

2022

## Biofilm Harvesters in Coastal Settings of the Early Palaeozoic

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### Original Publication Citation

Noffke, N., Mángano, M. G., & Buatois, L. A. (2022). Biofilm harvesters in coastal settings of the early Palaeozoic. *Lethaia*, 55(1), 1-18. <https://doi.org/10.1111/let.12453>

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# Biofilm harvesters in coastal settings of the early Palaeozoic

NORA NOFFKE , M. GABRIELA MÁNGANO  AND LUIS A. BUATOIS 

## LETHAIA



The ichnogenera *Syringomorpha* and *Daedalus* are here interpreted as products of infaunal biofilm harvesters. This study investigated: (1) *Syringomorpha nilssoni* and *Syringomorpha* isp. from the Cambrian Series 2-Miaolingian Campanario Formation, northwest Argentina; and (2) *Daedalus halli* from the Floian Grès et Schistes de la Cluse de l'Orb Formation, Montagne Noire, France. *Syringomorpha nilssoni* occurs in sandy to mixed intertidal to lower shoreface deposits, whereas *Syringomorpha* isp. in the lower intertidal zone. *Daedalus halli* occurs in a lagoon and intertidal to lower shoreface sands of a barrier island. *Syringomorpha* and *Daedalus* comprise a vertical J-shaped causative burrow and deep spreite. These ichnotaxa form monospecific assemblages (bioturbation index BI = 3–5) in quartzose medium- to fine-grained sandstone, recording colonization in high-energy tide- and wave-dominated settings. Lower abundances (BI = 1–2) are observed in silty sandstone. The abundance of both ichnogenera in mature sandstone is inconsistent with a classic deposit-feeding strategy because ‘clean’ sediments are commonly impoverished of organic detritus, this being particularly true in Cambro-Ordovician littoral settings lacking terrestrial plant detritus. Based on morphology, host sediment properties and comparison with modern structures, such those produced on intertidal and shallow subtidal setting by *Arenicola marina* and *Paraonis fulgens*, it is suggested that the diet of *Syringomorpha* and *Daedalus* producers may have consisted of biofilms colonising sand grains, associated eukaryotic microbes, and possibly meiofauna. Whereas *Syringomorpha* is a product of the Cambrian explosion, *Daedalus* is associated with the Ordovician Radiation. In contrast to most ichnotaxa, which display long temporal ranges, these two ichnogenera are restricted to the Cambrian and Ordovician-Silurian, respectively. The underlying reasons for the relatively restricted stratigraphic ranges of these ichnotaxa are unclear, but space competition, and increased predation pressure may have played a role. The feeding strategy of the *Daedalus* and *Syringomorpha* producers was less efficient than suspension feeding and passive predation, trophic types epitomized by the dominant macroinfauna that persisted in water-agitated nearshore sands during the rest of the Phanerozoic. □ Biofilm harvesters, Cambrian explosion, meiofaunal hunters, Ordovician Radiation, trace fossils.

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Ediacaran shallow-marine bottoms were characterized by widespread sediment-stabilizing microbial mats (Seilacher & Pflüger 1994; Seilacher 1999; Gehling & Droser 2009). As an adaptation to these stabilized substrates, Ediacaran organisms may have developed a variety of feeding strategies and benthic lifestyles, including mat encrusters, mat stickers, mat scratchers, mat grazers and undermat miners (Seilacher 1999; Buatois & Mángano 2012, 2016). During the early Cambrian, shallow-marine settings experienced ecosystem re-structuration from matground-related communities to a dominance of mixground-related, metazoan-dominated communities. This event is referred to as the ‘Agronomic Revolution’ (Seilacher & Pflüger 1994; Seilacher 1999; Mángano & Buatois 2017). Microbial mats were largely undisturbed by macroscopic life during the Precambrian, but they were forced to compete for space with

invading bottom dwellers during the terminal Ediacaran and the early Cambrian. If a microbial mat establishes within a few days, then most benthic organisms that rework the bottom sediment are being excluded from the mat-shielded areas; however, where the macrobenthos establishes before a microbial mat can develop, bioturbation precludes mat development, and only patchy ‘biofilms’ occur (Noffke 2010). Biofilms are initial stages of microbenthic colonization, visible only with a magnifying device. In modern sediments, biofilms look like organic envelopes surrounding mineral grains. The organic envelopes include prokaryotes, single-celled eukaryotes, such as diatoms, as well as fungi and other components. Many of these micro-organisms secrete mucilages, called extracellular polymeric substances (EPS), which are adhesive ‘slimes’ assisting the attachment of the biofilm to firm surfaces.

At suitable locations, biofilms can thicken and eventually coalesce to form large-scale microbial mats. Complex biofilms and microbial mats were formed by prokaryota already in the early Archean 3.48 Ga ago, constituting some of the oldest fossils in the rock record (Noffke et al. 2013).

During the Ediacaran-Cambrian transition, newly evolved macrobenthos exploited microbial mats and biofilms as food source (Seilacher 1999). Good examples are the classic Cambrian ichnotaxa *Oldhamia* and *Climactichnites* (Seilacher 1999; Seilacher-Drexler & Seilacher 1999; Buatois & Mángano 2012, 2012; Seilacher et al. 2005; Getty & Hagadorn 2009; Herbolch & Verniers 2011). Meiofaunal components may have also contributed to the producers' diet, as biofilms work as attractors to small metazoans, including both larval stages of macrofauna (i.e. facultative meiofauna) and obligate meiofauna. The rich Cambrian-Ordovician trace-fossil record reveals that benthic organisms displaying a wide variety of modern feeding strategies and ethologies were well established (Osgood 1970; Fillion & Pickerill 1990; Orłowski & Żylińska 1996; Jensen 1997, 2003; Seilacher 1999; Mángano & Buatois 2014, 2016, 2020; Buatois et al. 2016, 2020; Toom et al. 2019). However, various ichnotaxa, such as *Syringomorpha* and *Daedalus*, defy conventional ethological interpretations, the mode of life of their producers and preferred food resources being poorly understood. The objective of this paper is to explore the interpretation of two iconic early Palaeozoic ichnogenera, *Daedalus* and *Syringomorpha*, as possible biofilm harvesters, feeding on microbes and possibly meiofauna. Both ichnogenera have been included within the category of burrows with complex vertically oriented spreiten (Buatois et al. 2017). Our hypothesis is based primarily on morphology of the structure, inferred properties of the hosting sediment and comparisons with modern biogenic structures.

## Geological setting

### *The lower to middle Cambrian Mesón Group of northwest Argentina*

Specimens of *Syringomorpha nilssoni* and *Syringomorpha* isp. are present in Cambrian Series 2-Miaolingian strata exposed in various areas of northwest Argentina (Fig. 1A); these include Quebrada de Humahuaca (Angosto del Morro de Chucalezna, Angosto de Perchel, Tilcara and Cordon de Alfarcito) in the Jujuy Province and Cuesta de la Pedrera and Cerro Gólgota in Salta Province (Mángano & Buatois 2004). *Syringomorpha nilssoni* is present in lower intertidal

sand flat, middle intertidal mixed flat and lower shoreface deposits, whereas *Syringomorpha* isp. is restricted to the lower intertidal sand flat. These deposits accumulated in the Lower Palaeozoic Basin of Northwest Argentina that developed along the margin of Western Gondwana. The strata are included in the Mesón Group, which is divided, from base to top, into the Lizoite, Campanario and Chalhualmayoc formations (Turner 1960, 1963). The specimens studied occur in the Campanario Formation, which consists of planar cross-bedded and ripple cross-laminated medium- to fine-grained sandstone, thinly interbedded fine- to very fine-grained sandstone and mudstone and red mudstone (Fig. 2). Locally, hummocky cross-stratified, very fine-grained sandstone is present. Wrinkle structures are patchily preserved on rippled-top deposits formed in the most protected areas of the tidal flats recorded in the Campanario Formation of Argentina, suggesting the local presence of microbial mats.

### *The Floian (lower Arenigian) of the Montagne Noire, France*

The specimens of *D. halli* studied occur in Floian (lower Arenigian) outcrops exposed along the river Orb, close to the village of Roquebrun, in the southern Montagne Noire, France (Fig. 1B). These strata are part of the Synforme du Roquebrun, which tectonically constitutes the front of the Mt Peyroux Nappe. The Mt Peyroux Nappe builds up the southern part of the Massif Central, forming the Montagne Noire. From base to top, the Floian strata include five lithostratigraphic units, encompassing deposition in a variety of shallow-marine clastic settings of a cold-temperate climate zone: the Schistes et Grès de la Maurérie, formed in shelf environments below the storm-wave base; the Schistes du Setso recording a shallow coastal embayment; the Grès et Schistes de la Cluse de l'Orb, which include shelf, shoreface, foreshore, barrier islands, tidal flat and lagoonal deposits; the Foulon Formation, formed in shelf to offshore environments, the latter above the storm wave base; and the Landeyran Formation, which represents shelf settings below storm wave base (Courtessole et al. 1981, 1985; Noffke & Nitsch 1994). *Daedalus halli* is present in the Grès et Schistes de la Cluse de l'Orb, which consists of quartzose sandstone, siltstone and mudstone (Fig. 3). More specifically, this ichnotaxon occurs in fine-grained quartzose sandstone and silty sandstone formed in the lower shoreface of a barrier island, lower intertidal sand flat and lagoon. Widespread endobenthic and epibenthic microbial mats were abundant in this ancient marine environment, except in the highest energy settings (Noffke 2000).

