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Estrellichnus jacaensis from the Eocene Jaca Basin (NE Spain): new locality and new ethological interpretation

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New occurrences of *Estrellichnus jacaensis* in the deep-marine turbidite deposits of the Eocene Hecho Group (Fiscal, Huesca, NE Spain) are described. Most of them include specimens preserved as ‘urban fossils’ located in several villages of the South-Central Pyrenees. Well-preserved morphological features of the new specimens studied and their interactions with accompanying ichnotaxa allow reinterpreting the constructional process and functional significance of *Estrellichnus* and its rejection as a graphoglyptid. The comparison of this ichnogenus with lebensspuren recorded in oceans and seas around the world has allowed finding a plausible current analogue and proposing a likely tracemaker.
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Keywords

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Trace fossils bearing a radial morphology or architecture have been denominated as star-shaped, flower-like, spoke, stellate, rosette or radiating traces or structures (e.g. Häntzschel 1970; Książkiewicz 1970; de Gibert *et al*. 1995; Bromley 1996). Knaust (2012) proposed a hierarchical scheme corresponding to previous morphological classifications of trace fossils (e.g. Książkiewicz 1977). More recently, in order to evaluate the ichnodisparity of ichnotaxa, Buatois *et al*. (2017) defined 79 categories of architectural designs, 58 of them being referred to bioturbation structures.

Ichnogenera *Asterichnus*, *Capodistria*, *Chondrorhaphe*, *Cladichnus*, *Dactyloidites*, *Dendrorhaphe*, *Fascisichnium*, *Glockerichnus*, *Gyrophyllites*, *Haentzschelinia*, *Lorenzinia*, *Monocraterion*, *Parahaentzschelinia*, *Phoebichnus*, *Rotamedusa* and *Skolichnus* exhibit some kind of radial aspect that partially or completely characterize their morphology and/or architectural design that allow including them within the categories of 'sub-horizontal and unbranched burrows with radial shape', 'sub-horizontal and branched burrows with radial shape', 'complex and radial burrows' and 'branched and radial bioerosional trace fossils' proposed by Knaust (2012), or within the 'radial to rosette structures', 'radial graphoglyptids' and 'radial borings' of Buatois *et al*. (2017).

A new locality of *Estrellichnus jacaensis* Uchman & Wetzel 2001, from the Eocene Hecho Group (Huesca, NE Spain), is presented herein. This ichnotaxon was firstly interpreted as a graphoglyptid consisting of a complex burrow system composed of shallow sub-surface tunnels spreading out from a vertical shaft (Uchman & Wetzel 2001). However, the preservational features of the specimens from the new locality described herein, together with an exhaustive palaeobiological and palaeoethological analyses in correspondence to lebensspuren photographed on deep-sea floor all over the world, allow reinterpreting the architectural design of *Estrellichnus* and its formational and functional interpretation.

Geological and stratigraphical setting

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The studied trace fossils are found in a quarry located around 3.5 km northwest to the town of Fiscal (Huesca, NE Spain; Figs 1, 2). In a broad scale, the Palaeogene sedimentary rocks exposed in this area are part of the South-Pyrenean Foreland Basin. The development of this basin (together with that of the Aquitaine Foreland Basin) was induced by the formation of the Pyrenees, an orogenic belt formed as a consequence of collision between the Iberian and Eurasia plates throughout the Late Cretaceous to early Miocene (Roure *et al*. 1989; Roest & Srivastava 1991; Muñoz 1992; Teixell 1998; Vergés *et al*. 2002).

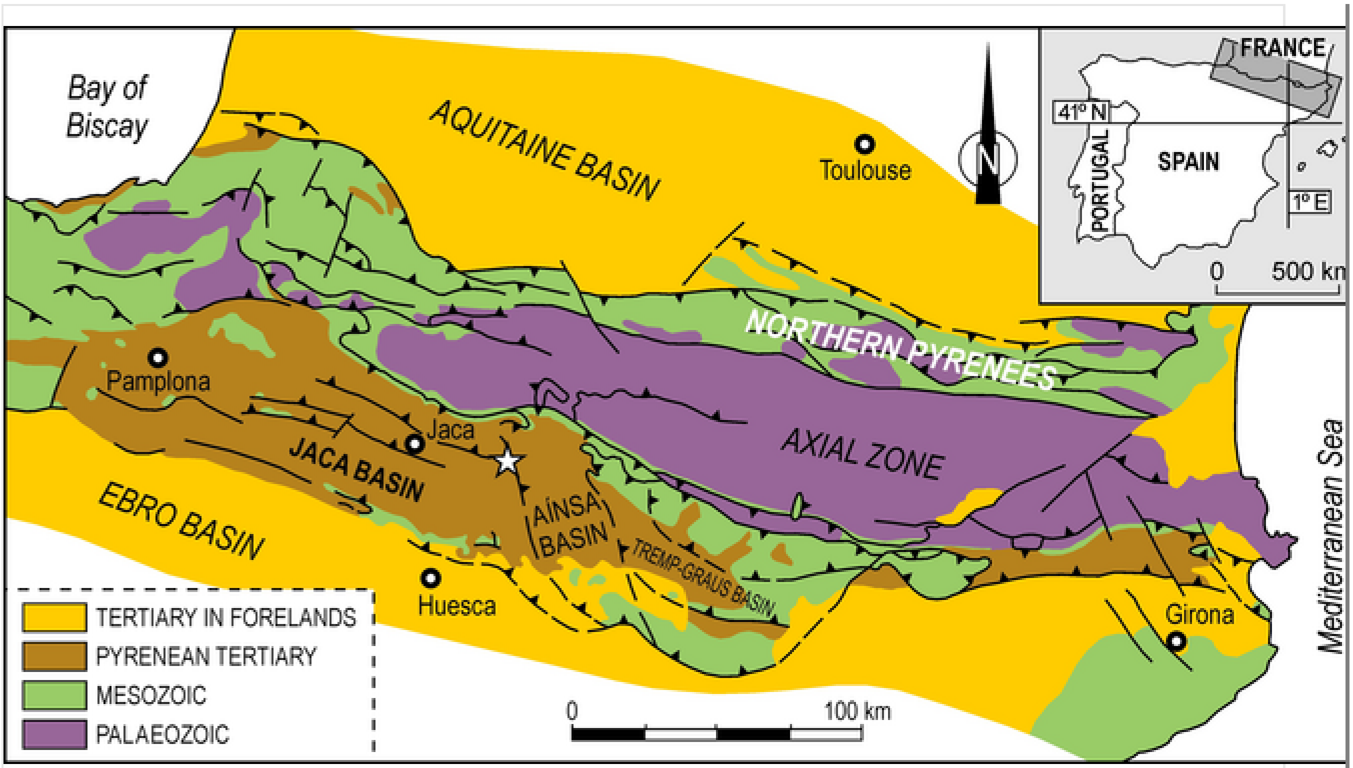

Fig. 1 Geographical and geological map of the Pyrenees including the studied locality (white star) (modified after Arbués *et al*. 2011 and Roigé *et al*. 2007 '2017' instead of '2007'). In the upper right corner is included an inset map, displaying the position of the considered area in the Iberian Peninsula.

