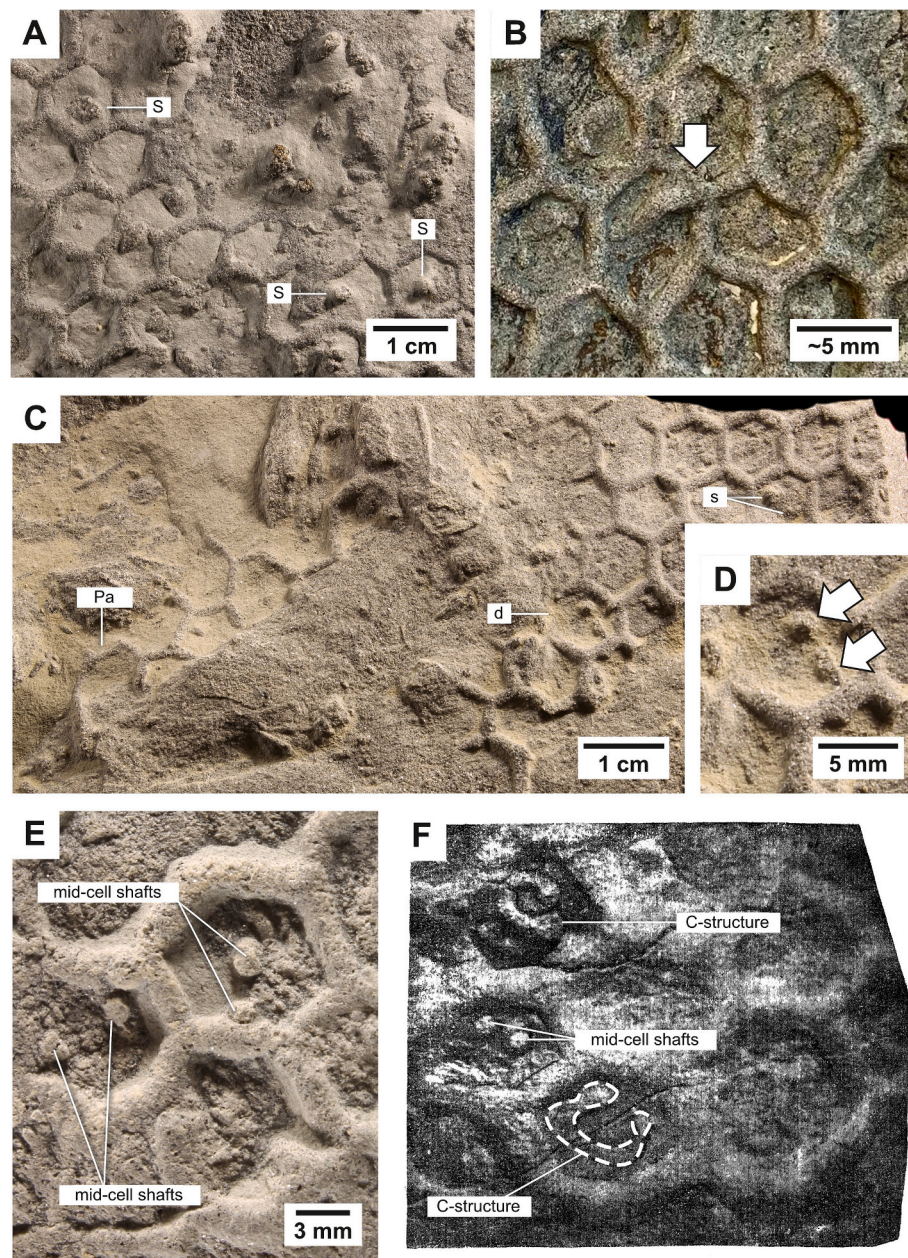


Fig. 10. Mid-cell structures in *Paleodictyon*. A. Single shafts (s). NHMP154. B. Tripod-like structure; arrow indicates where it overlays *Paleodictyon*. C. Vertical shafts at mid-cell positions (s, d); arrow 'd' points to the detail shown in D. NHMP348. A second specimen of *Paleodictyon* (Pa) is seen at a lower elevation. D. Paired shafts at mid-cell position, marked by arrows. E. Mid-cell paired shafts. NHMP153. F. Karpinsky's (1932) *Paleodictyon*, showing C-shaped structures at mid-cell, one highlighted by a dashed line. Paired shafts at mid-cell may correspond to the tips of C-shaped structures.

structures, present in some *Paleodictyon* but absent in others with similar morphology, suggests they may be facultative features. This variability could be linked to local environmental factors, substrate properties, or a specific developmental phase in *Paleodictyon*.

Specifically, the presence of shield-mounds in some modern specimens of *Paleodictyon*, as documented by Seilacher (2007), Rona et al. (2009), and Kikuchi and Naruse (2022), is a notable morphological feature in which the seafloor elevation reaches up to 5 mm at the central point. Recent research in the Aleutian region indicates that not all present-day *Paleodictyon* exhibit shield mounds (Míguez-Salas et al., 2023). The formation of mud mounds by various arthropod trace-makers, such as crabs (De, 2015), amphipods, and decapods (Baucon and Felletti, 2013), involves the sequential deposition of excavated sediment around burrow entrances, resulting in conical structures at singular burrow heads. In contrast, *Paleodictyon* mounds are

shield-shaped, with multiple openings. Despite these morphological differences, modern crustacean mounds suggest that *Paleodictyon* mounds may result from a similar process linked with arthropod activity.