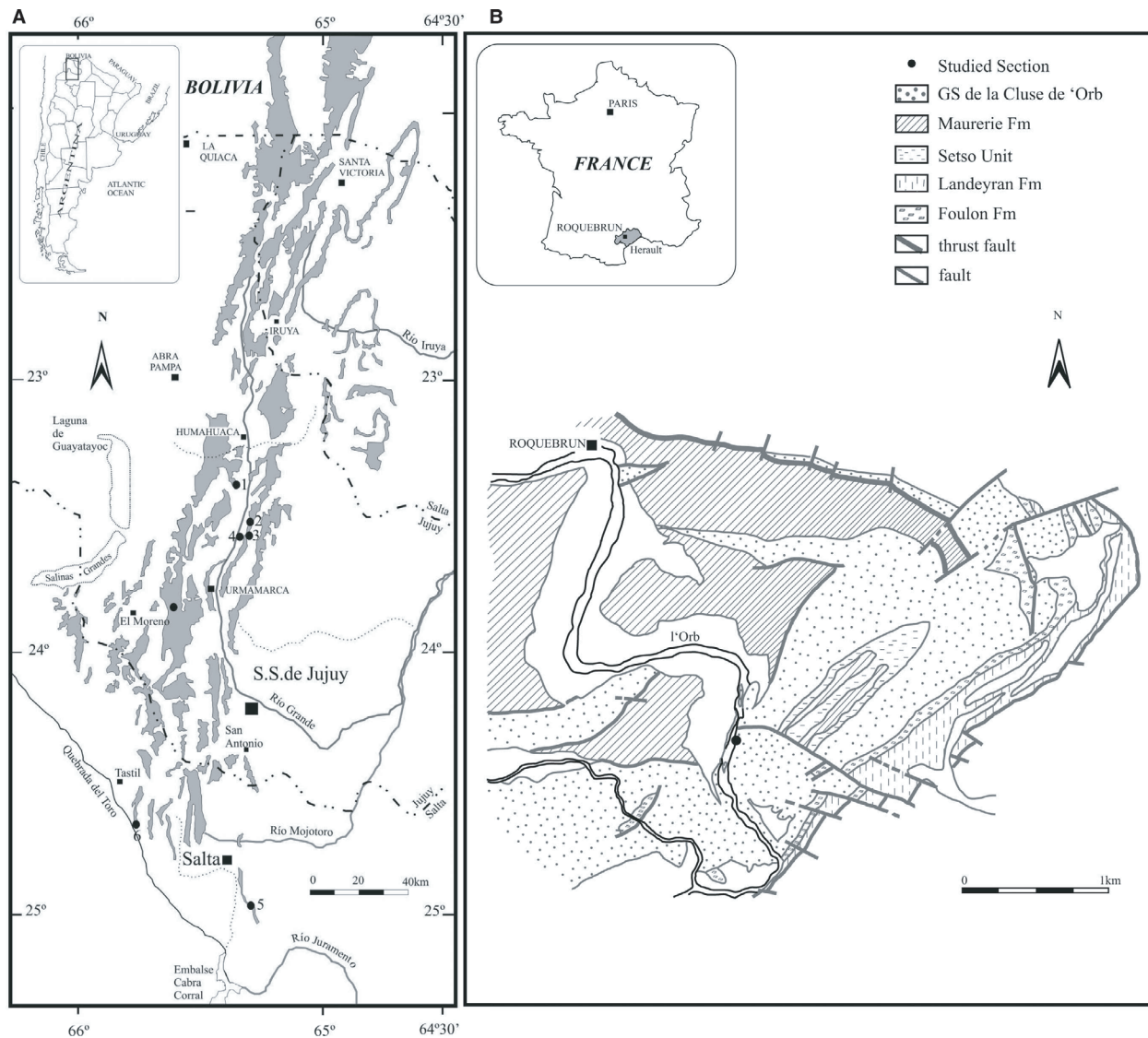


Fig. 1. Location maps of the studied field areas. A, regional distribution of outcrops of the Mesón Group in northwest Argentina (after Sánchez & Salfity 1999) showing position of the localities mentioned in the text. 1, Angosto del Morro de Chucalezna. 2, Angosto de Perchel. 3, Cordon de Alfarcito. 4, Tilcara. 5, Cuesta de la Pedrera. 6, Cerro Gólgota. B, location of the Floian succession in the Montagne Noire, France. The Grès et Schistes de la Cluse de 'Orb crop out along the river Orb and in abundant road cuts south of the village Roquebrun.

## Morphology and palaeoenvironmental distribution of *Syringomorpha nilssoni* and *Syringomorpha* isp

*Syringomorpha nilssoni* consists of a simple spreite formed by a single, J-shaped causative burrow (Fig. 4B–J), whereas *Syringomorpha* isp. comprises structure, J-shaped causative displaying a more complex morphology resulting in elongated, straight to curved structures on horizontal view (Fig. 5A, G) (Mángano & Buatois 2004). On bedding planes, the

spreite of *S. nilssoni* is seen as cm-scale short and straight segments, rarely crossing each other, whereas in *Syringomorpha* isp. the spreite is seen as relatively long straight to curved segments, trying to form semi-circles on bedding plane view. In *Syringomorpha* isp., overlap among spreiten of different individual structures is common. The causative burrow is 1.0–2.0 mm wide, whereas the horizontal expression of the spreite (observed on bedding-plane view) is 2.5–10 cm wide. The burrow is 10–30 cm deep. The infill of the structure is similar to the host rock, although an iron-oxide patina outlines the spreite, suggesting a mucus-lined structure.



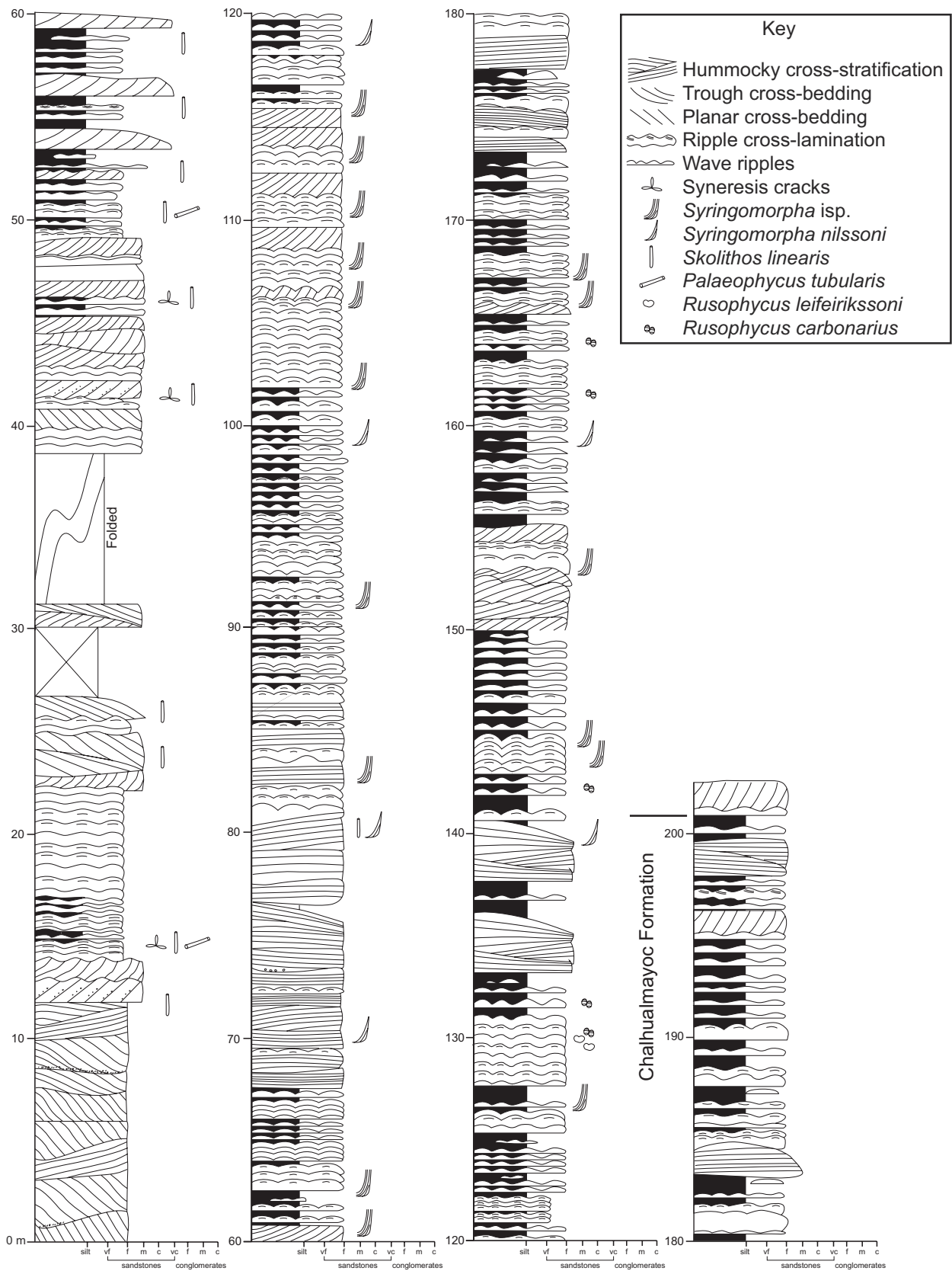


Fig. 2. Sedimentological log showing distribution of *Syringomorpha nilssoni*, *Syringomorpha* isp. and associated ichnotaxa in the Angosto del Morro de Chucalezna section.