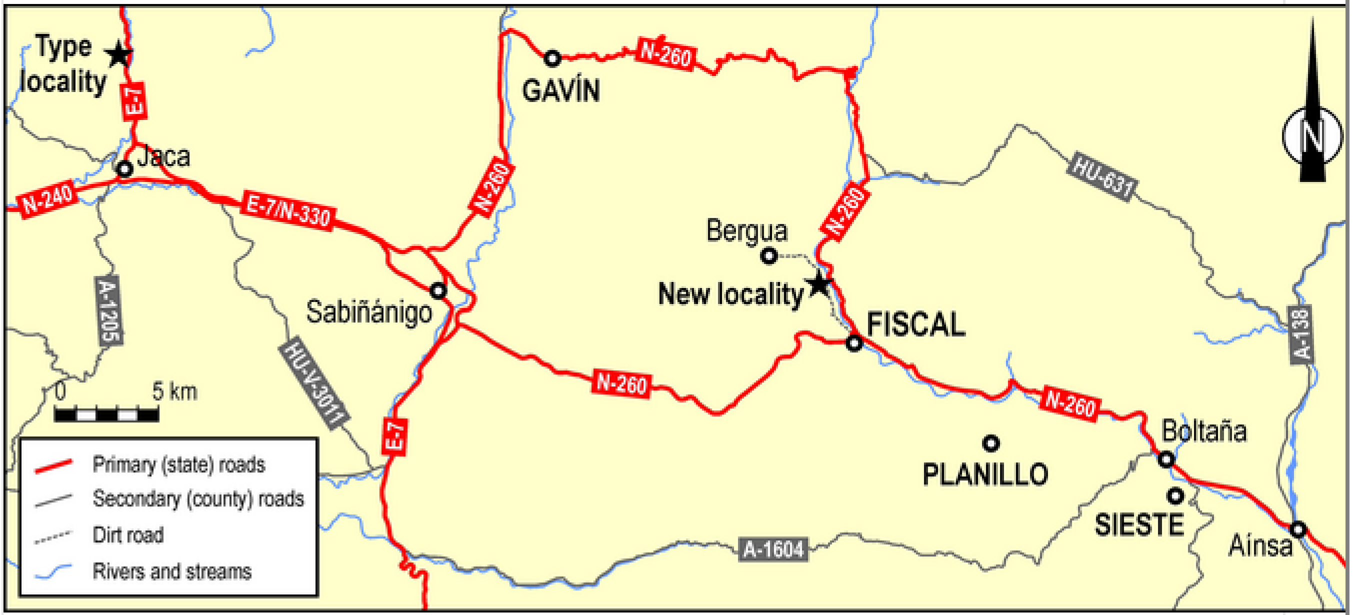

Fig. 2 Locality map showing the type-locality and the new one described herein (black star; 42°31′18.6″N, 0°08′12.4″W). The villages in capital letters and bold are those in which ‘urban specimens’ of *Estrellichnus* have been found and studied.

Puigdefàbregas *et al*. (1992) proposed four main episodes (Stages I–IV; from Upper Cretaceous, Santonian, to Oligocene) to explain the evolution of the South-Pyrenean Foreland Basin, a basin that remained opened towards the Atlantic until the Late Eocene (Puigdefàbregas *et al*. 1989). During early Eocene (Stage III of Puigdefàbregas *et al*. 1992), a strongly subsiding foredeep took place, including the development of the Aínsa and Jaca basins, and the associated piggy back Tremp-Graus Basin (Arbués *et al*. 2011; Fig. 1). Specifically, during Eocene times and in connection from east to west, the infill of the Tremp-Graus Basin was dominated by a fluvio-deltaic sedimentation, which fed the slope complex that characterizes the Aínsa Basin, which in turn fed the terrigenous basin-floor systems identified in the Jaca Basin (Roigé *et al*. 2007; Arbués *et al*. 2011; and references therein).

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Deep-marine deposits (turbidite-dominated) from the Jaca Basin are known as the Hecho Group (Ten Haaf *et al*. 1971; Mutti *et al*. 1972, 1981, 1985, 1988; Mutti 1977, 1985; Estrada 1982; Remacha *et al*. 1998a,b1998b), this group also being represented in the Aínsa Basin. The Hecho Group (Lower–Middle Eocene) in the Jaca Basin, mainly and axially fed from the eastern Aínsa and Tremp-Graus basins, is subdivided into four main sandstone-rich turbidite depositional systems related to sea-level changes and tectonic activity (from base to top: Fosado-Torla, Arrò-Broto, Gerbé-Cotefablo and Banastón-Fiscal systems *sensu* Mutti *et al*. 1985; see also Das Gupta & Pickering 2008; Heard & Pickering 2008). In this context, the trace fossils studied herein are a part of the Banastón-Fiscal system (the Fiscal Unit *sensu* Estrada 1982), specifically within the Lacort Subunit, just above the Megabed 5 or the Roncal-Fiscal Megaturbidite (*sensu* Estrada 1982; see also Barnolas *et al*. 1996 and references therein).

Main facies in the Hecho Group

Following Mutti (1977, 1984, 1985), and with respect to their distinctive sedimentological features, a series of thin-bedded turbidite facies can be distinguished in the Hecho Group: (1) channel margin facies; (2) inter-channel facies; (3) channel mouth facies; (4) lobe fringe facies; and (5) basin plain facies (see Fontana *et al*. (1989) or Remacha & Fernández (2003) for more information). In addition and combining sedimentological and ichnological data, Heard & Pickering (2008) proposed a palaeoenvironmental interpretation for the turbidite complex of the Aínsa and Jaca basins. Specifically, these authors differentiated between basin slope, upper-slope gully, canyon-fill, channel axis, channel off-axis, channel margin and outermost channel-to-levée–overbank environments for the more laterally confined and channel-dominated Aínsa Basin, and between channel–lobe transition, lobe, lobe fringe, fan fringe and distal basin-floor environments for the more unconfined and distal Jaca Basin.

The type-locality of *E. jacaensis*, around 5 km north of Jaca (Fig. 2; locality known as Puente de Torrijos; see Remacha & Picart 1991), is part of the Subunit C of the Jaca Unit, located just below the Megabed 8 or Jaca Megaturbidite (following Estrada 1982). Uchman (2001) and Uchman & Wetzel (2001) interpreted these deposits as lobe facies. This lobe facies mainly consists of a few metres to a few tens of metres of thickening-upward or symmetrical cycles, which contain thick-bedded coarse-grained to thin-bedded fine-grained, lithic sandstone turbidites (see Mutti 1977, 1984, 1985; Estrada 1982 and references therein).

Regarding the new locality studied herein (the quarry on the dirt road that connects Fiscal with

Bergua; Fig. 2), its deposits mostly consist of sandstone-dominated turbidites that mainly correspond to lobe facies, but are secondarily also attributable to lobe-fringe and channel–lobe transition environments (P. Arbués personal communication, 2018). Although both localities, the type-locality and the new one, have been dated to the Lutetian (Eocene; see Barnolas *et al*. 1982; Remacha *et al*. 1998b1998b; Oms *et al*. 2003; Pickering & Corregidor 2005; Scotchman *et al*. 2015; and references therein), the type-locality (Subunit C, Jaca Unit) is located stratigraphically above the new one (Lacort Subunit, Fiscal Unit; see Estrada 1982). AQ7

Material and methods

Many of the specimens studied herein were found as 'urban fossils' (see Belaústegui & Belaústegui 2017 and references therein), mainly as paving slabs of the streets of several villages in this area (i.e. Fiscal, Gavín, Planillo and Sieste; Fig. 2). These paving slabs were extracted from the Fiscal quarry (the new locality presented herein). All measurements were carried out using a Vernier calliper with a precision of 0.05 mm.

The holotype (MPZ 98/477) is housed in the Palaeontological Museum of the University of Zaragoza ('Museo Paleontólogico de la Universidad de Zaragoza'; see Uchman & Wetzel 2001). Except for those located in the type-locality (Uchman 2001; Uchman & Wetzel 2001), no more *in situ* specimens have been found.

Descriptive ichnology

The ichnospecies *Estrellichnus jacaensis*

This ichnotaxon has only been formally identified in the Eocene sedimentary rocks of Huesca (south-central Pyrenees, NE Spain). It was first reported by Lucas & Rech-Frollo (1964) as 'traces en rosette', and formally described by Uchman & Wetzel (2001; see also Uchman 2001). Risk (1973) recorded 'fan- or bugle-shaped traces' from the middle Silurian Thorold Sandstone (southwestern Ontario, Canada), which could correspond to initial ichnogenetic stages (see Belaústegui *et al*. 2016) of *E. jacaensis*, although their dimensions are much smaller.

Estrellichnus jacaensis is a hypichnial and radial trace fossil, which is composed of numerous (up to 60) and mostly rectilinear ridges (or grooves) that radiate from a unique and central conical mound (Figs 3–8 3 #let12346-fig-0004 #let12346-fig-0005 #let12346-fig-0006 #let12346-fig-0007 #let12346-fig-0008 All this should be deleted. (It must be an editing error... in the pdf is OK)). Ridges are around 1.9–3.75 mm wide and 177–302 mm long (i.e. a maximum diameter of 600 mm for a whole specimen). The proximal part of these ridges (i.e. the closest to the central mound) is commonly well marked, smooth and transversally hemi-cylindrical (Figs 3–6 3 #let12346-fig-0004 #let12346-fig-0005 #let12346-fig-0006 All this should be deleted. (It must be an editing error... in the pdf is OK)); their terminal part (ca. last 50–100 mm) exhibits a progressive widening (up to 16 mm) to form a slightly rough and convex bulge, more elevated than the proximal sections, which outline shows an elongate drop-shaped morphology (Figs 3B, 4A, B, 6D, 7A). The radiating ridges show two types of distal or terminal curvatures: (1) an upward bow which plane is perpendicular to the bedding (almost always present; e.g. Fig. 3A); and (2) an occasional winding parallel to the bedding and always oriented to the same direction (Figs 4B, 6C, D). The central mound exhibits a rounded and conical morphology, its maximum diameter ranges from 19 to 53 mm, and it shows a maximum height of 15 mm (Figs 3A, 4C, 5C, D, 6B, 8D–F). Occasionally and likely due to weathering, the mounds may display a volcano-shaped morphology which allows to observe an internal and concentrically laminated structure that surrounds a central, thinner and most likely conical termination of a shaft (Fig. 8D–F). The whole structure of this ichnofossil may or may not show a slight elevation with respect to the bedding plane in which it appears; it is almost inexistent in some specimens.