The presence of vertical structures at mid-cell positions is another intriguing but overlooked feature of *Paleodictyon*. These structures, located within the hexagonal boundaries of the cells, are not consistently associated with every *Paleodictyon*; however, they are not uncommon (e. g., they have been photographed by Malekzadeh and Wetzel (2020): fig. 7C). They comprise (1) single shafts (Figs. 6C, 10A), (2) paired shafts (Fig. 10C–E), (3) C-shaped tunnels (Fig. 10F), and (4) elliptical forms (Fig. 6B).

Understanding the three-dimensional form and behavioural significance of these structures is not straightforward, as they mostly occur as sections without physical connections to *Paleodictyon*.

The rarity of visible connections to the hexagonal network opens two possibilities: these structures could represent mid-cell constructions by the *Paleodictyon* tracemaker or independent traces produced by other organisms. The discovery of a three-dimensionally preserved tripod-like tunnel system (Fig. 10B) supports the idea that the *Paleodictyon* tracemaker produced at least some mid-cell structures. This tripod-like structure connects one branch to the primary *Paleodictyon* mesh; the other two branches extend towards a mid-cell position, possibly corresponding to single-shaft mid-cell structures.

One branch of the tripod-like structure is located at a higher level than the main hexagonal mesh (Fig. 10B), suggesting that *Paleodictyon* may exhibit vertical development, with multiple meshes at different stratigraphic levels. This idea receives further support from the observation of two specimens of *Paleodictyon* at two levels within the same layer (Fig. 10C). However, the absence of direct connections between the two specimens leaves this hypothesis unconfirmed.

Paired shafts are another recurrent vertical structure at mid-cell position (Fig. 10C-E). Their seemingly vertical orientation, together paired configuration, is consistent with a U-shaped three-dimensional geometry. We propose a C-shaped base, based on a *Paleodictyon* specimen photographed by Karpinsky (1932), which exhibits paired shafts associated with C-shaped tunnels featuring enlarged ends (Fig. 10F). The enlarged ends align in size and spacing with the paired shafts on the specimen.

Single and paired shafts reveal a circular outline, contrasting with elliptical forms, which show irregularly rounded shapes. Notably, the diameter of these structures is significantly larger than that of *Paleodictyon* tunnels, suggesting they may represent funnels or irregular bioturbation structures.

4.2. Taphonomy

Taphonomic features do not provide specific evidence either for or against an arthropod tracemaker. Nonetheless, the preservation of *Paleodictyon* supports its classification as an ichnofossil rather than a body fossil. Stratinomy suggests passive-fill preservation of *Paleodictyon*, as it is generally found in convex hyporelief at the base of turbidite layers, sharing major textural features with surrounding sediment. Consequently, *Paleodictyon* and other graphoglyptids are considered “open mud burrows that became uncovered and were immediately sandcast by low-velocity turbidity currents” (Seilacher, 1977: p. 289).

The sharp outlines of *Paleodictyon* suggest that the tunnel walls were reinforced by a particularly strong mucus film (Seilacher, 1977). The presence of a mucus film is also supported by Monaco's (2008) taphonomic analysis, which indicates that the walls of *Paleodictyon* were coated with a gluey film that trapped fine particles settling from suspension on the seafloor. The ichnological nature of *Paleodictyon* is evident from its common association with burrows preserved in the same style. This association implies a common origin as burrows rather than as a body fossil, as proposed by Seilacher (1977). Furthermore, the preservation evidence contradicts the body fossil interpretation, particularly the protist/xenophyophore hypothesis. It is unlikely that the delicate body of a xenophyophore could be preserved to form the sharp edges observed in *Paleodictyon* (Honeycutt and Plotnick, 2005). Additionally, *Paleodictyon* lacks xenophyophore-specific features such as xenophyae and exhibits traits inconsistent with this interpretation. Levin (1994, p. 38) identified significant discrepancies between *Paleodictyon* and xenophyophores, notably the absence of agglutinated particles typical of xenophyophores. Moreover, the precise hexagonal symmetry in *Paleodictyon* is not found in modern xenophyophores (Antcliffe et al., 2011).

4.3. Tracemaker

4.3.1. Motility

Evidence suggests that the producer of *Paleodictyon* was a highly

mobile and efficient burrower, consistent with arthropod features. Recent neoichnological investigations substantiate this observation. Boehringer et al. (2021) examined the re-establishment of *Paleodictyon* following experimental disturbances in modern deep-sea basins. Notably, new *Paleodictyon* appeared on substrates that had been disturbed just 17–18 days earlier in the Clarion-Clipperton Fracture Zone and 6 weeks earlier in the Peru Basin (Boehringer et al., 2021). This rapid re-establishment indicates that the tracemaker must have been highly motile and, if solitary, an exceptionally rapid burrower, traits consistent with arthropod behaviour.

Network analysis indicates that a solitary burrower would have travelled substantial distances relative to its body size to create and maintain *Paleodictyon* burrows (Honeycutt and Plotnick, 2005). A large *Paleodictyon* with a tunnel length of 230 m is approximately 250,000 times longer than the potential producer (Honeycutt and Plotnick, 2005). Consequently, researchers hypothesise that a single animal could not have constructed these structures, as the total tunnel length would far exceed the size of the organism if it traversed all paths (Fan et al., 2018; Honeycutt and Plotnick, 2005). Alternatively, if the organism were solitary, it would have had to exhibit extremely high burrowing efficiency.

The rapid production of *Paleodictyon* suggests it may have been produced by a colony rather than a single individual. This observation challenges the hypothesis of formation through modular growth, as suggested by Plotnick (2003). The rapid reformation of *Paleodictyon* within weeks following a disturbance further undermines the plausibility of a growth-based process, given that such a high growth rate is atypical for many organisms, including xenophyophores (Boehringer et al., 2021).