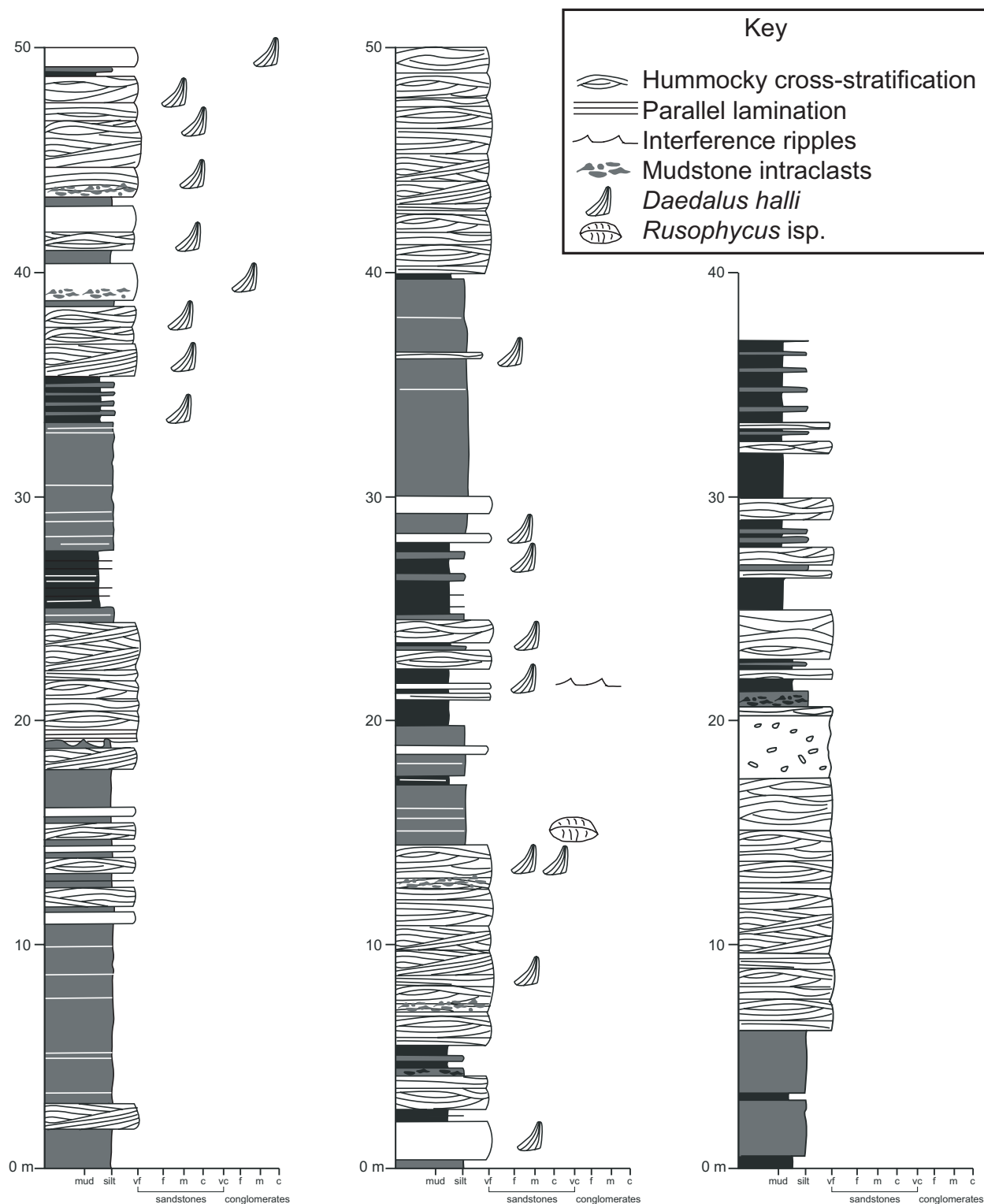


Fig. 3. Sedimentological log showing distribution of *Daedalus halli* and associated ichnotaxa in the Grès et Schistes de la Cluse de l'Orb section.

*Syringomorpha nilssoni* and *Syringomorpha* isp. occur in current-ripple cross-laminated and flaser-bedded, thin- to medium-bedded, medium- to very fine-grained quartzose sandstone formed in lower

intertidal sand flats (Table 1). *Syringomorpha nilssoni* is also present in current-ripple cross-laminated and wavy-bedded, very thin- to thin-bedded, fine- to very fine-grained sandstone formed in middle intertidal

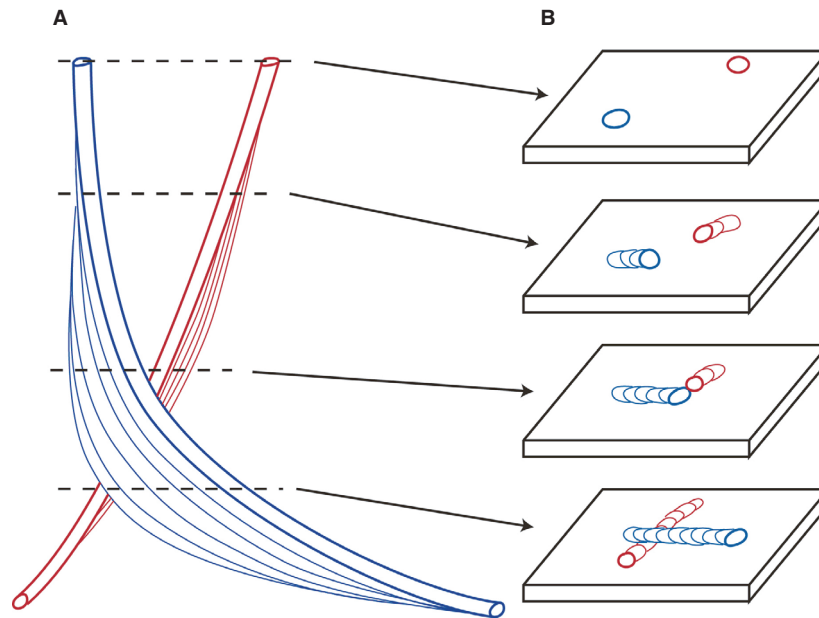


Fig. 4. Idealized three-dimensional reconstruction of *Syringomorpha nilssoni* (based on Seilacher 2007). A, vertical cross-sectional view showing cross-cutting of two individual specimens (see Fig. 5F, for intersection with slightly different angle in vertical cross-section). B, bedding plane and internal horizontal views illustrating causative burrow and spreite as sliced at different stratigraphic levels (see Fig. 5H). Multiple colonization surfaces result in the expression on the bedding plane of both the spreite and the causative burrow cross-cutting each other as seen in Figure 5J.

mixed flats and in hummocky cross-stratified, thick-to thin-bedded, very fine-grained sandstone formed in a transgressive lower shoreface (Mángano & Buatois 2004). No significant variation in burrow size is apparent in the different deposits. In the case of tide-dominated deposits, *S. nilssoni* and *Syringomorpha* isp. are present towards the base of fining-upward successions that are interpreted as tidal flat parasequences (Mángano & Buatois 2004). Sand flat assemblages tend to display the highest density of burrows. Degree of bioturbation in cross-section due to disturbance by *S. nilssoni* and *Syringomorpha* isp. is moderate to high (Bioturbation Index BI 3–5; index scales from Reineck 1963 and Taylor & Goldring 1993), in places mimicking piperock (Fig. 5 A). Density on bedding surface is up to approximately 400 individuals per m<sup>2</sup>. Most dense occurrences form composite ichnofabrics recording multiple colonization events resulting in palimpsest surfaces (Mángano & Buatois 2004; their Fig. 6). In the mixed flat deposits, *S. nilssoni* is rare (Mángano & Buatois 2004).