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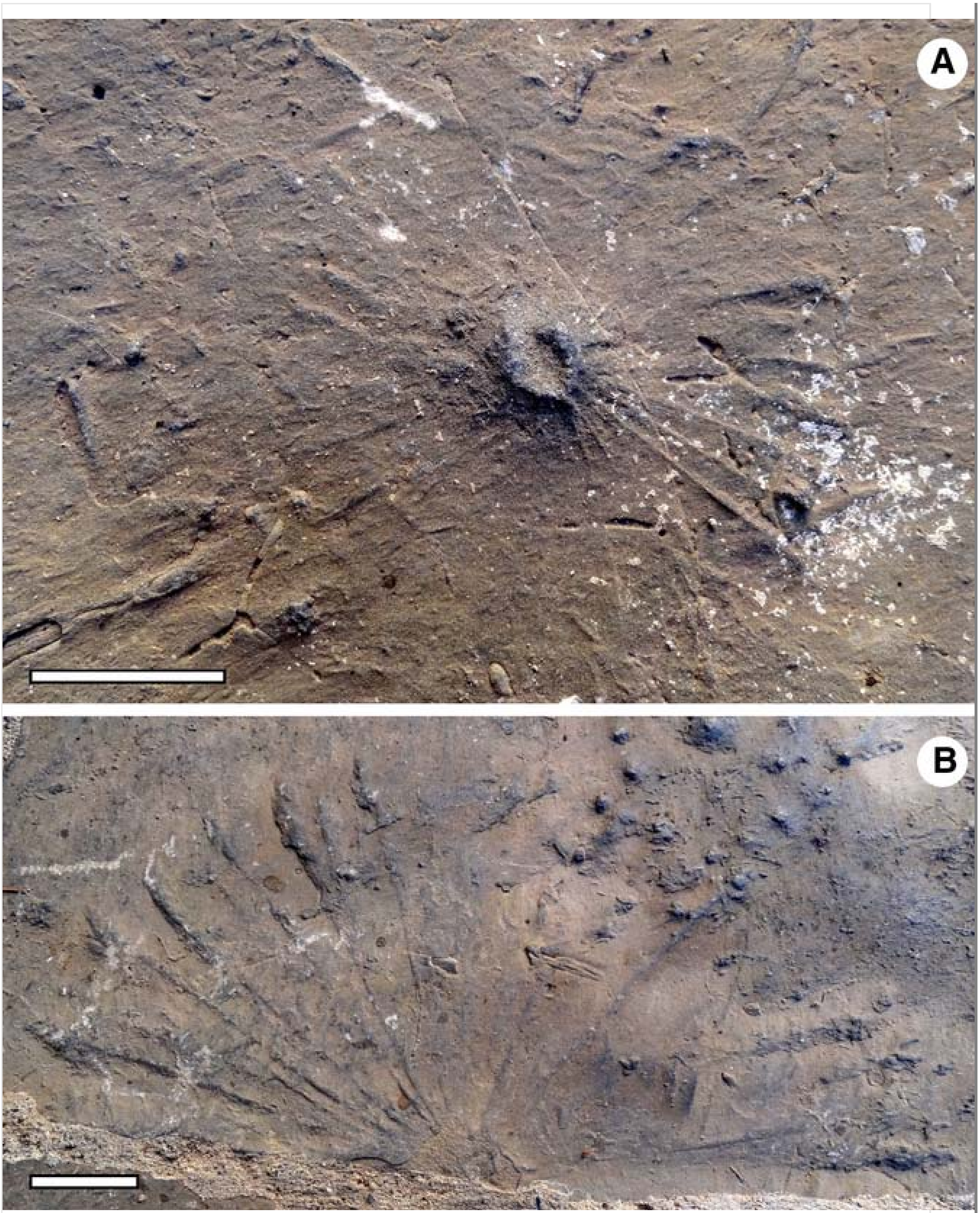

Fig. 3 *Estrellichnus jacaensis* from Fiscal. A, Complete specimen (the smallest observed); *Ophiomorpha annulata* with Y-shaped branching and pellets in the concave part (originally from the sandy roof side) is observable in the lower left corner. B, Partial specimen of *Estrellichnus* together with ?*Saerichnites* isp. Scale bars: 5 cm.

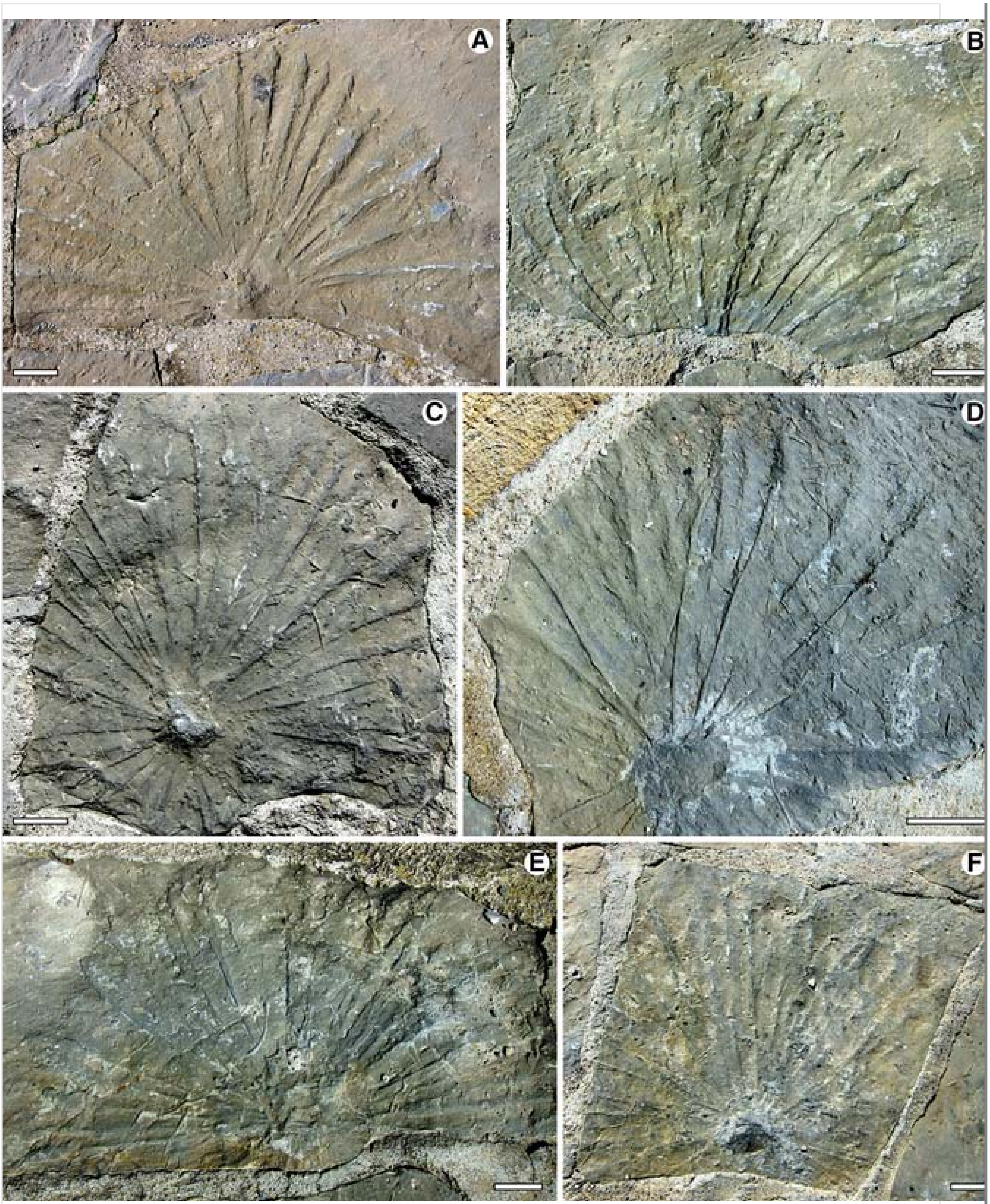

Fig. 4 *Estrellichnus jacaensis* from Gavín. A–F, Six partial to almost complete specimens of *Estrellichnus*; a clear winding of the ridges (to the right of the image) is observable in B (see details of associated ichnotaxa in Figs 7, 8). Scale bars: 5 cm.