4.3.2. Cognitive abilities of the *Paleodictyon* tracemaker

The geometry of *Paleodictyon* provides insights into the cognitive capabilities of its tracemaker, based on the information required to produce such a pattern. In other words, understanding what information guided the tracemaker in forming *Paleodictyon* allows us to infer general cognitive abilities. Spatial parameters, such as distance and angles, appear crucial (Garlick and Miller, 1993; Honeycutt and Plotnick, 2005; Seilacher, 1977). Therefore, the cognitive abilities of the tracemaker likely included orientation (the ability to perceive direction relative to a stable external reference) and odometry (the ability to estimate distance travelled). This hypothesis is supported by L-system models of *Paleodictyon* (Baucon, 2010b; Plotnick, 2003), which help define the minimal behavioural rules necessary to replicate the trace (Plotnick, 2003). Notably, only the turning angle and step size are required to simulate *Paleodictyon* digitally.

The tracemaker demonstrated not only the ability to process angle and distance information but also remarkable precision in orientation and odometry. The morphometric analysis of the Piacenza collection constrain this precision. In fact, angular control operated within ~7% of the 120° target (mean $\sigma_a = 8.5^\circ$), and odometric control within ~12% of the target step length (mean $\sigma_l = 0.5$ mm against a mean side length of 4.26 mm). Computer simulations by Garlick and Miller (1993) indicated that the tracemaker executed precise 120° turns at consistent intervals. As elaborated in Section 4.1.3, the formation of tessellation-like patterns indicates precise motor control during burrow construction. The organism had to perform tunnel-building movements that maintained consistent lengths, executed turns at exact angles, and compensate eventual deviations from the ideal 120° angle. The *Paleodictyon* producer must have possessed sophisticated navigational skills to execute precise turns at set distances (Seilacher, 1977; Garlick and Miller, 1993; Honeycutt and Plotnick, 2005).

The arthropod brain exhibits sophisticated cognitive features, potentially enabling the production of complex, regular patterns, such as those found in *Paleodictyon*. Arthropods demonstrate remarkable navigational skills and possess a diverse array of cognitive abilities (Heinze et al., 2018). Despite having smaller brains and fewer neurons, their

cognitive skills rival, and sometimes exceed, those of vertebrates, depending on the species in question (Cross et al., 2020; Pfeffer and Wolf, 2020).

Arthropods, such as honeybees, desert ants, and crabs, effectively utilise sophisticated odometry and orientation skills (Layne et al., 2003; Wolf, 2011; Yu and Kim, 2012). Foraging ants and bees employ techniques akin to those of birds and mammals, using path integration and memories of visual landmarks to navigate through familiar terrain (Collett and Collett, 2002). Some arthropods have a notable capacity to determine angles using a magnetic compass, as observed in the sandhopper *Talitrus saltator*. This species exhibits exceptional orientation skills, consistently directing itself towards ecologically significant cardinal directions, particularly its native beach, even when in complete darkness (Grob et al., 2021). Moreover, there is evidence that arthropod brains can generate mental maps, templates, and even foresight (Menzel and Greggers, 2015; Perry et al., 2013; Perry and Chittka, 2019), all of which are potentially important for constructing complex structures like *Paleodictyon*.

The cognitive capabilities of the *Paleodictyon* tracemaker are highlighted by the occurrence of shortcuts and irregular hexagons in its burrow designs. As discussed in Section 4.1.3, these tracemakers were able to identify and correct errors during burrow construction, as indicated by angular irregularities that do not produce tessellation gaps. This finding suggests that *Paleodictyon* is not merely the outcome of a fixed behavioural programme but also involves elements of foresight and planning. In other words, the *Paleodictyon* tracemaker displayed behavioural plasticity when the innate programme was less effective. In addition, the presence of shortcuts linking different areas of the burrow (Fig. 7D) poses the question of whether the tracemaker had a mental representation of the burrow layout.

Quantitative results confirm that the tracemaker identified and corrected errors, as indicated by angular irregularities that do not create tessellation gaps. Departures from the ideal 120° are small but not negligible, i.e., the mean within-cell angular deviation is $\sigma_a = 8.5^\circ$, and 90.6% of the 438 interior angles fall within 15° of 120°. The tessellation is nonetheless complete in nearly all specimens, implying that local errors were compensated during the development of *Paleodictyon*.

The within-specimen variation in mesh size (mean $\sigma_e = 0.19$ mm) is only about one-third of the within-cell variation in side length (mean $\sigma_l = 0.5$ mm), so deviations introduced in one cell did not propagate to the next. Had the tracemaker followed a rigid behavioural programme, errors would have accumulated throughout the network, and σ_e would have equalled or exceeded σ_l , rather than being markedly lower. Correction appears to have operated within the cell itself, vertex by vertex. In several cells the vertex with the largest interior angle is immediately adjacent to the vertex with the smallest — in one cell of NHMP153, for instance, the sequence runs 132.0° – 100.5° – 105.5° – 165.4° – 89.4° – 127.2°. The tracemaker therefore did not spread the compensation evenly around the cell; the error at the 165.4° vertex was offset at the very next vertex rather than distributed over the remaining five vertices, as would be expected if the organism detected the departure from 120° and compensated for it in the following move.

Such corrections imply sophisticated odometry and orientation skills, probably aided by the use of pre-existing tunnels as benchmarks. Adjacent cells share walls, providing a continuous physical reference that constrains the direction and length of each new segment and reduces reliance on internal odometry alone.