In the lower shoreface deposits, *S. nilssoni* occurs as monospecific suites in moderate to low densities, recording opportunistic colonization after storms. Degree of bioturbation in cross-section due to disturbance by *S. nilssoni* is low (BI 0–1). In these deposits, the *S. nilssoni* morphology is fully developed (i.e. without uppermost truncation) with causative burrows extending from the top of the tempestite and

forming a wide vertical spreite towards the lower part of the hummocky cross-division of the storm bed. Lower shoreface occurrences correspond to simple ichnofabrics representing a single bioturbation event following storm sedimentation (Mángano & Buatois 2004; their Fig. 6). In both, intertidal and shoreface examples, *Syringomorpha* is associated with moderate-to high-energy conditions due to tidal currents and waves, respectively.

## Morphology and palaeoenvironmental distribution of *Daedalus halli*

*Daedalus halli* in the Grès et Schistes de la Cluse de l'Orb consists of a steep, almost vertical spreite forming an inverted cone caused by a very slightly bended causative burrow oriented perpendicular to bedding (Noffke 1992; Noffke & Nitsch 1994; Seilacher 2000) (Figs 6, 7A–E). Distinctly cone-shaped examples have aperture angles ranging between 5° and 20°. Commonly, the top of the burrow is truncated by erosion (amalgamation). No indication of upward or downward displacement of sediment is apparent. Some well-preserved *D. halli* specimens show ring-like annulations in lateral view. On tops of mature, quartz-rich sandstone beds, the horizontal section of the spreite is visible (Fig. 7C). These



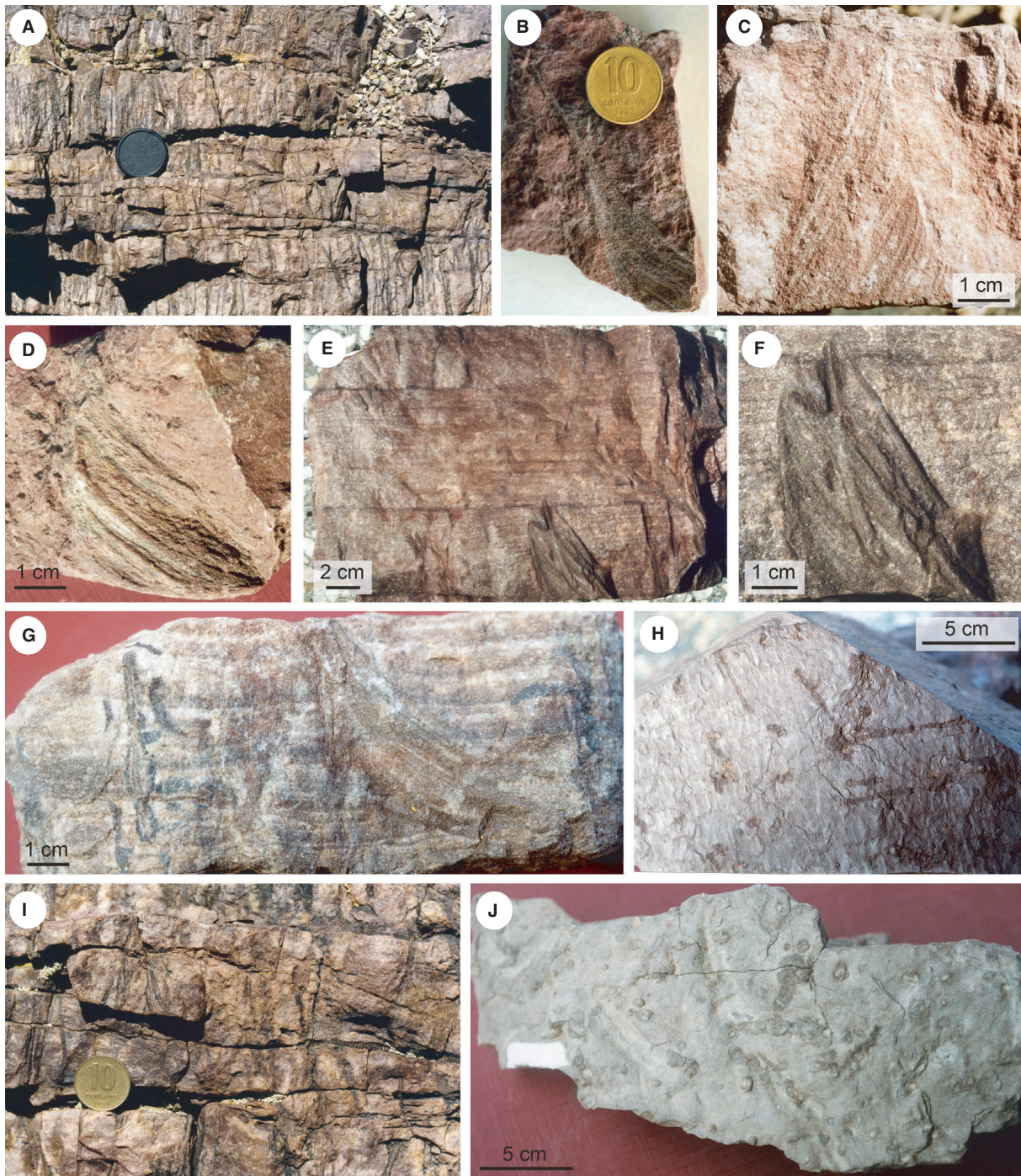


Fig. 5. *Syringomorpha nilssoni* and *Syringomorpha* isp., Campanario Formation, northwest Argentina. A, general view of intensely bioturbated sand flat deposits containing a high-density occurrence of *Syringomorpha* isp. Angosto del Morro de Chucalezna. Lens cap diameter = 5.5 cm. B, *Syringomorpha nilssoni* showing the typical causative burrow and spreite (see Fig. 4, blue specimen on the left). Cuesta de la Pedrera. Coin diameter = 1.8 cm. C, *Syringomorpha nilssoni* in sand flat sandstone. Spreite displays a slightly curved morphology generating a more three-dimensional form. Tilcara. D, *Syringomorpha nilssoni* in sand flat sandstone. Cordón de Alfarcito. E, low-density assemblage of *S. nilssoni* in amalgamated sandstone tempestites. The colonization surface is not visible, but these deep forms are clearly cross-cutting multiple beds. Angosto del Morro de Chucalezna. F, close-up of specimen in E. G, general view of a weathered outcrop displaying a moderate-density assemblage of *S. nilssoni*. Iron oxide differentially highlights causative burrows, spreite being only locally visible. Cerro Gólgota. H, bedding-plane view showing the horizontal expression of the *Syringomorpha* spreite in sand flat deposits. Note that more than one population representing different colonization surfaces are herein recorded. Angosto de Perchel. I, highly bioturbated sand flat deposits with *Syringomorpha* isp. Iron oxides differentially highlight some causative burrows, spreite being only locally visible. Angosto del Morro de Chucalezna. Coin diameter = 1.8 cm. J, bedding plane view displaying a palimpsest surface recording the horizontal expression of causative burrows and the spreiten of successive populations of *Syringomorpha* isp. in sand flat deposits. Angosto de Perchel.



Table 1. Summary of the main features of the occurrences of *Syringomorpha nilssoni* and *Syringomorpha* isp. in the studied deposits.

Subenvironment	Facies characteristics	Bioturbation Index (BI)	Density on bedding surface	Burrow size
Middle intertidal mixed flat (only <i>Syringomorpha nilssoni</i> present)	Light pink, laterally extensive, very thin- to thin-bedded, fine- to very fine-grained sandstone and red siltstone. Sand/mud ratio about 1:1. Ripple cross-lamination and wavy-bedding dominant. Subordinate flaser bedding. Variably shaped syneresis cracks. Soft-sediment deformation structures (e.g. load casts, ball and pillow). Bed tops undulated, with either symmetric or asymmetric ripples. Locally, thin-bedded, erosively normally based, graded coarse- to very fine-grained sandstone with flat mud pebble clasts and symmetrical ripples	2–3	Up to approximately 50 individuals per m <sup>2</sup>	Causative burrow diameter 1–2 mm; horizontal width of spreite 2.5–4.0 cm; burrow depth 16–20 cm
Lower intertidal sand flat	Light green to red, either erosively, sharp or gradationally based, laterally extensive, thin- to medium-bedded, medium- to very fine-grained quartzose sandstone. Sand/mud ratio high (>1) to infinite (100% sand). Gutter and pot casts locally present. Ripple cross-lamination dominant. Flaser bedding and mudstone drapes common. Wavy bedding rare. Variably shaped syneresis cracks in mudstone drapes and sandstone tops. Bed tops undulatory, with asymmetric ripples. Ripple patches, wrinkle marks, interference ripples, and flat-topped ripples	3–5	Up to approximately 400 individuals per m <sup>2</sup>	Causative burrow diameter 1–2 mm; horizontal width of spreite 2.5–10 cm wide; burrow depth 16–30 cm
Transgressive shoreface (only <i>Syringomorpha nilssoni</i> present)	Light pink, erosively based, thin- to thick-bedded, fine- to very fine-grained sandstone. Individual beds either tabular at outcrop scale or pinching out laterally. Locally scours filled with mudstone clasts. Lower hummocky cross-stratified or parallel-laminated division passing upwards to ripple cross-laminated division. Symmetrical to near-symmetrical ripples. Thin mudstone partings or layers in thinner beds. Bed amalgamation common	0–2	Up to approximately 15 individuals per m <sup>2</sup>	Causative burrow diameter 1.5–2 mm; horizontal width of spreite 2.5–4.0 cm; burrow depth 10–20 cm