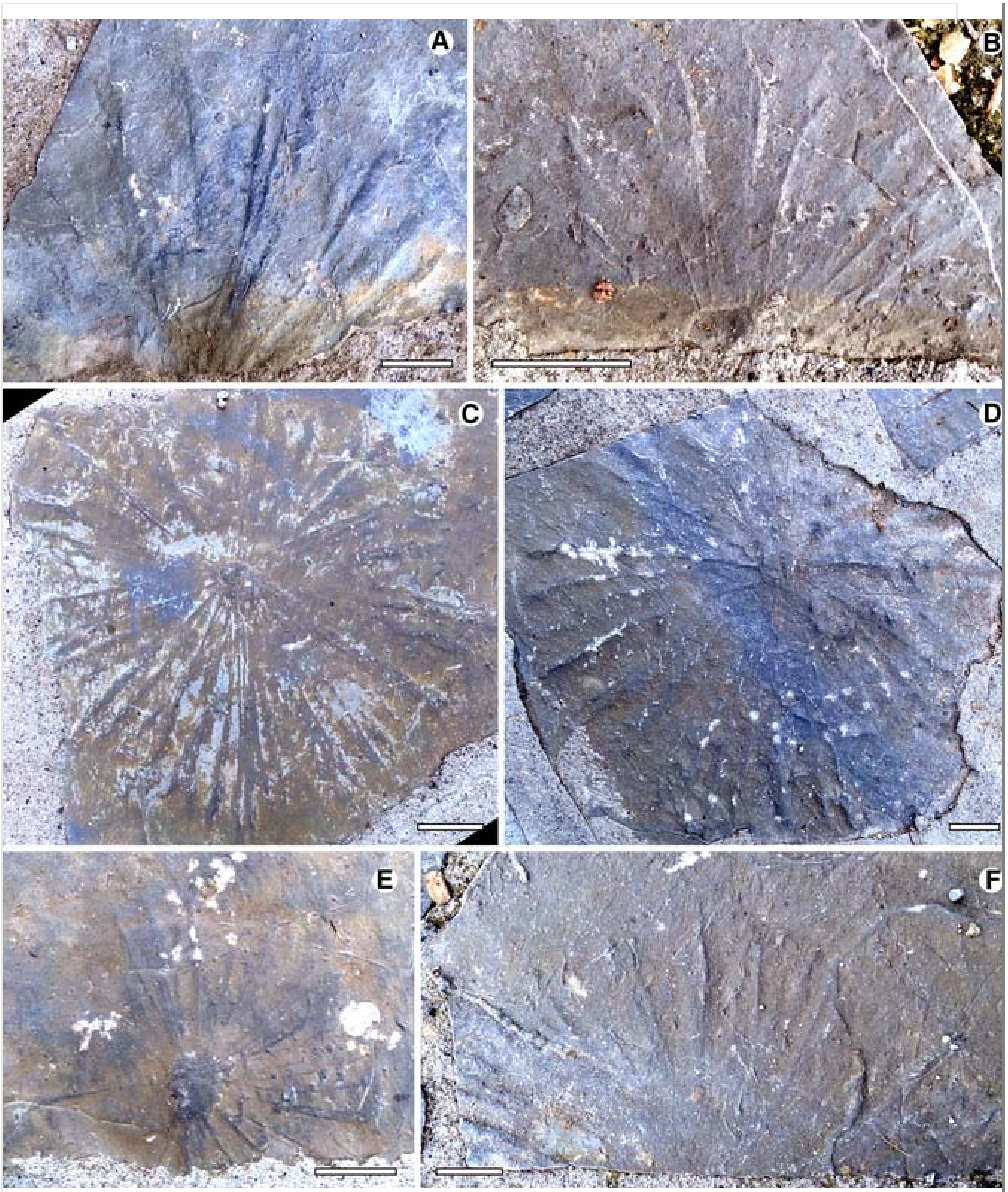

Fig. 5 *Estrellichnus jacaensis* from Planillo. A–F, Six partial to almost complete specimens of *Estrellichnus*. *Ophiomorpha annulata* and Without italics. *Ophiomorpha rudis* are observable in F (see details of associated ichnotaxa in Fig. 8). Scale bars: 5 cm.

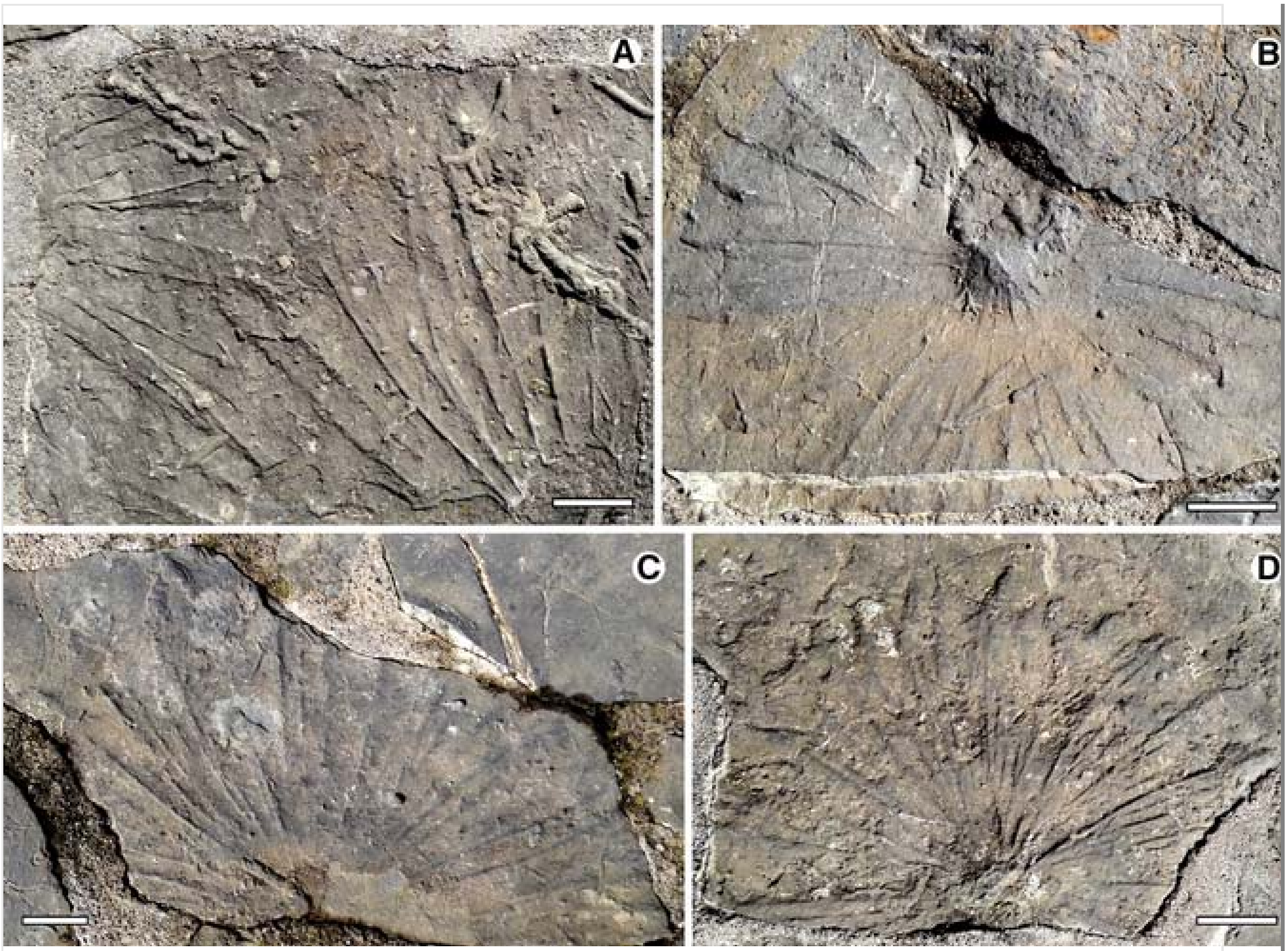

Fig. 6 *Estrellichnus jacaensis* from Sieste. A, Slab with two partial specimens of *Estrellichnus* together with *Ophiomorpha annulata* and *Ophiomorpha rudis*. B–D, Three partial specimens of *Estrellichnus*; a slight winding of the ridges (to the right of the image) is observable in C and D. Scale bars: 5 cm.