Research on arthropod fossils indicates that the neurobiological foundation for such advanced navigational skills was already established in the Cambrian. Fossils reveal that four fundamental brain types emerged over 500 Ma, corresponding to onychophorans and the three main extant euarthropod clades (Strausfeld et al., 2016). Given the evolutionary stability of these brain types, it is plausible that Cambrian arthropods possessed the neurobiological architecture necessary to support the skills required for producing *Paleodictyon*. This view is supported by the hypothesised “Cambrian Information Revolution,” a

coevolutionary increase in both the information content of the marine environment and in the ability to process it (Plotnick et al., 2010). Garlick and Miller (1993) concluded that the geometric precision required to create *Paleodictyon* is unlikely to be attributed to protists or vermiform organisms. They proposed that a small crustacean is more plausible. While annelids can orient themselves and navigate their immediate surroundings, they lack the complex, long-range navigational abilities observed in many arthropods. Although this hypothesis is plausible, further research into the cognition of infaunal invertebrates is necessary. Studies on navigation and cognition have seldom integrated data from both arthropods and worm-like phyla. Thus, the assumption that arthropods are generally superior navigators compared to annelids or other soft-bodied phyla remains plausible but unproven.

4.4. Stratigraphic distribution

The stratigraphic occurrence of *Paleodictyon* aligns well with the timing of arthropod tracemakers.

The appearance of *Paleodictyon* in the geological record, specifically in shallow-marine settings during the early Cambrian, is contemporaneous with the initial radiation of arthropods. *Paleodictyon* is indeed documented in early Cambrian shallow-marine deposits (Crimes and Anderson, 1985; Jensen et al., 2013; Malekzadeh and Wetzel, 2020), as confirmed by the Nozelos Quarry specimen. Correspondingly, the earliest ichnological evidence for arthropods appears within a few million years after the Proterozoic-Phanerozoic boundary (Daley et al., 2018; Gribet and Edgecombe, 2019). According to Daley et al. (2018), euarthropod trace fossils (e.g. *Rusophycus*, *Cruziana*) first appear at around 537 Ma and thus provide one of the oldest records for euarthropods, substantially predating the earliest arthropod (trilobite) body fossils at 521 Ma. This is further supported by Gougeon et al. (2025), reporting euarthropod trace fossils from the Fortunian deposits.

During the Late Cretaceous and early Cenozoic, *Paleodictyon* exhibited significant diversification, becoming a characteristic component of the deep-sea *Nereites* Ichnofacies (Seilacher, 1967a, 1967b, 1974; Uchman, 2004, 2007, 2009; Uchman and Wetzel, 2012; Neto de Carvalho et al., 2020; Míguez-Salas et al., 2023). This occurrence is particularly noteworthy as it coincides with the extensive colonisation of the deep sea by decapods. This supports the hypothesis that arthropods may be potential tracemakers of *Paleodictyon*. However, numerous other organisms also show a trend of deep-sea colonisation during the Mesozoic.

4.5. Environmental distribution

The environmental distribution of both modern and fossil *Paleodictyon* is consistent with that of arthropods, particularly crustaceans. However, numerous other tracemakers, including various worm-like phyla, exhibit similar distribution patterns.

Paleodictyon is a typical component of the *Nereites* Ichnofacies, one of the ichnofacies that shows the closest link to bathymetry (Buatois and Mángano, 2011; see also Neto de Carvalho et al., 2020). Although the *Nereites* Ichnofacies spans a wide bathymetric range, it typically occurs in deep-sea turbiditic deposits (Uchman and Wetzel, 2012). The specimens of *Paleodictyon* from the Piacenza Apennines fit well with the *Nereites* Ichnofacies, being associated with *Spirophycus*, *Chondrites*, *Halopoa*, and *Planolites* at the sole of sandy turbidites (Fig. 11A–D). Graphoglyptids and meandering trace fossils are the most representative traces of the *Nereites* Ichnofacies (Uchman and Wetzel, 2012).

The *Nereites* Ichnofacies comprises the *Nereites*, *Paleodictyon*, and *Ophiomorpha rudis* ichnosubfacies (Uchman, 2009). *Paleodictyon* is the most representative taxon of the eponymous ichnosubfacies, which is often typified by a high-diversity suite of graphoglyptids. The sequence of *Ophiomorpha rudis*, *Paleodictyon*, and *Nereites* ichnosubfacies indicates a proximal-to-distal gradient from the inner to the outer fan and a non-bathymetric trend from the channel axis to the overbank through levee