sections of the spreite appear as spirals of varying degrees of coiling. The visibility of the spreite on such bedding planes is enhanced due to slightly increased amount of goethite, representing weathered pyrite. No other difference in mineralogy and grain sizes between burrow and host sedimentary rock was observed. In a small percentage (ca. 5%) of specimen, the spiral width widens with increasing distance from the causative burrow (1–8 mm wide). A higher percentage of spirals (40–60% approximately) start from a vertical burrow indicating the eroded, uppermost part of the ichnofossil. Commonly, eroded specimens are recorded by subcircular depressions in bedding plane views (Fig. 7C). In basal bedding-plane views, spirals show both a left and a right direction of turning. The spiral shapes range from (rarely) almost straight or coily to double spirals showing opposite directions (Fig. 7D). Burrow depth is up to 100 cm (Fig. 7E). The infill of the structure is similar to the host sediment, suggesting passive infill. The degree of bioturbation is low to moderate (BI 1–4). There seems to be a correlation between sedimentary facies and density and size of *D. halli* (Table 2).

Amalgamated hummocky cross-stratified, very fine-grained sandstone beds, 20–120 cm thick, with 95% sand quartz composition, record the lower shoreface portion of a barrier island in a wave-dominated shallow-marine environment. In cross-section, *D. halli* shows a relatively high density (BI = 4). The tightly packed trace fossils likely record multiple re-colonization events triggered by frequent disturbances in this high-energy setting. In bedding plane view, specimen is overlapping to such degree that individual specimen is difficult to distinguish. However, in a few beds a trend towards equidistance is apparent. The horizontal widths of spreite are 7.8–37.4 cm, and burrow depths are 3–100 cm.

Micaceous, fine-grained quartz sandstone beds show interference ripple marks and flaser bedding, 5–10 cm thick, representing a lower intertidal sand flat. These deposits display a moderate amount of *D. halli* (BI = 3). One bed surface shows 172 individuals per m<sup>2</sup>. Here, the individual trace fossils are more or less equidistant, and no trend to clustering can be detected. There appears to be also no relation to any current direction. Rarely, the trace fossils touch each other, but cross-cutting or interpenetration is absent

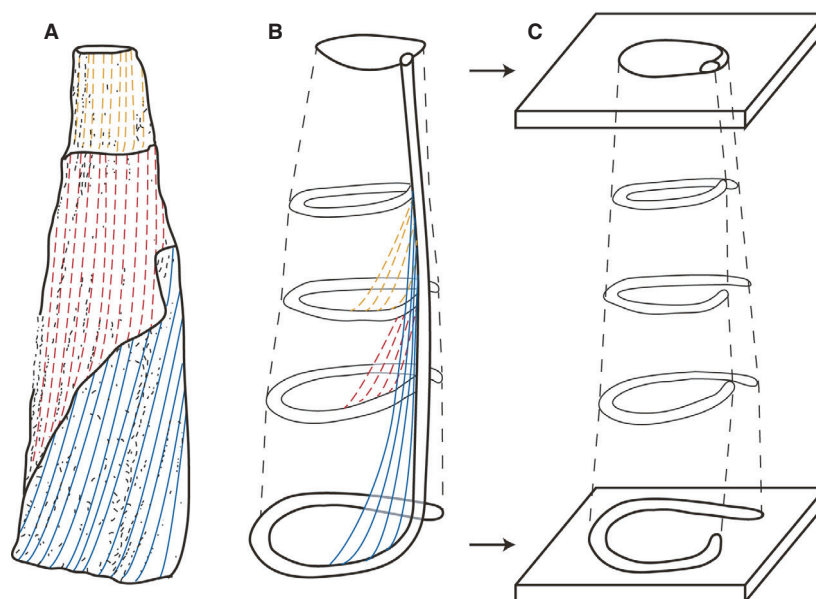


Fig. 6. Idealized three-dimensional reconstruction of *Daedalus halli* based on Seilacher (2000). A, cross-sectional view showing vertical development of spiral spreite (see Fig. 7A–C, E). B, constructional model of *Daedalus halli* (centre). Note protrusive J-shaped causative burrow responsible for the well-developed vertical spreite. C, different expressions of spreite on bedding plane or horizontal internal views (see Fig. 7D).

suggesting the work of one population. Causative burrow diameter is 2–5 mm; horizontal width of spreite is 1.9–7.6 cm; and burrow depth is 4.2–18.3 cm, specimens commonly crossed multiple beds.

Silty very fine-grained sandstone beds, 3–15 cm thick, were formed in a lagoon that appears to have been at least temporarily connected to the ocean (Noffke & Nitsch 1994). These silty sandstones display lower burrow densities (13–56 specimens per m<sup>2</sup>). Causative burrow diameter is ca. 1 mm; horizontal width of spreite is 0.4–0.9 cm; and burrow depth is 1.0–2.1 cm. BI is 1–2. *Daedalus halli* is absent (BI = 0) in black mudstone interpreted as recording the anoxic, deeper sediments of an still water lagoon, probably formed when the connection to the ocean was severed (Noffke & Nitsch 1994).

In conclusion, there is a positive correlation between grain size, trace fossil density and trace fossil size. The distribution patterns show that the producer of *D. halli* clearly preferred sandy substrates and avoided muddy, oxygen-depleted deposits.

## Discussion

### *Palaeoenvironmental distribution and potential controlling factors*

The palaeoenvironmental distribution patterns displayed by the trace fossils studied may allow more specific palaeoecological interpretations. Both

*Syringomorpha* and *Daedalus* tend to occupy near-shore, moderate to high-energy settings conducive to the establishment of the so-called high-oxygenated window *sensu* Pemberton *et al.* (2001) or subtidal pump *sensu* Riedl *et al.* (1972). This has been noted not only in the studied sections but elsewhere, in facies hosting *Daedalus* (e.g. Neto de Carvalho *et al.* 2016). Sediments in these settings are characterized by high water percolation. With *D. halli*, this is particularly evident in the case of the significantly larger specimens, whose producers seem to have preferred clean and well-oxygenated, porous substrates. In contrast, smaller specimens occur in finer-grained deposits in relatively quieter water, lower-energy settings. Three potential hypotheses may be suggested to explain this trend. First, similar trends in size have been observed in the modern polychaete *Arenicola marina* in connection with different ontogenetic stages (Newell 1948; Farke *et al.* 1979). Juvenile *A. marina* are present in silty to fine-grained sandy deposits in lagoonal areas of less hydrodynamic disturbance, whereas the adult population occupies outer, higher-energy areas of the tidal flats and the subtidal zones comprising fine- to medium-grained sands (Longbottom 1970; Farke *et al.* 1979). It may be argued that the similar distribution pattern of *D. halli* with smaller specimens in lower-energy deposits of an ancient lagoon and tidal flats and larger specimen in higher-energy deposits of the shoreface zone of the barrier island can also be explained by different ontogenetic stages (i.e. juveniles and adults)