Fig. 7 Interactions of *Estrellichnus jacaensis* with *Paleodictyon strozzii* and *Paleodictyon*

majus (this ichnospecies only in C). A–C, *Paleodictyon* is deformed and adapted to the convexity of the *Estrellichnus* ridges. D–F, *Paleodictyon* is crossed and partially removed by the radial ridges of *Estrellichnus*. *Helminthorhaphe flexuosa* and *Ophiomorpha annulata* in E. (All pictures are from Gavín; A and B are details of Fig. 4B; C is a detail of Fig. 4D; D is a detail of Fig. 4F; and E is a detail of Fig. 4C.) Scale bars: 5 cm.

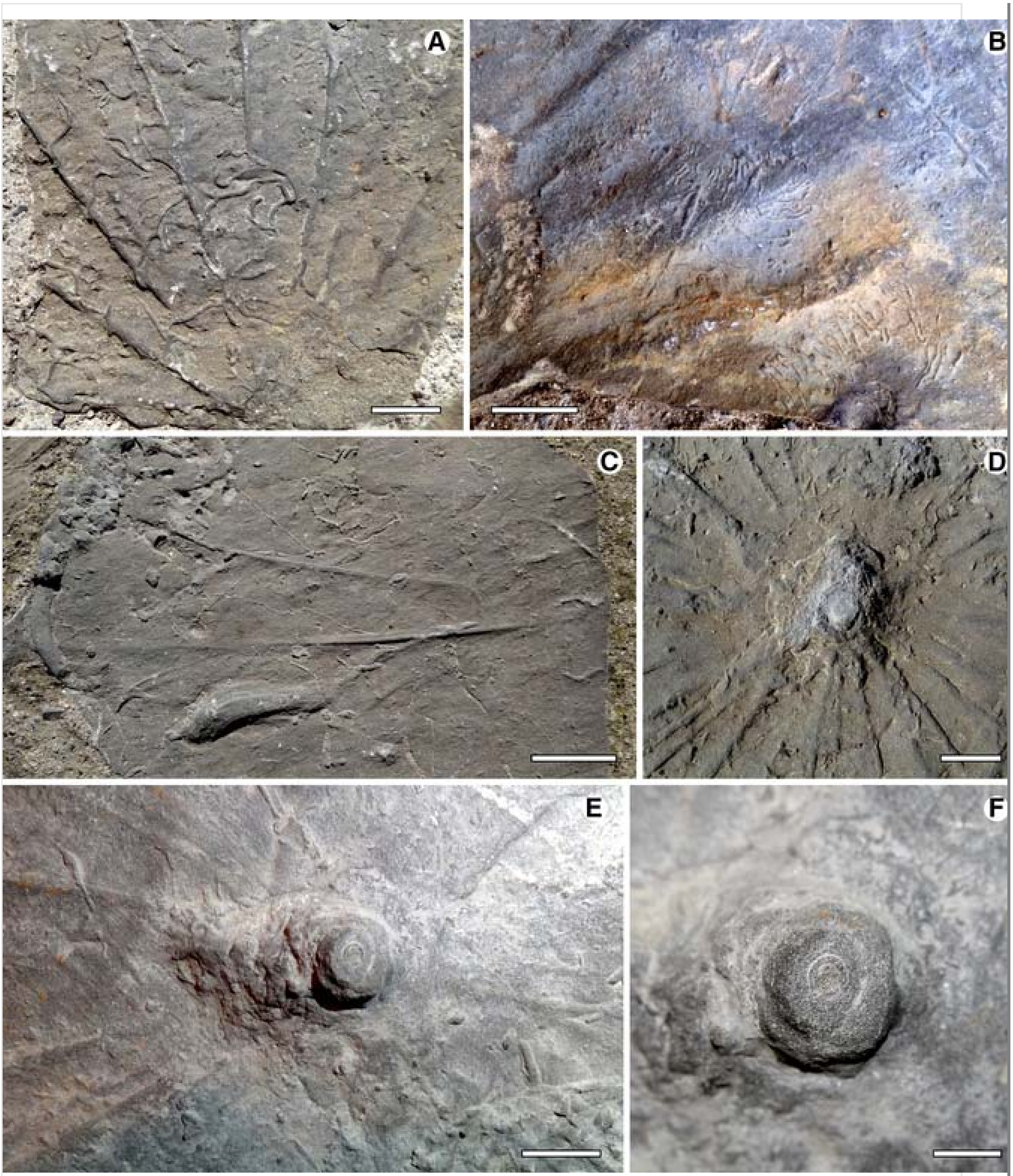

Fig. 8 Other interactions and details of *Estrellichnus jacaensis*. A, *Estrellichnus* and *Megagrapton submontanum* (Gavín; scale bar: 1 cm). B, Six ridges (distal part) of *Estrellichnus* and *Helminthorhaphe flexuosa* (detail of Fig. 5A; Planillo; scale bar: 2 cm). C, Initial ichnogenetic stage of *Estrellichnus* (only two ridges are observable); *Curvolithus* cf. *multiplex* is observed in the centre of the bottom of the photograph; moreover, *Ophiomorpha annulata* and *Ophiomorpha rudis* are present (Sieste; scale

bar: 5 cm). D–F, Details of the central conical mound; a concentric laminated lining is observable (Gavín; D is a detail of Fig. 4C; scale bars: 2 cm, except for F that is 1 cm).

Thanks to ongoing activity in the Fiscal quarry, around 30 specimens were observed on the same bedding plane on a surface of approximately 130 m by 30 m (around 4000 m^2), that is around one specimen/100 m^2.

Accompanying ichnotaxa

Several (27) pre- and post-depositional ichnotaxa occur in strata bearing *Estrellichnus* (Figs 3, 5F, 6A, 7, 8, 9). Since the most part of these ichnotaxa have been commented in several papers (e.g. Seilacher 1977; Uchman 1995, 1998, 2001), only those unrecorded (until today) in this area are described. Their ethological interpretation and distribution in the new locality (‘Fiscal quarry’) and in the villages studied are presented in Table 1.