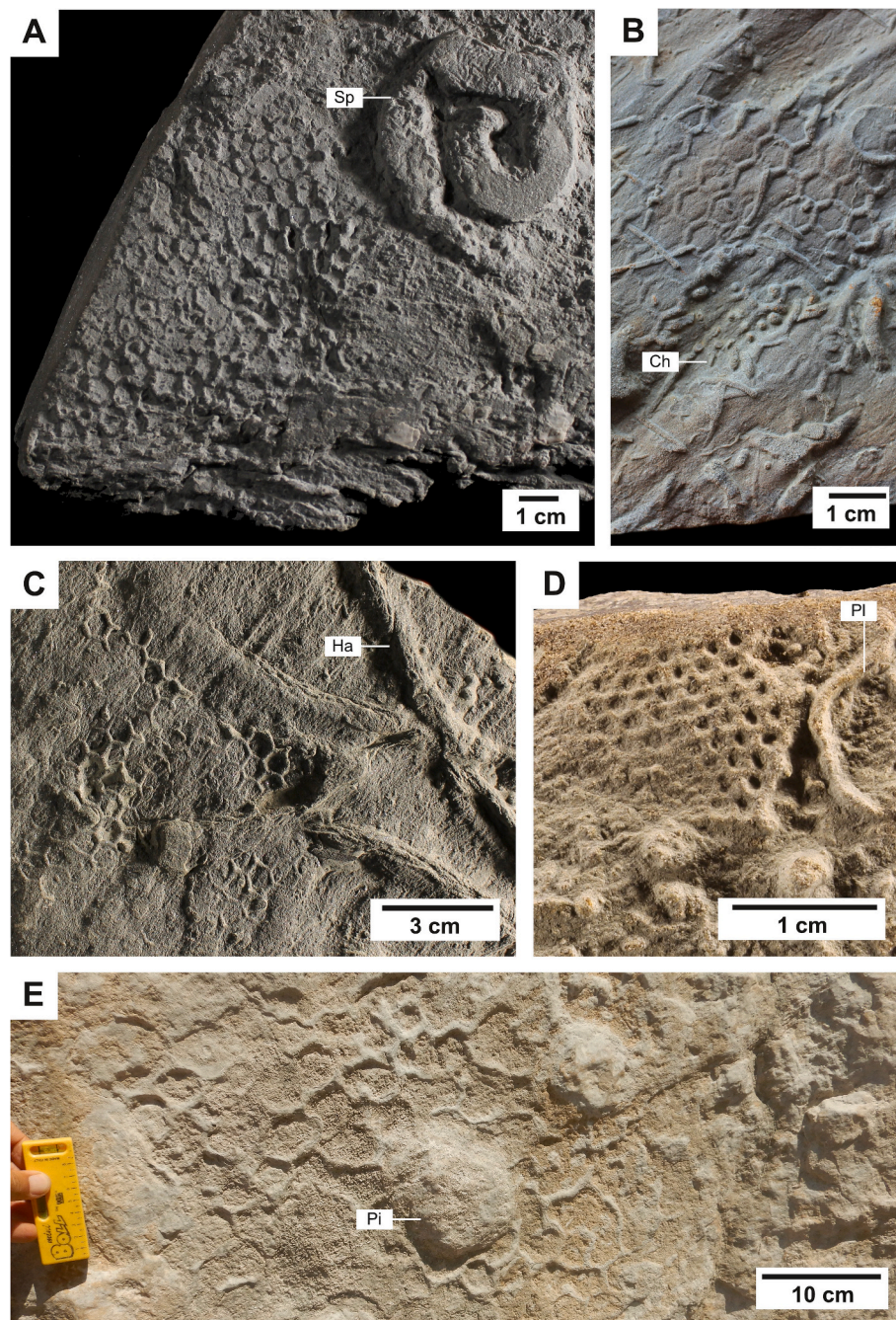


Fig. 11. Trace fossils associated with *Paleodictyon* and *Paleodictyon*-like traces. A. *Spirophycus* (Sp) co-occurring with *Paleodictyon*. NHMP002. B. *Paleodictyon* with passively filled *Chondrites* (Ch). NHMP459. C. *Halopoa* (Ha) associated with *Paleodictyon*. NHMP158. D. *Paleodictyon minimum* with *Planolites* (Pl). NHMP382. E. *Piscichnus* (Pi) co-occurring with a *Paleodictyon*-like burrow boxwork (cf. *Thalassinoides*). Andreis, Triassic.

settings (Uchman, 2009; Uchman and Wetzel, 2012). Although *Paleodictyon* is often associated with the specific *Paleodictyon* ichnosubfacies, evidence from the modern deep-sea floor shows it has a wider distribution. Its distribution appears more limited due to the specific processes required for its preservation, such as delicate scouring and casting, which are characteristic of the *Paleodictyon* ichnosubfacies (Uchman, 2009).

The producers of *Paleodictyon* were also capable of colonising diverse environments beyond deep-sea areas, such as slope and middle-to-deep shelf regions (Fürsich et al., 2007; Kikuchi, 2018; Malekzadeh and Wetzel, 2020; Neto de Carvalho et al., 2020). In fact, *Paleodictyon* first appeared in shallow marine deposits, with evidence of its presence in deep-sea sediments extending back to the Cambro-Ordovician (Fig. 5A;

Seilacher, 2007; Malekzadeh and Wetzel, 2020). Malekzadeh and Wetzel (2020) documented 18 occurrences of *Paleodictyon*, ranging from nearshore to outer-shelf environments and spanning the Cambrian to the Cretaceous.

The presence of *Paleodictyon* in shallow-sea environments presents a dilemma (Miguez-Salas et al., 2023): did the tracemakers repeatedly colonise these areas, or was their presence continuous? Malekzadeh and Wetzel (2020) contend that the frequent absence of *Paleodictyon* in many shallow-sea successions implies that its presence was rare, thereby favouring the hypothesis of recurrent colonisation over a sustained presence in shallow-marine settings.

An additional argument for an arthropod tracemaker of *Paleodictyon* emerges from morphologically similar trace fossils that are assigned to

other ichnotaxa yet confidently attributed to shallow-water crustaceans. In the Triassic peritidal deposits of Andreis, a large boxwork with polygonal cells is documented together with *Piscichnus*, which probably represents the work of fish predators searching for the producer of the boxwork (Fig. 11E). This *Thalassinoides*-like structure displays bedding-parallel orientation, straight segments, polygonal cells, and angles close to 120°, mirroring some of the most prominent features of *Paleodictyon*. Another shallow-marine example is *Thalassinoides horizontalis*, a regularly branching network, as documented by the Ordovician specimen described by Neto de Carvalho and Bayet-Goll (2023: fig. 6D). This specimen shares horizontal orientation, straight segments and polygonal cells. Since *Thalassinoides* is attributed to arthropods, these boxworks reinforce the notion of an arthropod tracemaker for *Paleodictyon*.