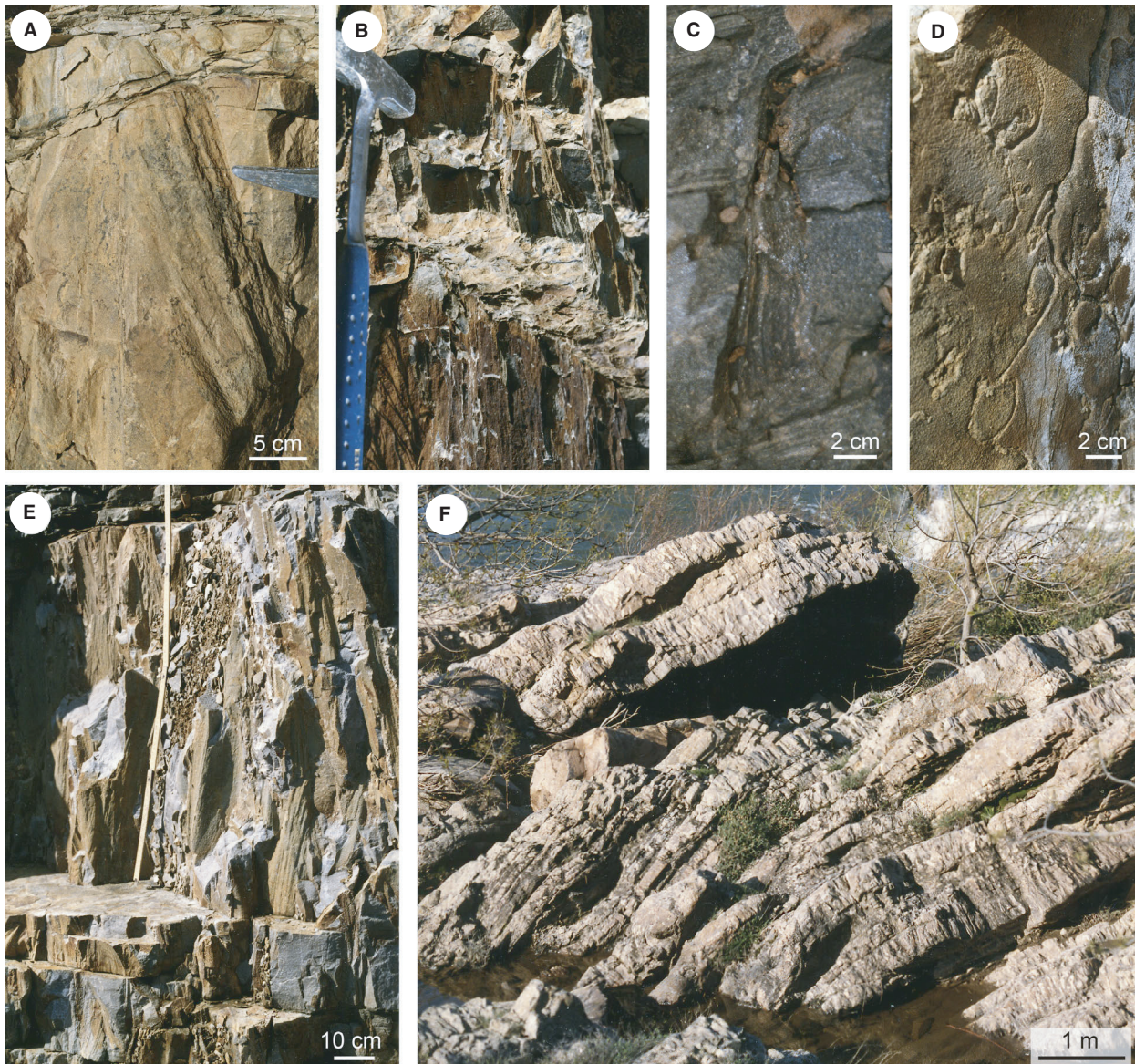


Fig. 7. *Daedalus halli*, Grès et Schistes de la Cluse de l'Orb, France. A, vertical view of spreite of a *D. halli* specimen. Commonly the inverted cone morphology is evident in well-preserved specimens. B, cross-sectional view of a high-density assemblage of *D. halli*. Note bedding plane views revealing subcircular depressions recording weathered uppermost incomplete specimens. C, specimen showing uppermost part of the structure connected to spreite. Width of hammer = 1 cm. D, spiral-shaped and double-spiral-shaped structures representing horizontal expressions of individual *D. halli* spreite. E, highly bioturbated quartz sandstone; individual *D. halli* specimen not recognizable. Burrow depths reach almost 100 cm. F, sparsely to highly bioturbated succession in the Grès et Schistes de la Cluse de l'Orb.

living in different substrates. Lower-energy sites may have provided appropriate conditions for larva recruitment and growth (Woodin 1991). This fits with the scenario of tidal flats as 'nurseries' (Reise 1985).

Second, size reduction may reflect decreased oxygenation, as trace fossils in oxygen-depleted environments tend to be smaller than their fully oxygenated counterparts (Savrda 2007). The silty very fine-grained sandstone containing small specimens of *D. halli* was formed in a lagoonal environment. This

restricted setting is characterized by relatively stagnant, oxygen-depleted waters negatively impacting on the distribution of benthic macrofauna. This scenario is consistent with the lack of trace fossils in the inter-bedded lagoonal black mudstone.

Third, small size may reflect increased stress linked to freshwater dilution of normal marine salinity in lagoonal areas. Restricted water bodies, such as lagoons and embayments, typically display reduced salinity in comparison with marine open waters. Size reduction is a common phenomenon in brackish-



Table 2. Summary of the main features of the occurrences of *Daedalus halli* in the studied deposits.

Subenvironment	Facies characteristics	Bioturbation Index (BI)	Density on bedding surface	Burrow size
Lower shoreface of a barrier island	Light grey, erosively based, thick-bedded, amalgamated, hummocky cross-stratified very fine-grained sandstone. Commonly, beds pinch out laterally. Some erosional bases may include rounded mudstone intraclasts. Shallow scours may occur, but are rare. Predominance (95%) of quartz	4	Individual specimen almost not distinguishable due to overlap	Causative burrow diameter 2–8 mm; horizontal width of spreite 7.8–37.4 cm; burrow depth 3–100 cm
Lower intertidal sand flat	Micaceous, thin- to medium-bedded, fine-grained quartz-arenite. Flaser bedding and interference ripple marks common, rare desiccation cracks	3	One bedding plane has 172 individuals per m <sup>2</sup>	Causative burrow diameter 2–5 mm; horizontal width of spreite 1.9–7.6 cm; burrow depth 4.2–18.3 cm
Lagoon, temporarily connected to ocean	Thin-bedded, silty fine-grained sandstone, quartz-rich with only low amount of mica	1–2	13–56 individuals per m <sup>2</sup> upper bedding planes	Causative burrow diameter ca. 1 mm; horizontal width of spreite 0.4–0.9 cm; burrow depth 1.0–2.1 cm

water trace-fossil assemblages (Pemberton & Wightman 1992).

In the case of *S. nilssoni* and *Syringomorpha* isp., no trend in burrow size in the different sedimentary facies is apparent. However, there is a clear increase in density of burrows from the mixed to the sand flat, also suggesting a clear preference for well-sorted, clean, sandy substrates affected by relatively intense tidal currents and waves. In addition to hydrodynamic energy and substrate, the lower intertidal sand flat is less subject to the stress factors associated with the more proximal positions in the intertidal area, such as longer periods of subaerial exposure and more extreme changes in temperature and salinity (Mángano *et al.* 2002; Mángano & Buatois 2004). *Syringomorpha nilssoni* is too rare in lower shoreface deposits to allow for further elaboration on trends, other than an obvious preference for high-energy, well-oxygenated, sandy settings.

### Food resource and feeding behaviour

The well-developed spreite displayed by the two ichnogenera is reminiscent of the feeding spreite of many stationary deposit feeders. However, it has long been noted that the dominance of both ichnogenera in well-sorted, and clean sandstone is inconsistent with a classic deposit feeding strategy because these sediments are commonly well oxygenated and depleted of organic detritus (Seilacher 2000; Mángano & Buatois 2004; Neto de Carvalho *et al.* 2016). Therefore, an alternative food resource must have been available to the producers.

The overall and fine morphology of the two ichnogenera and the sedimentological context suggest that their producers were most likely biofilm harvesters,

exploiting epigranular microbes and probably available associated meiofauna. Biofilms are major contributors to primary productivity and substrate stability in near-shore sands. A diverse community of microbes, in close association with meiofauna, are fundamental pillars of the food web in modern intertidal and shallow subtidal environments (Coull 1990; Carpentier *et al.* 2014). The meiofauna represents an operationally defined group of eukaryotic organisms that passes a sieve of 1 mm mesh sizes, but that are trapped by the microfauna sieve (typically 44 µm) (Giere 2009). Common modern examples include large foraminifers, ciliates, nematodes, copepods, ostracods, polychaetes and oligochaetes. The importance of meiofauna in ecosystem processes and functions, for example in provisioning food to higher trophic levels, is being increasingly recognized (Giere 2009; Schratzberger & Ingels 2018).

In high-energy sandy beaches, Malan & McLachlan (1985) found significant concentrations of meiofauna and bacteria occurring up to 60 cm deep. Contrary to the misconception of sandy, high-energy environments affected by waves and strong tides as barren and inhospitable habitats, these settings host rich microbe communities: the so-called micropsammion which includes autochthonous microbes (i.e. bacteria, fungi and protozoa) and allochthonous components (e.g. pathogens) (Whitman *et al.* 2014). High hydrodynamic conditions may result in erosion and transport of microbes attached to grains, but also in resuspension of benthic microbes in the water column and vertical transport (Whitman *et al.* 2014). Strong intra-sediment water percolation is an important factor to transport microbes through the different reservoirs within the sediment. In particular, biofilms on grains provide an optimal habitat space,

where microbes concentrate. Modern studies show that biofilms record the highest microbe diversity compared to any other sediment habitat spaces (Whitman *et al.* 2014). In fact, total abundance of bacteria associated with biofilms on sand grains is much greater than that in water-filled pore spaces by several orders of magnitudes (Gobet *et al.* 2012; Whitman *et al.* 2014). Moreover, Boehm *et al.* (2014) and McLachlan & Defeo (2017) showed that the bacteria cell counts for pore spaces increase dramatically after sediment was affected by groundwater or tidal flushing. Hence, it appears that disintegration of biofilms and mobilization of bacteria can be caused through water motion during high-energy hydrodynamic events. As a counterpart, microbes and particularly prokaryotes tend to migrate and form a biofilm when lower-energy conditions prevail. Microbes are commonly coupled to meiobenthic communities (Gerlach 1978; Malan & McLachlan 1985; Giere 2009; McLachlan & Defeo 2017). Meiofaunal grazers are attracted to bacterial concentrations and crop on them, and at the same time meiofauna excretes dissolved metabolites containing N and P fostering bacterial growth (Giere 2009). Meiofauna is commonly concentrated in the upper 10 cm of sediment, but in high-energy settings meiofauna seem to replicate increased microbial communities in well-oxygenated, clean sandy substrates reaching much deeper levels within the sediment (Malan & MacLachlan 1985; Giere 2009). Overall, the meiobenthos is directly or indirectly tightly coupled to bacteria (Giere 2009). The occurrence of meiobenthic metazoans preserved as small carbonaceous fossils in Cambrian sandstone has proved that meiofaunal elements were already diverse and a significant component of the benthic ecosystem since the early Phanerozoic (Harvey & Butterfield 2017). As in modern coastal ecosystems, microbe-rich biofilms attached to grains and enriched pockets of meiofauna must have constituted an abundant food provision for harvesting by the producers of *Syringomorpha* and *Daedalus*.