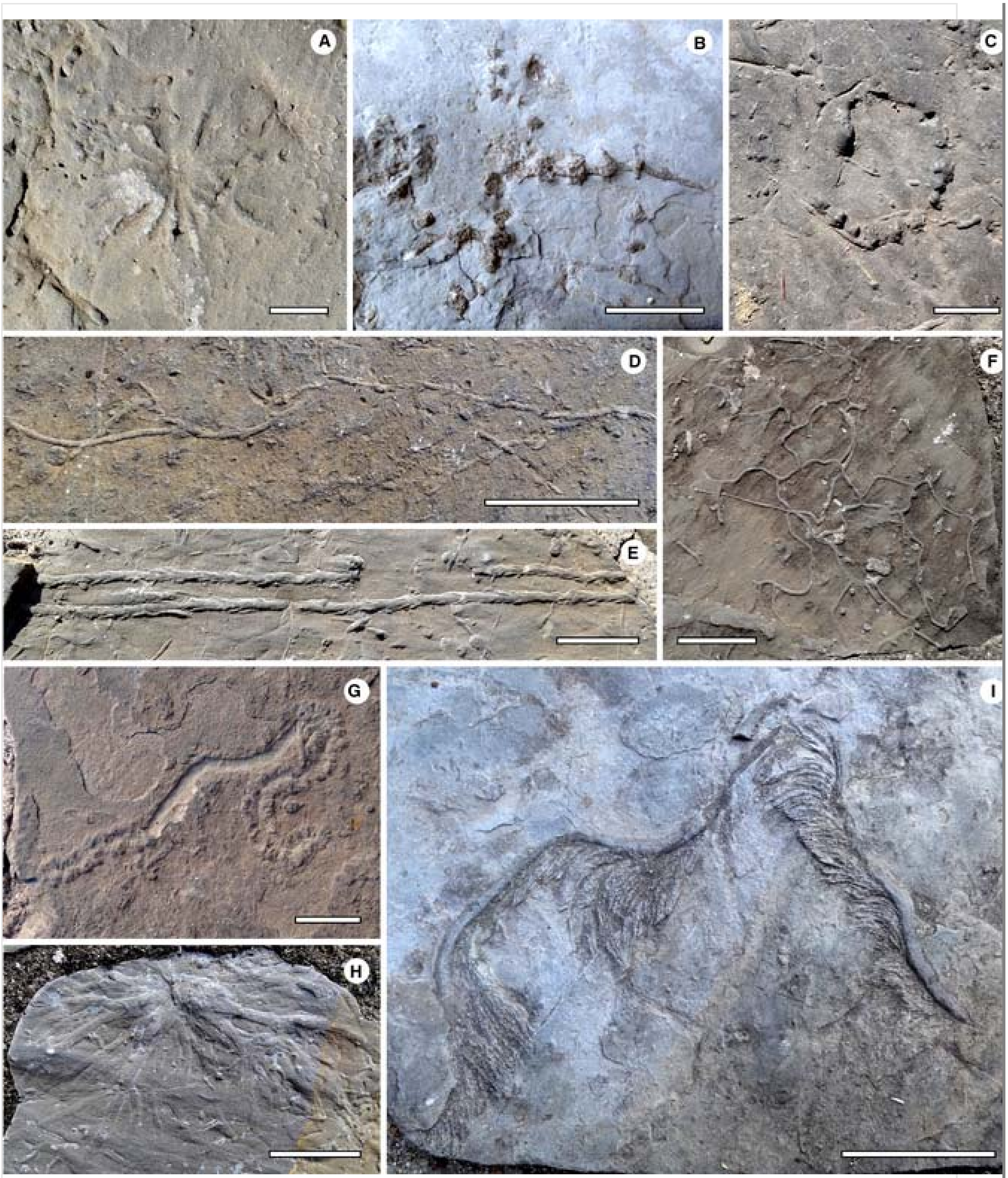

Fig. 9 Associated ichnotaxa. A, *Glockerichnus* isp. (Gavín; scale bar: 2 cm). B, *Halimedides* isp. (Planillo; scale bar: 2 cm). C, *Lorenzinia* isp. (Fiscal; scale bar: 2 cm). D, ?*Halopoa* isp. B (Fiscal; scale bar: 5 cm). E, *Halopoa storeana* (Gavín; scale bar: 5 cm). F, *Megagrapton irregulare* (Gavín; scale bar: 5 cm). G, *Nereites* isp. (Fiscal; scale bar: 2 cm). H, Radial trace A (Sieste; scale bar: 5 cm). I, *Zoophycos* isp. (Planillo; scale bar: 5 cm).

Table 1

Associated ichnotaxa. Those in bold occur on the bedding plane with *Estrellichnus* (cal – callichnia; dom – domichnia; fod – fodinichnia)

Ichnotaxon	Ethological category	Fiscal quarry	Villages ('urban fossils')				Figs
			Fiscal	Gavín	Planillo	Sieste	
Bergaueria isp.	Domichnia					x	–
Chondrorhaphe bifida	Agrichnia		x				–
Cosmorhaphe sinuosa	Agrichnia	x	x		x		–
Curvolithus cf. *multiplex*	Pascichnia					x	8C
Glockerichnus isp.	Agrichnia			x			9A
Halimedides isp.	pas/dom/?cal				x		9B
Halopoa imbricata	Pascichnia		x		x		–
Halopoa storeana	Pascichnia	x	x	x		x	9E
Halopoa isp. A	Pascichnia		x		x	x	–
?*Halopoa* isp. B	Pascichnia		x		x	x	9D
Helminthoidichnites isp.	Repichnia				x		–
Helminthopsis isp.	Repichnia					x	–
Helminthorhaphe flexuosa	Agrichnia		x	x	x	x	7E, 8B
Lorenzinia isp.	Agrichnia		x				9C
Megagrapton irregulare	Agrichnia	x	x	x		x	9F
Megagrapton submontanum	Agrichnia		x	x		x	8A
Nereites isp.	Pascichnia	x		x			9G
Ophiomorpha annulata	dom/fod	x	x	x	x	x	3A, 5F, 6A, 7E

Ophiomorpha rudis	dom/fod	x	x	x	x	x	5F, 6A
Paleodictyon strozzii	Agrichnia	x	x	x			7, 9A
Paleodictyon delicatulum	Agrichnia		x				–
Paleodictyon majus	Agrichnia			x			7C
?*Saerichnites* isp.	dom/fod	x				?	3B
Scolicia isp	Pascichnia		x				–
Thalassinoides isp.	dom/fod	x	?				–
Zoophycos isp.	Fodinichnia				x		9I
Radial trace A	Fodinichnia					x	9H

Curvolithus cf. *multiplex* Fritsch 1908 (Fig. 8C) is a slightly curved, flat-topped ridge, which is 11 mm wide and about 80 mm long. It shows indistinct, narrow, side bevels. The ridge plunges into the bed from both sides. The ridge is elevated aside of the middle part.

Halimedides isp. (Fig. 9B) is a horizontal series of oval, rhomboid to heart-shaped in outline chambers interconnected by a cylindrical tunnel, preserved in full relief and filled with sand coarser than the surrounding slab. The chambers are 3–5 mm wide, 2–4 mm apart. The tunnel is 1.0–1.5 mm wide.

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Halopoa isp. A is a hypichnial, cylindrical, straight, rope-like structure, 8–14 mm wide, composed of barrel-like of rhomboid segments, which are 10–15 mm long. The structure shows constrictions between the segment joints. The segments are covered by longitudinal wrinkles.

?*Halopoa* isp. B (Fig. 9D) is a hypichnial, cylindrical, slightly winding string, which is about 2 mm wide. It shows segments, which are 15–20 mm long and separated by transverse discontinuities. The segments show irregular, longitudinal wrinkles.

Helminthoidichnites isp. is a horizontal, irregularly, slightly winding, semicircular ridge, about 1 mm wide.

Radial trace A (Fig. 9H) is a hypichnial, incompletely preserved structure, which is composed of straight to slightly curved, low ridges, which are about 5 mm wide. The ridges overlap in proximity of a common centre and spread out up to a distance of about 100 mm and weld with the bedding plane at their termination. Close to the centre, an elliptical mound is present.

Discussion

Construction and function

According to the architectural features of *Estrellichnus*, it is quite plausible that this ichnotaxon is the result of the burrowing activity of an invertebrate that possess some protrusible element that successively left surface feeding traces radiating from a single burrow (currently of unknown morphology).

Among the marine invertebrates that are able to generate this kind of bioturbation structures, the traces resulting from the bioturbation of echiurids constitute a good analogue for this ichnogenus. Echiuridae, a group of annelids closely related to Capitellidae, are secondarily unsegmented worms with a distinctive and extensible pre-oral proboscis (Brusca *et al*. 2016). This proboscis, which may reach lengths of 1–2 m, is used as a non-selective food-collecting device (covered by mucus and probably chemoreceptors) that directs material along its ciliated gutter towards the mouth (Barnes *et al*. 1991; Brusca *et al*. 2016). Such feeding behaviour has been widely documented (Chuang 1962; Otha 1984; Lampitt 1985; de Vaugelas 1989; Gage & Tyler 1991; Bett & Rice 1993; Hughes *et al*. 1993, 1994).

Although modern echiurids are able to produce simple blind shafts as well as U- or J-shaped burrows (to which the proboscis traces are associated; see Chuang 1962; Otha 1984; de Vaugelas 1989; Anker *et al*. 2005), the complete morphology of the central burrow has not been observed in the studied specimens of *Estrellichnus*. However, a concentrically laminated lining has been observed in the transverse section of the central elevation in some specimens (Fig. 8D–F); the mucus secretion and the peristaltic movements performed by some echiurids (see Meglitsch 1972; Risk 1973) could be attributable to the formation of such structure.

Therefore, both *Estrellichnus* and modern echiurid lebensspuren are considered herein as the combination of dwelling and feeding structures (fodinichnia). Since the morphology and depth of the lower termination of *Estrellichnus* are unknown, it is not possible to determine the full tiering position of this ichnotaxon which could correspond to a middle- or even deep-tier deposit feeder.

Tracemaker

The identification of tracemakers is often not a straightforward mission, since a majority of soft-bodied producers show low fossilization potential. Therefore, a good preservation of their architectural details, especially the ‘bioprints’ of Rindsberg & Kopaska-Merkel (2005) or the ‘fingerprints’ of Seilacher (2007), together with a wide knowledge of modern tracemakers is crucial. Fortunately, both parameters are available in the case of *Estrellichnus*.

Lucas & Rech-Frollo (1964) attributed this trace fossil to the epi- and endobenthic activity of large bivalves, specifically those belonging to the genera *Mya* or *Lutraria*, also compared *Estrellichnus* with the life traces currently produced by the smaller tellinoid bivalve *Scrobicularia plana* (see also Häntzschel 1934). Later, Häntzschel (1970) discarded crabs and bivalves and proposed worms (or at least worm-like animals) as their most likely producers. Finally, Uchman & Wetzel (2001) considered echiurid worms, large annelids or crustaceans as possible tracemakers. Due to their interpretation of *Estrellichnus* as a permanently open burrow system, these authors did not relate the lebensspuren generated by such organisms (mostly surface traces) to this ichnotaxon.

Nowadays, more and more neoichnological studies are being carried out, contributing to a better knowledge of burrowing and boring faunas from shallow- to deep-marine environments (e.g. Seike *et al*. 2012; Ayranci & Dashtgard 2013; de Gibert *et al*. 2013). Among them, the radial or rosette lebensspuren that share more analogies with *Estrellichnus* are those produced by echiurids or the spoon worms (Annelida: Polychaeta).

