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Reply to: The Cabrières Biota is not a Konservat-Lagerstätte

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 Check for updates

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REPLYING TO L. A. Muir & J. P. Botting *Nature Ecology & Evolution* <https://doi.org/10.1038/s41559-024-02559-6> (2024)

The Cabrières Biota (France) is a new diverse fossil assemblage that provides insights into Ordovician polar ecosystems¹. This assemblage comprises fossils of algae, sponges, cnidarians, trilobites, non-biomineralized arthropods, molluscs, brachiopods, hyoliths, hemichordates, worms and lobopodians¹, as well as trace fossils. Muir and Botting² question whether the site is a Lagerstätte by reinterpreting sponges, algae, hemichordates, worms and cnidarians as trace fossils. Here we show that their arguments do not follow an evidence-based approach and the specifics of their trace fossil claims do not engage with the standard protocols for distinguishing between trace and body fossils. We provide comprehensive evidence that the Cabrières Biota is a diverse and exceptionally preserved fossil Lagerstätte including algae and animals, representing a high-latitude refugium during the warm Early Ordovician.

When new fossil sites are discovered, there is usually an initial publication that establishes the locality both stratigraphically and geographically and describes the main assemblage components, environment and mode of preservation. This is then followed over subsequent years, or even decades, with more detailed analyses of the environment and community, taxonomic monographs and taphonomic work. Our publication¹ showing evidence of non-mineralized fossil preservation in the Cabrières Biota represents the initial presentation of this faunal element; detailed follow-up work is in progress. This work takes time and, as always in science, the conclusions are constantly questioned and refined as newly collected evidence comes to light. Of course,

different scientists will have differing opinions, but these opinions must be evidentiary to contribute to the scientific discourse, and the reinterpretation of body fossils as trace fossils by Muir and Botting² is not backed by new evidence or observations. Here, problems with the structure of their main arguments are addressed, followed by a specific rebuttal against each of their trace fossil reinterpretations (summarized in Table 1).

Muir and Botting² acknowledge that reanalysis of fossil material and magnified views are critical for robust interpretation. When discussing the lobopodian specimens, they attribute their morphology to being an artefact that “is due to the differential hardness of the concretions and the surrounding sediment”. This, like other statements they make, would be testable should the authors examine magnified views or the fossil material housed at a public institution.

There are several instances of faulty logic presented in the Matters Arising². For example, in reinterpreting specimens of the cnidarian *Sphenothallus* as a trace fossil, they state that the specimen does “appear to be sediment filled and could therefore be reasonably interpreted as a burrow”. This is a false equivalence because being sediment filled does not indicate something is a trace fossil. Any fossil of appropriate shape (containing a chamber of some kind) could be sediment filled because all objects can be filled with sediments under appropriate burial conditions. It is inappropriate to imply that something is a diagnostic criterion when it is not exclusive or indicative of a single affinity.

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Table 1 | Table summarizing the arguments regarding the identification of fossils from the Cabrières Biota