Modern occurrences of *Paleodictyon* are found in the deep sea. Notable observations include those at a depth of ~3500 m on the Mid-Atlantic Ridge (Rona et al., 2009), at depths ranging from 1400 to 4000 m in the South Atlantic (Ekdale, 1980), and at depths of 1300–2200 m in the eastern margin of Australia (Przeslawski et al., 2012). *Paleodictyon* specimens in the Clarion-Clipperton zone occur at depths of approximately 4000 m but are most prevalent between 3430 and 3500 m (Durden et al., 2017). Miguez-Salas et al. (2023) proposed a bathymetric constraint for its tracemaker, noting Subarctic occurrences over 4500 m but none beyond 5000 m. They identified an upper depth limit of approximately 1400 m (Miguez-Salas et al., 2023).

The modern occurrences of *Paleodictyon* suggest that the bathymetric range for its tracemakers is between ~1300 and ~5000 m. Within this range, numerous infaunal arthropods with body widths suitable for *Paleodictyon* openings are found, including isopods, amphipods, copepods, and decapods. Isopods represent one of the most abundant and diverse macrofaunal groups in the deep sea (Hessler et al., 1979; Hessler and Strömberg, 1989). The burrowing isopod *Macrostyliis metallica* inhabits the polymetallic nodule fields of the Clarion-Clipperton Zone (Riehl and De Smet, 2020), an area also known for the presence of *Paleodictyon* (Durden et al., 2017). This extensive region is also notable for its diverse decapod fauna (Christodoulou et al., 2022).

Amphipod crustaceans represent another abundant component of deep-sea macrofaunal assemblages across all latitudes (Frutos and Jazdzewska, 2019; Lacey et al., 2018; Senna, 2010).

The majority of deep-sea amphipods exhibit a benthic lifestyle (Frutos and Jazdzewska, 2019), as demonstrated by the Phoxocephalidae family. These benthic amphipods often display a burrowing behaviour (Senna, 2010).

These examples suggest that modern occurrences of *Paleodictyon* may be attributed to deep-sea arthropods, particularly crustaceans, but other groups cannot be discounted. In the Clarion-Clipperton Zone, a region of approximately 6 million km² where *Paleodictyon* has been observed (Amon et al., 2016; Durden et al., 2017), the most diverse metazoan phyla are Arthropoda (27%), Annelida (18%), and Nematoda (16%) (Rabone et al., 2023). Xenophyophores dominate in abundance, being nearly twice as common as Cnidaria in a polymetallic-nodule area of the E Clarion-Clipperton Zone (Amon et al., 2016).

The fauna associated with modern *Paleodictyon* also does not provide resolute insight into identifying the tracemaker. Rona et al. (2009) documented fauna in direct association with *Paleodictyon*, including a diminutive isopod crustacean and a polychaete worm. Miguez-Salas et al. (2023) observed “tentacle-like structures” near *Paleodictyon* openings; however, the image resolution was insufficient to determine their nature.

As observed for the bathymetric distribution, the latitudinal distribution of *Paleodictyon* fits with an arthropod tracemaker, although it does not exclude soft-bodied phyla as the producers. Predominantly, modern occurrences are documented in tropical and subtropical zones, with some isolated findings extending to Subarctic regions (Miguez-Salas et al., 2023, and references therein). Specifically, these occurrences are mainly located between 30° N and 30° S (Durden et al., 2017: fig. 1).

A key requirement for modern *Paleodictyon* is the presence of soft, fine-grained sediments, even when found alongside isolated hard substrates (Miguez-Salas et al., 2023; Boehringer et al., 2021). Notably, Miguez-Salas et al., 2023 observed that the size of *Paleodictyon* (mesh size and number of openings) correlates with particulate organic carbon (POC) flux to the seafloor. Smaller *Paleodictyon* are associated with more eutrophic environments. However, this does not conclusively determine the identity of the tracemaker.

Modern *Paleodictyon* is predominantly found in well-oxygenated, cold environments (Miguez-Salas et al., 2023). Well-oxygenated conditions are well-suited for the presence of arthropods, as evidenced by the reduced occurrence of deep-sea amphipods in low-oxygen conditions (Frutos and Jazdzewska, 2019). While this supports the hypothesis of an arthropod tracemaker for *Paleodictyon*, it does not preclude the involvement of other tracemakers, as oxygen availability is a critical limiting factor for most deep-sea animal phyla, including annelids.

Paleodictyon is typically found in oligotrophic settings characterised by low sedimentation rates (Wetzel, 2010). However, some occurrences suggest this association may not be absolute (Durden et al., 2017; Miguez-Salas et al., 2023). Durden et al. (2017) observed that modern *Paleodictyon* is present in areas with higher sedimentation and absent in regions with lower rates. The fossil occurrences documented by Fürsich et al. (2007) also challenge the impact of sedimentation rates, suggesting that trophic conditions may not have inhibited tracemaker colonisation in nearshore eutrophic environments, possibly highlighting an essential role of taphonomic factors in determining the presence of *Paleodictyon* within the fossil record (Fürsich et al., 2007).

4.6. Function

Interpretations of *Paleodictyon* as a burrow suggest functions such as a grazing trail (pascichnia), trap (irretichnia), bacterial farming (agrichnia) and brooding (calichnia), potentially compatible with an arthropod tracemaker. However, these interpretations remain speculative and could also align with worm-like phyla, thus not providing conclusive evidence for an arthropod origin.