Heezen & Hollister (1971) described 'spoke burrows' produced by the proboscis of echiurids from southern Peru–Chile Trench (3626 m deep). Through aquarium observations of live specimens of the echiurid *Listriolobus pelodes* Fischer collected from Santa Barbara Channel (southern California), Risk (1973) documented 'fan-like' traces emerging from a single burrow that could be interpreted as the first ichnogenetic stages of a complete and radial (360°) *Estrellichnus*-like trace. Hollister *et al*. (1975) figured 'spoke-like impressions radiating from a central hole' that attributed to echiurid worms (but without discarding bivalves and polychaetes) from the southeastern Indian Ocean. Otha (1984) recorded the presence of 'star-shaped foraging traces' which resulted from the bioturbation activity of echiurid worms on the deep-sea floor (ca. 2600–5000 m deep) of the Bay of Bengal, specifically describing five different types of radial traces (I to V), types II and III being the most similar to *Estrellichnus*. Bett *et al*. (1995) described six types of 'spoke burrows' attributed almost certainly to echiurids from the Cape Verde Abyssal Plain (ca. 4600 m deep); among them, the most abundant 'type 3' ('simple spoke burrows') is almost identical to *Estrellichnus*. Dundas & Przeslawski (2009) documented 'large rosettes' produced by echiurids (Bonelliida) and other polychaetes (terebellid, trichobranchid, ampharetid) from the Eastern (1310–2178 m deep) and Western (1571–4091 m deep) Australian margin. Bell *et al*. (2013) also described echiurid 'large rosettes' from the bathyal Mid-Atlantic Ridge.

Not directly related to echiurids, Ewing & Davis (1967) ordered abundance of lebensspuren on the basis of photographs of the seafloor. Among the six basic subdivisions (I to VI) proposed by these authors, the third one ('IIIB1b. Sets of grooves radiating from a common point and with many rays') includes specimens (IIIB3 to IIIB11) that share many similarities with *Estrellichnus*; observations were carried out in the Pacific (southeast area and Polynesia) and Indian (Seychelles area) oceans, and in all cases, the producer was not identified (see Ewing & Davis (1967) for more details). Young *et al*. (1985) documented a 'rosette' produced by an unknown tracemaker in the Venezuela Basin (Caribbean Sea). Huggett (1987) described the presence of small (from 25 to 50 cm in diameter), medium (from 50 to 200 cm) and large (greater than 200 cm) 'spoke burrows' attributed to the activity of worm-like organism from the Madeira Abyssal Plain (5100–5450 m deep); among them, the medium ones share a lot of analogies with *Estrellichnus*. Gaillard (1991) also recorded 'star- and fan-like (incomplete star) traces' of unknown producers from the deep-sea floor of New Caledonia (Southwestern Pacific).

Additionally and in relation to shallow marine environments, Farrow (1971) described the burrowing activity of *Arenicola* in a lagoon sandflat of the southeast of the 'Île d'Esprit' (Seychelles Archipelago, western Indian Ocean; see also Risk 1973); following the description of this author, the traces of this polychaete consist of frequent U-shaped burrows associated with radiating feeding trails which could also be comparable to initial ichnogenetic stages of *Estrellichnus*. Nevertheless, the radial surface traces produced by *Arenicola* are wider and shorter than the typical ones of that ichnogenus.

Taphonomic aspects

Uchman & Wetzel (2001) interpreted the *Estrellichnus* as a burrow system having permanently open radial tunnels emanating from a likely vertical central shaft; the latter would be preserved as semi-reliefs, which resulted from scouring of sub-surface tunnels and their casting, a common preservational mode of graphoglyptids (e.g. *Paleodictyon*). In fact, Uchman & Wetzel (2001) proposed that *E. jacaensis* would share a comparable architectural pattern with *Capodistria vettersi* Vyalov 1968~~;~~. Subsequently, Knaust (2012) proposed a hierarchical scheme to classify trace fossils and catalogued *Estrellichnus* as 'sub-horizontal and unbranched 'branched' instead of 'unbranched' burrows with radial shape and passive fill'. Later and trying to measure the ichnodisparity of the trace-fossil record, Buatois *et al*. (2017) defined a series of categories of architectural designs and included *Estrellichnus* within 'radial graphoglyptids', together with other ichnogenera such as *Dendrorhaphe*, *Glockerichnus* or *Lorenzinia*. By contrast, ichnogenus *Capodistria* was included within the category 'radial to rosette structures' (Buatois *et al*. 2017). More recently, Fan *et al*. (2018) carried out the topological analysis of graphoglyptid trace fossils (79 ichnotaxa from 28 ichnogenera) and proposed 3 major groups (line, tree and net graphoglyptids), 13 minor groups and 19 topological prototypes to classify them. Following this classification, *Estrellichnus* would be a 'tree graphoglyptid' that represents the 'stellate topological prototype'.

Besides its strong resemblance with echiurid lebensspuren (see the previous subsections), the preservational features of the new material studied herein allow reinterpretation and classification of *E. jacaensis* as 'radial to rosette structures' instead of 'radial graphoglyptids' (cf. Buatois *et al*. 2017; Fan *et al*. 2018). In the same way, the adscription to 'sub-horizontal and unbranched 'branched' instead of 'unbranched' burrows with radial shape and passive fill' is considered as a non-suitable category (cf. Knaust *et al*. 2012) herein; by contrast and in our opinion, none of the categories proposed within the classification of Knaust (2012) seem appropriate for *Estrellichnus*.

AQ10

In particular, several *Estrellichnus* specimens occur together with other ichnotaxa, including *Paleodictyon strozzii* and *Paleodictyon majus*, the co-occurrence of which is enlightening (Figs 7, 8, 10). These interactions may occur in two main ways: (1) *Paleodictyon* is crossed and partially truncated by the radial ridges of *Estrellichnus* (Figs 7D–F, 10C); and (2) *Paleodictyon* is deformed and adjusted to the convexity of the *Estrellichnus* ridges (Figs 7A–C, 10D). Assuming that *Estrellichnus* could have been produced by an echiurid worm or at least by an organism with a protrusible element such as proboscis, in both cases the final result would have been a consequence of the pressure exerted by that proboscis on the seafloor during the probing (Fig. 10A). Hence, this assumption implies that (1) the relation to *Paleodictyon* was totally incidental, and the proboscis of the *Estrellichnus* producer simply scraped it on the way (Fig. 10A; t1–t3) (no signal of predation/interest such as deflections or higher density of ridges close to *Paleodictyon* specimens has been observed); (2) the consistency or cohesiveness of the sediment could also have been a limiting factor, being slightly higher in the second case and allowing thus the deformation of the *Paleodictyon* systems together with the micro-strata on which they were formed (Fig. 10A; t3'A, t3'B, t4); (3) the producers of *Estrellichnus* and *Paleodictyon* were nearly contemporaneous and, therefore, both trace fossils are considered as pre-depositional; and (4) after the deposition of a turbidite, while *Paleodictyon* was preserved as semi-reliefs resulting from scouring and casting, *Estrellichnus* would be preserved in the same way but by scouring and casting of the undertraces transmitted to the depth of a millimetre scale (Fig. 10A; t3–t4) by the proboscis. The same taphonomic aspects affect other associated pre-depositional trace fossils, such as the graphoglyptids *Helminthorhaphe* or *Megagrapton*. Other associated post-depositional trace fossils, for example *Halopoa* and *Ophiomorpha* (see Table 1), have been produced later than *Estrellichnus*.