Saleh et al. ¹ interpretation	Specimen number	Rationale or description	Original figures ¹	Muir and Botting ² identification	Muir and Botting ² arguments for different interpretations	Additional comments
Sponge	UCBL-FSL713601	Long monaxons suggesting possible leptomitid affinity	Fig. 1d and Extended Data Fig. 4	Sponge anchoring structure	Coarse isolated spicules without soft tissues	Muir and Botting ² agree on its sponge affinity but not on its exact position within sponges
Sponge	UCBL-FSL713604	Spiculate skeleton	Fig. 2a and Extended Data Fig. 6	Trace fossil (lined burrow containing pellets)	None given	Specimen shows an organized skeleton (Extended Data Fig. 6e) ¹ and lacks sharp outlines of purported lined burrow or faecal pellets ²⁸ ; sponge affinity is maintained
Sponge	UCBL-FSL713605	Presence of ostia with two types of organic material under multispectral imaging	Fig. 2b,c	Trace fossil (<i>Alcyonidiopsis</i>)	None given	An irregular 3D structure that could be confused with <i>Alcyonidiopsis</i> ; however, multispectral imaging shows two types of organic material indicative of a decaying carcass, probably a sponge
Sponge	UCBL-FSL713607	Characteristic leptomitid spicules	Extended Data Fig. 5	Trace fossil (lined burrow)	Organic lining and presence of sediment infill (refer to the main text for discussion)	Specimen does not show evidence of sediment infilling, lacks relief and does not penetrate the matrix; a burrow lining (that is, a clear, sharp delineation between the inner and outer parts of a burrow ²) would have been visible all along the structure, which is not the case; oxidized organic material on the surface of the sediment is delicate and fragmentary; probably a decayed sponge
Sponge	UCBL-FSL713602	Presence of ostia and possible spicules	Extended Data Fig. 10	Trace fossil (burrow)	None given	Specimen with very irregular width used to investigate chemical signature and diagenesis; probably a decayed sponge with heavy oxidation
Alga	UCBL-FSL713606	Bifurcating 2D organic structure with irregular branch width	Fig. 2d and Extended Data Fig. 7a,b	Trace fossil (<i>Quebecichnus</i>)	None given	Specimen does not show pellets, has no vertical component or relief and has branches differing in width, unlike <i>Quebecichnus</i> ⁹ ; represents algae
Alga	UCBL-FSL713607	Bifurcating 2D organic structure with irregular margins	Fig. 2e and Extended Data Fig. 7c,d	Trace fossil (burrow)	None given	Specimen consists of a horizontal structure lying on the surface of the sediment with no vertical component; the material is delicate and fragmentary; probably algae
Alga	UCBL-FSL713608	Bifurcating 2D organic structure with complex ornaments	Fig. 2f and Extended Data Fig. 7e,f	Trace fossils (<i>Avetoichnus</i> or <i>Cladichnus</i>)	None given	The specimen is a horizontal structure on the surface of the sediment that is delicate and fragmentary; unlike <i>Avetoichnus</i> , it lacks the regular organization of a horizontal helix and shows no central core ¹⁰ ; it also lacks the vertical development, radiating arrangement of horizontal tubes with regular width and thick backfilled menisci showing a width:thickness ratio of 1:1, as in <i>Cladichnus</i> ¹ ; probably algae
Hemichordate	UCBL-FSL713609	Fibrous composition with an elaborate pore architecture and characteristic branching angles	Fig. 2g	Trace fossil (burrow containing pellets)	None given	Muir and Botting ² state that there is a lack of distinctive reticulate structures of benthic hemichordate tubes; however, morphological variations exist in hemichordate tubes ^{12,13} ; the specimen is slightly oblique on the bedding plane, with four clear nodes of equally spaced bifurcating tubes at similar angles to the hemichordate <i>Margaretia</i> and leading down to a single main pillar attaching to the benthos; the texture and porosity might have been partially removed due to decay
Unidentified vermiform organism	UCBL-FSL713615	Overall body shape, possible presence of a gut, and complex ornaments	Fig. 4a	Trace fossil (burrow with diagenetic artefacts)	Sediment infill and pellet infill (refer to the main text for discussion)	Specimen has variable width and very irregular outlines, atypical of burrows; pellets not identified and it is unclear what sort of diagenetic minerals could form similar textures; probably a worm showing the remains of external morphology and a decaying gut
Lobopodians	UCBL-FSL713616 and UCBL-FSL713617	Elongated 2D soft bodies with mineralized plates; multiple specimens showing consistent plate placement	Fig. 4b–e	Trace fossil (lined burrows with diagenetic concretions)	Lobopodican plates would be paired and with clear, consistent morphology	<i>Microdictyon</i> plates have various morphologies ¹⁴ ; multiple specimens show an elongated 2D body, with irregular outlines and a variable width, which is uncharacteristic of lined burrows ¹⁵ ; comparison to similar concretions placed at regular intervals in a burrow is not demonstrated by supportive literature; multiple specimens also show consistent placement of the plates, which would be impossible in an abiogenic scenario; probably a decaying organism, such as a lobopodian

Sponges, algae, hemichordates, worms, lobopodians and other enigmatic animals are present in the assemblage.