4.6.1. Deposit and detritus feeding models

Initial ichnological interpretations of *Paleodictyon* regarded it as a grazing trace. Seilacher (1955) classified it within pascichnia, later suggesting a trapping and farming function (Seilacher, 1977). Similarly, Nowak (1959) argued that *Paleodictyon* represented the feeding trace of an annelid. Osgood (1970) also described *Paleodictyon* as a pascichnion but recognised it as an unusual fossil, noting that it is “one of the most unusual fossil forms and could be properly labeled as a ‘problematicum’” (Osgood, 1970: p. 384). Corbo (1979) further supported this classification by including *Paleodictyon* among the pascichnia.

Röder (1971) and Seilacher (1977) offered a critical reevaluation of this interpretation, identifying inconsistencies with the fundamental traits of *Paleodictyon*. They particularly noted that the branching nature of *Paleodictyon* contradicts the continuous scanning strategy inherent in the pascichnial model. Furthermore, the open burrow structure of *Paleodictyon* allows revisiting, further challenging the original hypothesis (Seilacher, 1977). Baucon's (2010b) fractal analysis revealed that *Paleodictyon* has a fractal dimension lower than that of typical grazing traces such as *Nereites*. Additionally, taphonomic evidence and observations of modern specimens clearly indicate that *Paleodictyon* functions as a burrow rather than a trail, which contradicts the requirements of the pascichnion model. Its geometry seems excessively regular compared to most detritus-feeding trails and deposit-feeding burrows, which are often (but not exclusively) irregular due to local resource variations. Nevertheless, neoichnological evidence does not entirely discount deposit feeding and other strategies for *Paleodictyon*. Complex branching burrows are produced by thalassinid crustaceans, who may act as deposit feeders, drift catchers, or filter/suspension feeders (Griffis and Suchanek, 1991).

4.6.2. Trapping model

The trapping model holds that numerous graphoglyptids functioned as traps for migrating organisms. This hypothesis draws on the morphological analogy with the spiral burrows of the modern polychaete *Paraonis*, which were believed to serve as diatom traps due to their mucus-coated walls (Röder, 1971). The morphological similarities between graphoglyptids and *Paraonis* spirals include mucus-lined walls and occasionally branching tunnels (Röder, 1971; Seilacher, 1977). Additionally, both are open burrows and maintain consistent spacing between tunnels (Seilacher, 1977; see also discussion in Lehane and Ekdale, 2013). According to the trapping model, *Paleodictyon* and other graphoglyptids are comparable in function to a spider web, acting as “search nets” (Seilacher, 1977: p. 293).

However, analysis by Lehane and Ekdale (2013) challenged this interpretation, suggesting that *Paraonis* should be considered a selective deposit feeder rather than a trapper. For these reasons, the authors argue that it is inappropriate to classify graphoglyptids as traps if this interpretation rests merely on initial misunderstandings of *Paraonis* behaviour. In other words, if the morphological similarities between graphoglyptids and *Paraonis* burrows suggest a possible shared feeding strategy, that strategy should be deposit feeding (Lehane and Ekdale, 2013).

4.6.3. Farming model

Seilacher (1977) supported the trapping model for *Paleodictyon*, but specifically for specimens with few vertical shafts. This is exemplified by a two-opening *Paleodictyon* depicted as a trap (Seilacher, 1977: fig. 15). Conversely, the author proposed an evolutionary shift in the function of *Paleodictyon* with the introduction of additional openings during the Mesozoic. Accordingly, *Paleodictyon* transformed into a well-ventilated farming burrow, facilitating the utilisation of non-refractory food by symbiotic microorganisms. According to Seilacher (1977), the emergence of multiple openings across various graphoglyptid lineages coincided with the diversification of angiosperms. The farming model suggests that *Paleodictyon* acted as a sort of “mushroom garden”, with its geometry promoting water flow through tunnels. This process likely encouraged microbial growth on the walls, with the microbes serving as a food source for the *Paleodictyon* tracemakers.

Both behaviours (trapping and farming) were initially classified within the ethological category of agrichnia (Ekdale et al., 1984; Bromley, 1996), but Lehane and Ekdale (2013) subsequently differentiated farming traces (agrichnia) from trapping traces (irretichnia), a distinction supported by Vallon et al. (2016).

The agrichnial hypothesis remains a topic of debate. Although farming behaviour is often assumed for *Paleodictyon* and other graphoglyptids, there is no direct actualistic evidence supporting this hypothesis. Kitchell (1979) argued against microbial farming, citing the slow metabolic rates of deep-sea bacteria (see also Hsieh et al., 2019). Kitchell (1979) further contended that the absence of fecal pellets and bioglyphs in farming burrows, which would be expected if these burrows had long-term inhabitants, challenges the agrichnial hypothesis. Seilacher (1977) supported the agrichnial interpretation based on the fact that the geometry of *Paleodictyon* efficiently covered an area, thereby enhancing ventilation; however, this interpretation is also compatible with other functions, such as osmotrophy or brooding (Hsieh et al., 2019).

4.6.4. Nesting model

According to McMenamin (2012, 2016), *Paleodictyon* might be a nest, potentially marking the earliest known parental behaviour in the fossil record. The hypothesis proposes that *Paleodictyon* and other graphoglyptids functioned as microbial farms, akin to the agrichnial model, but were produced for the care and feeding of hatchlings. The nesting hypothesis posits that arthropods are the tracemaker, supported by early evidence of brood-rearing in arthropods from the Early Cambrian (McMenamin, 2012, 2016).

