

Original Article

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Enigma variations: characteristics and likely origin of the problematic surface texture *Arumberia*, as recognized from an exceptional bedding plane exposure and the global record

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Abstract

Arumberia is an enigmatic sedimentary surface texture that consists of parallel, sub-parallel or radiating ridges and grooves, most commonly reported from upper Neoproterozoic – lower Palaeozoic strata. It has variably been interpreted as the impression of a small metazoan, a ‘vendobiont’, a physical sedimentary structure formed on a substrate with or without a microbial mat covering, or a non-actualistic microbial community. In this paper we contribute new insights into the origin of *Arumberia*, resulting from the discovery of the largest contiguous bedding plane occurrence of the texture reported to date: a 300 m² surface in the lower Cambrian Port Lazo Formation of Brittany, NW France. We compare the characteristic features of *Arumberia* at this locality with 38 other global records, revealing four defining characteristics: (1) the three-dimensional (3D) morphology of exposed *Arumberia* lines (either positive relief ‘ridges’ or negative relief ‘grooves’) records fully preserved cords within clay laminae; (2) lines may transition laterally into reticulated patterns; (3) characteristic parallel and sub-parallel *Arumberia* lines can become modified by desiccation on emergent substrates prior to interment; and (4) *Arumberia* are streamlined with palaeoflow in successions showing evidence of unidirectional currents, but are organized parallel to ripple crests where strata were sculpted by oscillatory flows. These characteristics indicate that *Arumberia* records a 3D entity, distinct in material properties from its host sediment, which occurred in very shallow water settings where it was prone to passive reorganization in moving water, and desiccation when water drained. A literature survey of all known *Arumberia* occurrences reveals that the most reliable examples of the form are stratigraphically restricted to a 40 Ma interval straddling the Ediacaran–Cambrian boundary (560–520 Ma). Together these characteristics suggest that *Arumberia* records the remains of extinct, sessile filamentous organisms (microbial or algal?) that occupied very shallow water and emergent environments across the globe at the dawn of the Phanerozoic Eon.

1. *Arumberia*: a globally recognized sedimentary surface texture

Arumberia is a sedimentary surface texture comprising a series of low-relief, sharply defined sub-parallel lines (Fig. 1), which is often recognized on Precambrian and lower Palaeozoic bedding planes. It was originally reported from the Ediacaran Arumberia Sandstone of Australia by Glaessner & Walter (1975), who interpreted it as an impression fossil of a small cup-shaped metazoan. Subsequent *Arumberia* discoveries have shown that the cup-shaped gross morphology of the original specimens is not indicative of its true form, which can extend over multiple square metres on planar or rippled bedding planes (Fig. 1i; Table 1). The characteristic features of *Arumberia* have been explained in several mutually exclusive ways. Dominant among these are hypotheses that the texture is either the ‘body-fossil’ impression of a mat-like organism or community attached to a sedimentary substrate (Bland, 1984; Kumar & Pandey, 2008, 2009; Kolesnikov *et al.* 2012, 2015; Arrouy *et al.* 2016), or a physical sedimentary structure formed with or without a microbial mat covering (Brasier, 1979; McIlroy & Walter, 1997; Jensen *et al.* 2005; McIlroy *et al.* 2005; Allen & Leather, 2006; Seilacher, 2007; Netto, 2012; Liu *et al.* 2013; Sharma & Mathur, 2014; Becker-Kerber *et al.* 2020). Notable among previous work is the 1984 review paper by Bland, which described and reviewed all prior known *Arumberia* occurrences. Bland concluded that only a fraction of reported *Arumberia* specimens exhibited the original diagnostic criteria of Glaessner & Walter (1975), and that they represented large impression fossils restricted to uppermost Precambrian and lower Cambrian strata deposited in very shallow-marine to non-marine environments.