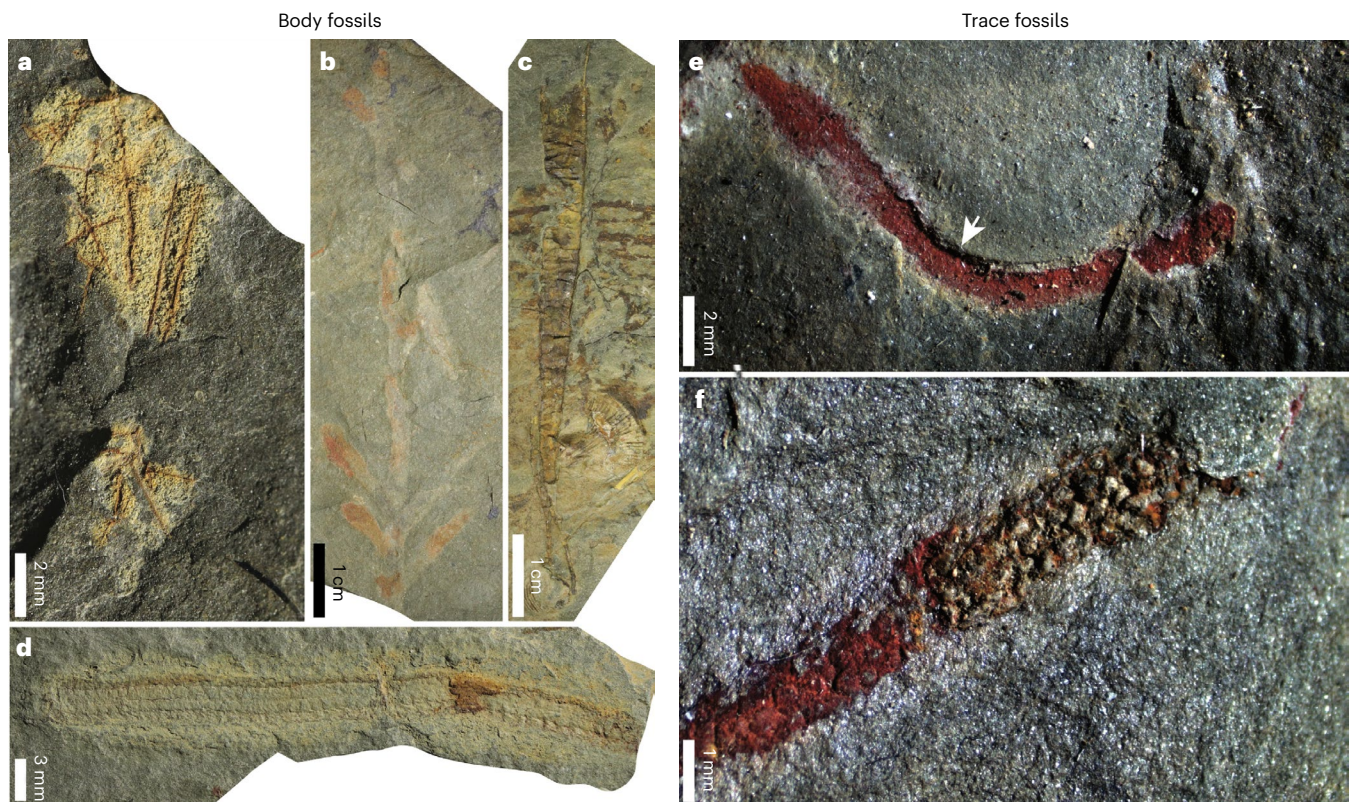


Fig. 1 | Body and trace fossils from the Cabrières Biota. a–e, Sponge spicules (a; UCBL-FSL713619), branching algae (b; UCBL-FSL713620), brachiopods attached to *Sphenothallus* (c; UCBL-FSL713621), a worm (d; UCBL-FSL713622) and a *Planolites montanus* burrow with distinct outlines, a regular width, a massive infill and a change of position within the vertical plane (marked with a white arrow) (e; UCBL-FSL713623), all of which represent a set of ichnologic criteria