4.6.5. Communication network model

The topology of *Paleodictyon* suggests a function beyond feeding, and we propose that the burrow served as a network through which colonial organisms propagated acoustic, hydraulic, and/or chemical signals. Efficient communication provides essential survival benefits for colonial organisms. It enables (1) rapid colony-wide predator alerts, (2) coordinated foraging or predation behaviour, and (3) synchronised reproduction, thereby enhancing ecological success. For instance, eusocial sponge-dwelling shrimp (*Synalpheus* spp.) uses multimodal communication, including acoustic signals (cavitation snaps), chemical cues (pheromones), and hydraulic signalling (water pumping), to coordinate colony defence, resource distribution, and reproductive activities (Hultgren et al., 2017).

The communication-network hypothesis relies on the observation that *Paleodictyon* topology exhibits properties characteristic of optimised communication networks, particularly (1) isotropic propagation of signal, (2) robustness, (3) high local clustering, and (4) scalability.

First, the topology of a hexagonal communication network promotes an even distribution of signals in all directions. This topology ensures that every member of the colony receives information uniformly, effectively preventing any areas from becoming unmonitored and therefore vulnerable.

Second, several alternative paths connect any two points of a hexagonal communication network. As a result, connectivity is maintained even with significant network damage. A hexagonal burrow network would enable a colony to maintain coordination even if many tunnels were damaged by predators or physical processes.

Third, the network hexagonal structure, in which each vertex connects to three neighbouring ones (see Honeycutt and Plotnick, 2005), improves detection reliability. The hexagonal topology supports signal averaging by allowing signals to reach nodes simultaneously via multiple routes, thereby improving detection reliability. This configuration is ideal for forming consensus through multiple confirming inputs and strengthening weak signals through local reinforcement.

Finally, a hexagonal communication network is scalable, enabling growth by simply adding hexagons while preserving communication efficiency. This scalability allows the colony to expand without necessitating a complete redesign of its connection architecture.

The communication-network hypothesis is supported by both topology and the active maintenance of *Paleodictyon* over time, as evidenced by specimens showing tunnel repair. Burrow maintenance would be necessary to preserve the integrity of the communication network, akin to maintaining a communication infrastructure. It is important to highlight that the communication-network hypothesis does not exclude previously proposed models. In fact, it is compatible with a range of functions, including trapping, farming, brooding, and deposit feeding.

The foremost counterargument of the communication-network model lies in its speculative nature. This model proposes a behaviour lacking direct empirical evidence, particularly since no extant colonial arthropod has been documented constructing burrow networks similar to those attributed to *Paleodictyon*. Consequently, further research is necessary to substantiate the model and explore alternative explanations for *Paleodictyon*.

5. Conclusions

This review provides robust evidence supporting arthropods as the most plausible producers of *Paleodictyon*. Peracarid crustaceans such as amphipods and isopods emerge as likely tracemakers, particularly for post-Ordovician occurrences. Multiple lines of evidence consistently converge to favour arthropod producers over previously proposed alternatives such as vermiform, hexactinellid, or protist tracemakers:

- The morphological features of *Paleodictyon*, including straight tunnels and pointed corners, indicate a tracemaker with a rigid exoskeleton and jointed appendages, characteristic of arthropods.

The 3D geometry of modern *Paleodictyon* remains poorly understood, as most research has documented burrow openings rather than comprehensive 3D analyses. To address this gap, resin-casting and micro-CT scanning studies are recommended. The geometry of fossil *Paleodictyon* is better defined, but the relationship between the hexagonal mesh and mid-cell structures remains ambiguous.

- Producing regular hexagonal networks requires mobility and advanced spatial skills, including accurate orientation and odometry. These abilities are consistent with arthropod neurological structures which govern spatial navigation. This observation highlights the need for further investigation into the influence of specific cognitive skills on burrow morphology.
- The first appearance of *Paleodictyon* coincides with the early Cambrian diversification of arthropods rather than with the Ediacaran, by which time vermiform taxa were already established. While this timing does not exclude a vermiform tracemaker, it favours an arthropod one. Future biostratigraphic work could test this hypothesis by correlating the episodic presence of *Paleodictyon* in shallow seafloors with arthropod radiation events in shallow-sea settings. Clades that expanded into shallow waters concurrently with *Paleodictyon* are likely candidates for its production.
- Based on the topology of *Paleodictyon*, we propose that it may have served as a communication network for a colony of organisms, regardless of their feeding strategy. Although the agrichnial hypothesis has garnered considerable support, it lacks direct evidence. To address this, in situ cameras could provide real-time observation of organisms producing these structures. However, a significant obstacle is that the behavioural activity occurs beneath the seafloor, making it challenging to capture tracemaker activity. In addition, no computational models have tested a colonial origin for *Paleodictyon*.

Direct neoichnological observations have the potential to address most of the above-mentioned gaps in our understanding of *Paleodictyon*. We propose establishing “*Paleodictyon* observatories” in areas where *Paleodictyon* is actively being produced (e.g., the Clarion-Clipperton Fracture Zone in the Pacific Ocean). The observatory infrastructure should incorporate three crucial components. First, autonomous time-lapse systems like Bathysnap for capturing hourly seafloor imagery over year-long periods. This would enable automated detection algorithms to trigger targeted sampling when new structures appear on the seafloor. It is recommended to integrate imaging systems with both visible light and Underwater Hyperspectral Imagers (UHIs), as they provide optical signatures beyond standard RGB capabilities. UV fluorescence may also reveal hidden macrofauna or biofilms.

Secondly, in-situ environmental DNA samplers should be employed to compare genetic profiles of both fresh and ancient *Paleodictyon*, distinguishing between tracemaking organisms and subsequent colonisers. Third, deploying a Sediment Profile Imagery system (SPI) on newly formed *Paleodictyon* could allow observation of tracemaker activity within the burrows. This multi-proxy approach would increase the probability of identifying the *Paleodictyon* tracemakers, presenting a promising solution to this longstanding palaeontological enigma.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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