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Fig. 1. (Colour online) Global *Arumberia* examples. (a) Maturin Ponds Formation, Canada. Note frequent bifurcations. (b) Synalds Formation, United Kingdom. Note the lack of intermittent bifurcations. Coin has diameter of 19 mm. (c) Ferryland Head Formation, Canada. (d) Maturin Ponds Formation, Canada. Coin has diameter of 16.25 mm. (e) Synalds Formation, United Kingdom. (f) Crown Hill Formation, Canada. In this instance *Arumberia* lines follow the direction indicated by the underlying linguoid ripple marks. Coin has diameter of 16.25 mm. (g) Arumbera Sandstone, Australia. (h) Maturin Ponds Formation, Canada. White arrow highlights an instance where multiple fine, superimposed, *Arumberia* cords are observed to comprise an 'individual' *Arumberia* line. (i) Ferryland Head Formation, Canada, an instance where contiguous *Arumberia* lines extend across a large surface area (exceeding 3 m²). Contiguous *Arumberia* examples rule out the original hypothesis that *Arumberia* records the remains of a small cup-shaped organism (Glaessner & Walter, 1975). (j) Crown Hill Formation. *Arumberia* are overprinted by rain-drop marks (implying *Arumberia* was an ineffective buffer against droplet impact; Davies *et al.* 2016). (k) Maturin Ponds Formation. (l) Gibbett Hill Formation, Canada. (m) Crown Hill Formation, Canada. (n) Ferryland Head Formation. (o) Crown Hill Formation, Canada. (p) Maturin Ponds Formation, Canada.



In this study we critically assess the nature of *Arumberia* using new evidence from the largest reported instance so far discovered in the global rock record: a 300 m² bedding plane in the lower Cambrian Port Lazo Formation of Brittany, France (Fig. 2). Isolated *Arumberia* have previously been reported from this locality (Bland, 1984), but the extensive low-lying coastal outcrop we describe here was fortuitously exhumed during an interval when the modern beach profile was lowered. Supporting this case study, we revisit Bland's (1984) assessment of *Arumberia* in light of 22

subsequent reports, in addition to the 18 instances that he previously reviewed (Tables 1, 2). Our literature survey has been grounded by field visits to six of these *Arumberia*-bearing formations (Table 1; the Arumbera Sandstone of Northern Territory, Australia; the Crown Hill, Ferryland Head, Gibbett Hill and Maturin Ponds formations of Newfoundland, Canada; and the Synalds Formation of Shropshire, England). These sites have provided further observations to supplement evidence from the Port Lazo bedding plane and support our interpretation of *Arumberia*.