unseen in algal material from the Cabrières Biota. f, *Alcyonidiopsis longobardiae* with distinct, small faecal pellets (UCBL-FSL713624). The photographs of the fossils in a–d were taken using a Canon 800D camera coupled with a Canon MP-E 65 mm macro lens, whereas the photos of the trace fossils shown in e and f were taken using a Zeiss SteREO Discovery V8 stereomicroscope equipped with a camera.

Muir and Botting² repeatedly alter the terminology being applied to a specimen to assert an alternative interpretation of that specimen without providing justification, evidence or argument as to why that terminology is appropriate. For example, spaces in the skeleton of a sponge are termed “pellets” and the hemichordates are “pellet-filled burrows”. These are not primary observations, but interpretations based on no presented rationale. “Pellet” is a term that would be applied once the genesis of the object has been established and it cannot be asserted to establish the nature of the specimen—simply stating it does not make it true.

We agree with Muir and Botting² that differentiating between algae, simple tubular organisms and trace fossils such as burrows is challenging. Nevertheless, clear criteria exist to differentiate between them. Burrows are structures excavated within the sediment by animals³. As such, they are three-dimensional (3D) objects and typically show evidence of sediment displacement and distinct regular outlines. Furthermore, as any tracemaker has a given body size, burrows do not substantially vary in width along their length or in between probes of a branching burrow system. The counter-example chosen by Muir and Botting² to suggest that width can vary substantially along a burrow is a problematic structure re-interpreted as inorganic and related to ptygmatic folding⁴. Exposed on a bed surface, a burrow either shows a bulge or depression that is distinct from the surrounding host rock or is cut through as an intersecting 3D object^{3,5}. A burrow does not lie flat on the surface of the sediment and its terminations are typically distinct and result from the change in the vertical level of the tracemaker. None of the specimens described as animal or algal body fossils in the Cabrières Biota meets all of these criteria. Instead, the specimens depicted possess distinct diagnostic characteristics that

enable their classification within the taxa to which they were initially assigned (Table 1). Additionally, the Cabrières Biota contains abundant trace fossils (Fig. 1e,f), meaning that direct comparisons are possible between traces that meet the criteria listed above and body fossils (Fig. 1a–d) possessing markedly different characteristics than trace fossils from the same depositional setting.

The substantive conclusion of Saleh et al.¹ is that the Cabrières Biota was an Ordovician polar ecosystem at a time of high global temperatures and this remains unchallenged. Muir and Botting² questioned only the quality of fossil preservation and extent of biodiversity. However, our arguments show that their reinterpretations are invalid (Table 1). The Cabrières Biota contains sponges (Fig. 1a), algae (Fig. 1b), hemichordates, worms (Fig. 1d), lobopodians and enigmatic animals such as *Sphenothallus* (Fig. 1c), together with and distinct from trace fossils (Fig. 1e,f). The Cabrières Biota fits in traditional and more recent Lagerstätte definitions for both its body and trace fossils⁶. We also emphasize that the studied material is available in public collections and can be accessed for study by any scientist. Interested researchers are welcome to join the team and work collaboratively with us to uncover the secrets of this ecosystem. The Cabrières Biota will continue to provide unique insights into Ordovician polar ecosystems.

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Author contributions

G.J.-M.P. and V.J. took photographs of the fossils. F.S. produced the figures and tables. F.S., R.G., J.B.A. and B.L. discussed and wrote the response with the help of L. Lustri, P.G., G.J.-M.P., F.P.-P., L. Laibl, V.J., A.V., A.C.D., M.N., C.D., S.S., E.B., S.L., H.B.D., R.V., M.V., E.M., S.M., J.-P.K. and M.-H.K.

Competing interests

The authors declare no competing interests.

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