AQ11

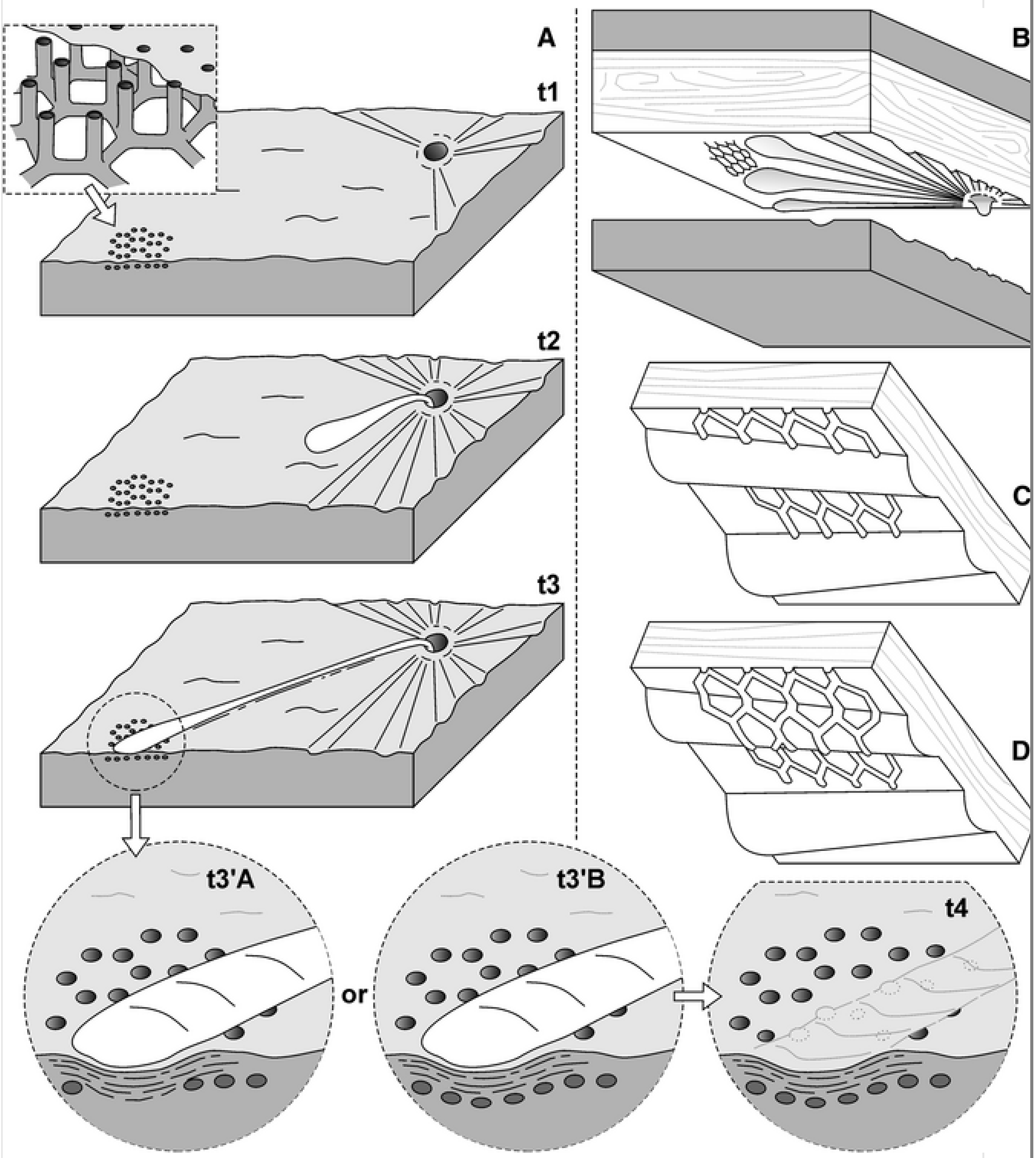

Fig. 10 Diagram showing the taphonomic and constructional aspects of *Estrellichnus*. A, Time lapse (t1, t2 and t3) of the proboscis emerging from the central burrow and incidentally affecting a previous *Paleodictyon* burrow system; t3'A and t3'B represent how the proboscis can affect this *Paleodictyon* burrow system, removing or deforming it,

respectively; t4 represents the resulting trace (e.g. t3'B) after the retraction of the proboscis. B, Stratigraphical sketch showing the common preservation way (hypichnial semi-relief) of the ichnogenus *Estrellichnus*. C, Fossil equivalent of t3'A. D, Fossil equivalent of t3'B.

In relation to the previously exposed, Rona *et al*. (2009) documented modern lebensspuren from the axial valley of the Mid-Atlantic Ridge (water depth 3430–3575 m) that are identical to those belonging to *Paleodictyon nodosum*; the authors described the presence of a shield- or dome-shaped elevation in the most superficial part of these structures. Such elevation, assuming that all *Paleodictyon* ichnospecies had it, would provide a few extra millimetres of sediment that could also promote the partial preservation of the overall burrow system by cushioning the proboscis of the *Estrellichnus* producer during its superimposition.

Some of the *Estrellichnus* specimens exhibit a slight winding of the ridges (Figs 3A, 4C, 6B). This curvature, in the plane of bedding, could point out a slight current that affected and bended the extended proboscis of the producer; the orientation of this winding, always towards the same direction, would support this idea.

Palaeoenvironmental significance

Estrellichnus has been identified in two localities of the Eocene Hecho Group (Huesca, NE Spain), in both cases in turbidite deposits (see the previous sections). Uchman (2001) and Heard & Pickering (2008) carried out the most detailed ichnological studies of the Hecho Group. In particular, Uchman (2001; see also Uchman & Wetzel 2001) interpreted the *Estrellichnus*-bearing deposits from the type-locality as lobe deposits characterized by a ichnoassemblage typical of the *Ophiomorpha rudis* ichnosubfacies within the archetypal deep-sea *Nereites* ichnofacies, the accompanying ichnotaxa being *O. rudis*, *O. annulata*, *Planolites beverleyensis*, *S. plana*, *Helminthorhaphe flexuosa*, *Urohelminthoida appendiculata*, *Megagrapton irregulare*, *M. submontanum* and *P. strozzii*. Following the palaeogeographical interpretations of the Aínsa and Jaca basins proposed by Heard & Pickering (2008), the new locality of Fiscal would also correspond to lobe environments; however, the area of Fiscal was not specifically studied by these authors. For Heard & Pickering (2008), the lobes of the distal Jaca Basin exhibit an assemblage that is more typical of the *Paleodictyon* ichnosubfacies (*sensu* Seilacher 1974), with some trace fossils which are more typical of the *O. rudis* ichnosubfacies (*sensu* Uchman 2001, 2009). Indeed, the ichnoassemblage associated with *Estrellichnus* in the new locality (i.e. the Fiscal quarry), with diverse graphoglyptids (*Paleodictyon, Helminthorhaphe, Megagrapton, Chondrorhaphe, Lorenzinia*; Table 1), fits well to that description of Heard & Pickering (2008). In summary, the ichnoassemblage described herein and in the type-locality of *Estrellichnus* is very similar. Nevertheless, proximal parts of at least some lobes in the region, dominated by thick-bedded sandstones, show the *O. rudis* ichnosubfacies.
AQ12

Modern echiurids are marine and benthic organisms, found from the intertidal zone to more than 10,000 m depth (Risk 1973; Brusca *et al*. 2016; and references therein). While higher populations are characteristic of shelf depths, an increase in the number of echiurid species has been observed in the transition from bathyal to hadal or ultra-abyssal environments (see

Risk (1973) and references therein). At the Cape Verde Abyssal Plain (around 4600 m deep), Bett *et al*. (1995) observed a density of 'spoke burrows' of 870 specimens per hectare (10 specimens/100 m^2) with an estimated density of some tens of producers (most likely echiurids) per hectare; these data are relatively higher than those observed in the quarry of Fiscal (ca. one *Estrellichnus* per each 100 m^2).

In any case, the time lapse between the deposits of the successive turbidites had to be enough long to allow fully developed of *Estrellichnus*, that is to generate complete radial structures (360°) that in some cases can exhibit up to 70 spokes. Assuming echiurids as the most likely tracemakers of *Estrellichnus*, it would imply enough time to protrude and retract the proboscis more than 70 times from the same burrow; neoichnological observations have shown that this kind of feeding behaviour could last minutes to even days (e.g. Chuang 1962; Bett & Rice 1993; Hughes *et al*. 1993). It is not excluded that the same spokes were used several times.

Conclusions

A new locality of the ichnospecies *E. jacaensis* is presented herein, also from the Eocene Hecho Group (Huesca, NE Spain), stratigraphically below the type-locality and located 35 km southeast of it.

The taphonomic features of the new specimens studied herein together with their interactions with other ichnotaxa allow reinterpreting the overall architecture of *Estrellichnus* and discard its adscription to graphoglyptids.

Through more detailed palaeobiological and palaeoethological analyses, together with a deep review of comparable lebensspuren, echiurid worms are presented as the most likely tracemakers of *Estrellichnus*. Today, these organisms exhibit a shallow-to-middle tier deposit feeding behaviour that results in a central burrow from which radiate several surface traces (fodinichnia). With respect to the fossil record, only future occurrences and further study will promote a better understanding of this ichnotaxon such as the discovery of the currently unknown sub-surface architecture of *Estrellichnus*.

AQ13
AQ14

The new locality of *Estrellichnus* described herein (i.e. the Fiscal quarry) mainly corresponds to lobe facies; the observed ichnoassemblage is ascribed to the *Paleodictyon* ichnosubfacies, with some presence of the elements of the *O. rudis* ichnosubfacies.

Most of new specimens are urban fossils. They provided a huge amount of data. This confirms their importance as an additional and easily accessible resource to get a better understanding of the palaeontological record.

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