### Morphology and functional interpretation

The overall morphology of *Daedalus* and *Syringomorpha* suggests a producer with an elongated, cylindrical body. Although fine morphology has not been described for *Syringomorpha*, some exceptionally preserved specimens of *Daedalus* display ring-like annulations that have been related to a vermiform, most likely annelid producer (Seilacher 2000, 2007). How did the animal move through the sediment? Seilacher (2000) suggested that 'We must visualize a worm-like animal, whose body passed through the

sediment like a straight stick stirring the sand, with the upper end fixed to the surface' (Seilacher 2000, p. 249). Meanwhile this is a useful image to visualize the overall morphology of the structure, it may not accurately reflect their mode of construction. The presence of annulations imprinted on burrow lining indicates a segmented body and suggests a peristaltic burrowing mechanism in the producer. The fact that the causative burrow of *Daedalus* and *Syringomorpha* is essentially a blind, originally mucus-lined structure suggests that porewater bioadvection, in addition to the physical pumping, may have been involved in fertilizing and mobilizing prokaryote and eukaryote micro-organisms, potentially promoting the concentration of meiofauna associated with microbial communities. The anterior end of the producer may have pointed downward, as spreite expansion shows this is the active end (Noffke 1992). Although there is no modern producer that can account for these extinct behaviours, lessons can be learned from some modern inhabitants of the littoral area. In particular, *A. marina* provides some valuable clues in terms of the mode of life and feeding strategy.

*Arenicola* is an example of a head-down deposit feeder that ventilates and irrigates a blind burrow (Krüger 1971). Lugworms produce L- or J-shaped burrows, including a long vertical to horizontal component ('the gallery') and the uppermost short part of the vertical component ('tail shaft'), of which the inner wall is covered with mucilage (Wells 1945; Krüger 1971; Rijken 1979). They live at 10–40 cm deep, feeding on fresh detritus transported to depth at the blind end of the burrow due to their feeding activities (Wells 1945, 1966; Woodin 1985). From this blind end, a vertical, narrow column of reworked sand connects to the surface ('head shaft'). At the top of the sedimentary surface, the head shaft forms a small funnel in the sand ('feeding pit'). In this head shaft, no hollow tube, mucus lining or wall exists, but mobile sand grains and labile organics move advectively downward ('quick sand column'; Hüttel 1990) as result of the lugworm underneath feeding activity and ventilation. The water current is generated by peristaltic movement of the body and passes dorsally from the posterior to the anterior end, returning to the surface via the head shaft. Pumping reverses flow from head to tail during burrowing and defecation, the latter representing about 12% of the animal's time expenditure (Krüger 1969; Wetthey *et al.* 2008; Woodin & Wetthey 2009). The constantly pulsing water currents facilitate sand grain movement in the head shaft and transporting sand and labile detritus from the surface towards the mouth of the polychaete. In an opposite direction, ventilation enhances advective

supply of nutrients from the deeper sediment promoting primary productivity at shallow depth and on the sediment (Woodin *et al.* 2010; Chennu *et al.* 2015). The pumping activity of the segmented worm includes a 'wave' of thickening–thinning of the body that migrates dominantly from the posterior to the anterior during feeding maintenance (>60% of the animal's time budget; Woodin & Wetthey 2009). Interestingly, such peristalsis or pulsing body 'wave' pressing against the tube wall may well have been the cause for the ring-like annulations visible in some specimens of *D. halli*. The modern *A. marina* excretes the digested sand grains episodically by moving backward in the tail shaft towards the sedimentary surface and expelling elongated, worm-shaped sand accumulations (fecal casts) devoid of any organic matter.

Although sharing some basic morphologic traits (e.g. J-shaped burrow), *Syringomorpha* and *Daedalus* differ in significant ways from the modern structures produced by arenicolids. There is no feeding pit, neither there is any evidence of a fecal cast pile associated with these ichnotaxa. The absence of fecal cast piles formed at the sediment–water interface is not surprising, however, and could be explained as a simple taphonomic bias. High-energy, clean sandstones are associated with *Syringomorpha* and large *Daedalus* specimens, the uppermost part of these trace fossils being typically lost by erosion or amalgamation (i.e. upper end of the structures is typically not preserved). As it is the case with *Daedalus* and *Syringomorpha*, *Arenicola* burrows do not occur in muddy, low porosity, diffusive deposits, suggesting that as in the case of the modern polychaete, the feeding strategies of the ancient producers may have benefited from the higher porosity and permeability of the sediment and the bioadvective potential fuelling primary productivity (Chennu *et al.* 2015). Based on his detailed study of *Abarenicola pacifica* and *Abarenicola vagabunda*, Hylleberg (1975) proposed gardening as a feeding strategy for these arenicolids, here understood as the stimulation of bacterial growth as a way to enrich the sediment with digestible components to be subsequently used as food (Hylleberg 1975). Similar to *Arenicola* and other arenicolids in modern sediments, ancient producers may have enhanced nutrient supply resulting in higher productivity and increased microbial and meiofaunal content in sediments that were characterized by low standing stocks of organic matter. In this sense, *Syringomorpha* and *Daedalus* producers could have developed low-level farming strategies (Schultz *et al.* 2005; Hsieh *et al.* 2019) grading to ecosystem engineering in which physiologic or behavioural activities create the conditions for positive feedbacks and proliferation of food resources (Hsieh *et al.* 2019).

On the other hand, high-level farming, as understood based mostly on complex fungiculture behaviour in social insects, requires additional components (i.e. evidence of planting, defence and protection, fertilization and harvesting; Schultz *et al.* 2005; Hsieh *et al.* 2019), being only exceptionally found in the fossil record (Genise 2017). Moreover, whether or not such a strict definition of farming can be adopted in marine ichnology needs to be further explored.

The fact that the low-organic content sandy intertidal sediments of the Wadden Sea support dense populations of *A. marina* has triggered considerable discussion on food sources (Andresen & Kristensen 2002; Chennu *et al.* 2015). Recent experimental and field studies point to *A. marina* as a detritus feeder advecting organic particles and microphytoplankton from the sediment surface. Contrastingly, *Syringomorpha* and *Daedalus* producers most likely relied on intrastratal microbial and meiofaunal resources, as suggested by their deep, mucus-reinforced spreite edifice. In fact, the well-developed spreite and particularly the spiral architecture of *Daedalus* could be suggestive of a mucus trap, an attractor for microbes on grain and burrow surfaces, and concomitant meiofauna. This favours comparison with another modern polychaete structure created by *P. fulgens* in moderate- to high-energy tidal flats (Röder 1971; Bromley 1996). *Paraonis fulgens* creates a mucus-lined burrow system of interconnected horizontal spirals, one above the other (see Bromley 1996; his fig. 4.38), that were interpreted as traps capturing microorganisms and particularly diatoms during vertical migration, controlled by the tidal cycle (Röder 1971; Bromley 1996). Defying the rules of preservation, a *Paraonis*-like spiral structure has been recovered from Permian tidal flat deposits of the Robledo Mountains, south-western USA (Minter *et al.* 2006). However, the intrastratal *Paraonis*-trap model has been challenged based on actualistic observations in Willapa Bay that suggest a selective deposit feeding strategy (Lehane & Ekdale, 2013). Although the robustness of *Syringomorpha* and *Daedalus* contrasts with the delicate, ephemeral, stacked spirals created by *P. fulgens*, the vertical-curtain-like, slimy spreite can certainly be envisioned as a functional trap to mobilized protists, eukaryotic microbes and interstitial organisms in a world devoid of diatoms. However, high-resolution morphological evidence to support the trap hypothesis (e.g. revisitation) is not available.

Whether *Syringomorpha* and *Daedalus* were both biofilm harvesters and to which degree meiofaunal elements were part of the producers' diet is an open question (Neto de Carvalho *et al.* 2016). Reise & Ax (1979) showed that the sediment in the vertical head



shaft of *A. marina* is oxygenated to such extent that meiofauna occurs at higher densities than in the surrounding, non-mobilized deposits. In a comparable way, the sediments hosting *Syringomorpha* and *Daedalus* were well oxygenated via hydraulic and biological processes generating the right conditions for enriched interstitial biota. That said, stable isotope analysis indicates that at least *A. marina* appears to be selective in nutrition sourcing, being particularly dependent on microphytobenthos (Herman et al. 2000; Chennu et al. 2015). The polychaetes seem to avoid meiofauna, merely grazing on bacteria and single-celled eukaryotes accumulated in the pore space of the turbulently reworked sand inside the head shaft (Krüger 1971; Hüttel 1990). Perhaps a similar selective behaviour existed in the producers of *Syringomorpha* and *Daedalus*.

In modern nearshore areas, high-energy sands similar to the ones inhabited by the *Syringomorpha* and *Daedalus* producers, opheliid polychaetes such as *Euzonus furciferus* or *Euzonus mucronata* (producers of *Macaronichnus*) are thought to feed from biofilms around sand grains typically supplemented by dissolved and particulate organic matter as well as other micro-organisms (Kemp 1987; de Souza & Borzone 2007). Such 'deposit feeding' records an active vagile strategy that contrasts with the mostly stationary exploration model of *Syringomorpha* and *Daedalus* producers, most likely reflecting very different physiologies. The highly active *Macaronichnus* producer is able to generate a thoroughly bioturbated, mottled texture of the sediment that reflects combined locomotion and feeding (Pemberton et al. 2001; Seike 2009; Quiroz et al. 2010, 2019; Seike et al. 2015). In contrast, the overall morphology of the spreite in *Syringomorpha* and *Daedalus* is suggestive of domiciles with persistence for months and probably years, most likely recording long-term occupation. Other complex, well-known, spreite stationary burrows, such as *Zoophycos*, have been interpreted as whole-life microbial farming structures in more stable offshore to basin settings (Bromley 1990, 1996; Löwemark 2015). However, the distinct size range in *D. halli* with smaller size populations in more proximal deposits is suggestive of an animal able to abandon the structure, migrate and relocate into an adjacent littoral environment, a behaviour that has long been known in *A. marina* (Wells 1966). Moreover, it has also been suggested that *Syringomorpha* and *Daedalus* may represent opportunistic colonization after storms, which implies shorter persistence of weeks to months (Mángano & Buatois 2004; Neto de Carvalho & Baucon 2014; Neto de Carvalho et al. 2016).

### *The nearshore microbial gardens of the early Palaeozoic*

The Agronomic Revolution marks the global onset of pervasive vertical bioturbation strongly modifying substrate properties (Seilacher & Pflüger 1994; Seilacher 1999; Mángano & Buatois 2017). Early Palaeozoic nearshore sandy substrates include elaborate spreite structures that are hard to interpret using the paradigm of mining organic-rich resources in the sediment. The vertical spreite is best interpreted as recording feeding activities to exploit an intrasementary resource: bacteria-enriched biofilms on grains and newly evolved meiofaunal components. Whereas *Syringomorpha* seems to be a product of the Cambrian explosion, *Daedalus* is associated with the Ordovician Radiation (Buatois et al. 2016). Most ichnotaxa have long temporal ranges. In contrast, *Syringomorpha* and *Daedalus* are restricted to the Cambrian and Ordovician-Silurian, respectively. The recently introduced ichnospecies *Syringomorpha cyprensis* occurs in deep-marine settings (Miguez-Salas et al. 2019), and its functional and ichnotaxonomical affinities with Cambrian *Syringomorpha* remain uncertain. The highly restricted stratigraphic ranges of *Syringomorpha* and *Daedalus* are remarkably unusual for trace fossils and suggest that these ichnotaxa reflect extinct behaviours within the context of an anactulistic ecology. Most likely, this restriction may reflect a combination of the prevalent conditions of early Palaeozoic nearshore ecosystems typified by the absence of plant-derived organics, relatively low predation pressure, low competition and limited efficiency of macrofaunal grazers and deposit feeders.

*Syringomorpha*, together with other vertical burrows, such as *Skolithos*, *Arenicolites* and *Diplocraterion*, illustrates the colonization of relatively high-energy environments. Colonization of this type of settings took place during Cambrian Age 2 and became particularly widespread in Cambrian Ages 3–4 (Mángano & Buatois 2014). A significant increase in the intensity of bioturbation is also evidenced in low-energy fully marine environments during this time as well (Mazurek 2014; Gougeon et al. 2018). This was a time of profound changes in shallow-marine ecosystems, signalling the appearance of a Phanerozoic-style ecological structure characterized by multiple tiers and inferred complex ecological relationships. The vast majority of the infauna in nearshore, high-energy settings comprised passive predators and suspension feeders, which may have consumed significant amounts of seston (i.e. suspended particles) and filtered vast volumes of water (Mángano & Buatois 2014, 2017). The appearance of *Syringomorpha* may record a new use

of an old resource: biofilms. Ediacaran grazers and deposit feeders were vagile, inhabiting microbial mats and shallow levels within the sediment. Contrastingly, *Syringomorpha* is a stationary structure recording a novel strategy to exploit a new infaunal niche in high porosity and permeability sediments poor in organic matter. While *Syringomorpha* architecture and fine morphology illustrate the Agronomic Revolution, the producer's diet was most likely linked to biofilms and microbes, bridging Ediacaran and Phanerozoic ecologies.

Cambrian *Syringomorpha* has only been recorded from strata of Ages 2–4, whereas *Daedalus* range from the Floian to the Wenlock (Seilacher 2000; Jensen *et al.* 2013; Buatois *et al.* 2016; Neto de Carvalho *et al.* 2016). Accordingly, their stratigraphic ranges do not overlap. However, architectural similarities and environmental preferences suggest that both producers occupied a similar niche, perhaps representing convergent evolution or a phylogenetic relationship not revealed by trace-fossil evidence. In fact, *Syringomorpha* resembles *Daedalus*, but the spiral tendency of the latter is absent in *Syringomorpha*. The 3D spiral pattern in *Daedalus* design is considered a first-order ichnotaxobase, as it determines form and implies an additional element of complexity.

The causes for the disappearance of this mode of life and feeding strategy in younger strata are far from clear (Neto de Carvalho *et al.* 2016). However, competition with more actively moving infauna and evolution of diverse nektonic and benthonic predators provide plausible scenarios. While the diversity of nearshore, high-energy ichnofaunas has not increased significantly during the Palaeozoic, it is likely that the feeding strategy of a quasi-sessile organism slowly sweeping sediment grains was replaced by highly motile infaunal feeding strategies that allowed quick movement from one harvesting ground to the next and efficient predator avoidance (e.g. *Macaronichnus* producer strategy).

Although arthropod predators have been a signature of early Phanerozoic ecosystems with significant presence in shallow marine communities (Maas *et al.* 2004), Cambrian littoral environments have been envisioned as refuge environments based on ichnological evidence (Mángano & Buatois 2004). An increase in predation pressures took place during the mid-Palaeozoic as indicated by a radiation of marine predators, including placoderm and chondrichthyan fishes, and phyllocarid and eumalacostracan arthropods (Signor & Brett 1984; Brett & Walker 2002; Klug *et al.* 2010). Although this increase in predation pressures roughly coincides with the disappearance of *Daedalus*, it cannot be invoked to explain the

extinction of *Syringomorpha*. Most importantly, both ichnogenera record the activities of deep burrowers and the deep infaunal ecospace is typically considered as a refugium from predators (Vermeij 1987).

Regardless of the underlying cause for their disappearance, it seems that the mode of life employed by the *Daedalus* and *Syringomorpha* producers was not viable in the long term. Passive predators, suspension feeders and effective, vagile biofilm harvesters comprised the dominant macroinfauna that persisted in nearshore agitated sands during the rest of the Phanerozoic. In particular, vertical burrows, such as those that are in places associated with *Daedalus* and *Syringomorpha* (e.g. *Arenicolites*, *Diplocraterion*, *Skolithos*), were the ones that remained being common in water-agitated settings, becoming the typical elements of the archetypal *Skolithos* ichnofacies.

*Acknowledgments.* – The study on *Daedalus halli* in the Floian (lower Arenigian) of the Montagne Noire, France, was part of the diploma thesis by Noffke. Mángano and Buatois studied *Syringomorpha* in the Cambrian of northwest Argentina. We thank valuable comments by an anonymous reviewer and the editor. We dedicate this paper to Dolf Seilacher, with whom we have had memorable interactions. Financial support for this study was provided by Natural Sciences and Engineering Research Council (NSERC) Discovery Grants 311727-15/20 and 422931-20 awarded to Mángano and Buatois, respectively. The Tübinger Stipendienstiftung and the Deutsche Forschungsgemeinschaft (DFG) funded the study by Noffke. Mángano thanks additional funding by the George J. McLeod Enhancement Chair in Geology.

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