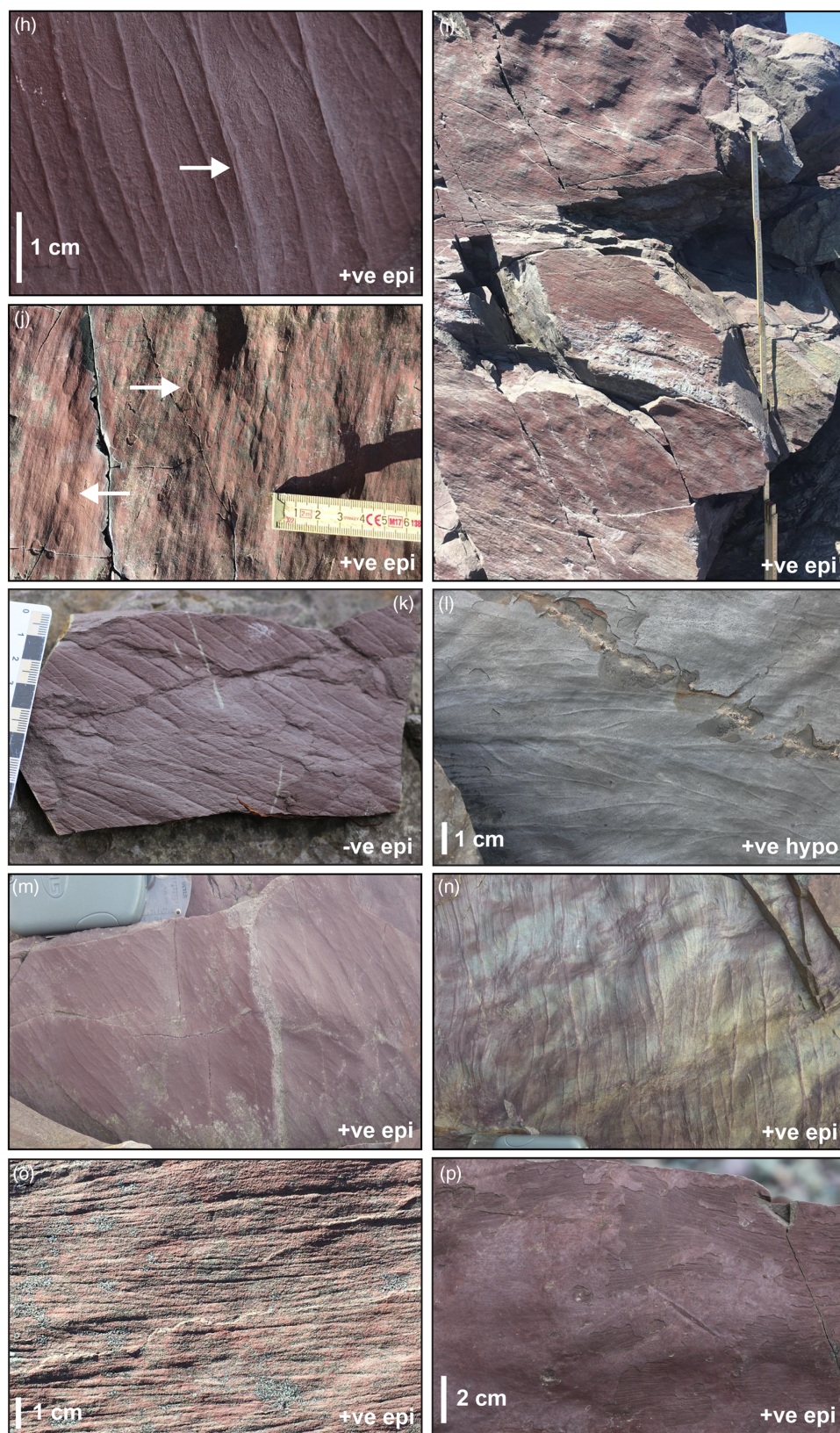


Fig. 1. Continued

2. Existing challenges and purpose of this paper

Universal diagnostic criteria for *Arumberia* have proved challenging to isolate (Glaessner & Walter, 1975; Bland, 1984; McIlroy *et al.*

2005; Kumar & Pandey, 2008, 2009; Kolesnikov *et al.* 2012; Retallack & Broz, 2020), resulting in continuing uncertainty surrounding its affinities and origin (Table 3). Three factors have hampered understanding, described in the following.

Table 1. Details of *Arumberia* morphologies documented by the present authors (in bold) or by previous workers (listed in Table 2). We searched for *Arumberia* in the Erquy Formation, Lightspout Formation, Rozel Conglomerate and Portway Formation, but without success. Features previously reported as *Arumberia* in the Diabaig Formation have been studied by us and are not considered to be equivalent (Section 5). Epi – epirelief; Hypo – hyporelief; +/- – positive/negative.

	Spatial extent (m ²)	Line width (mm)	Line spacing (mm)	Line relief	Line sinuosity	Relationship to current	Bifurcating?	Dimple-pimples?	Lithology	Environment
Africa										
1. Auborus Formation	c. 0.1	?	?	+epi	Low	?	No	No	Mudstone	Emergent
2. Kuibis Subgroup	?	2–4	< 0.5–1	+epi	Low	?	?	No	Sandstone	Shallow marine
3. Nudaus Formation	?	2–4	< 0.5–1	+epi	Low	?	?	No	Sandstone	Coastal
Asia										
4. Bhima and Kaladgi–Badami Sequence	?	?	?	?	?	?	?	No	Sandstone	Terrestrial–shallow marine
5. Bundi Hill Sandstone	?	?	?	?	?	?	?	No	Sandstone	Emergent
6. Jodhpur Sandstone	?	1–4	1–2	+epi, +hypo	Low	Parallel	Yes	Yes	Sandstone	Shallow water
7. Maihar Sandstone	?	1	1–3	+epi	Low	Parallel	Yes	Yes	Sandstone	Shallow marine/tidal
8. Masirah Bay Formation	c. 0.005	0.2–0.4	?	+epi	Low	Perpendicular	No	No	Sandstone	Offshore
9. Shichang Member	0.008	12–15	6–9	+epi	Low	?	No	No	Limestone	Marine
Australia										
10. Arumberia Sandstone	> 10	0.3–7	0.5–7	+epi, –hypo	Low	Parallel	Yes	Yes	Siltstone–sandstone	Shallow subtidal
11. Bonney Sandstone	?	?	?	?	?	Perpendicular	?	No	Siltstone–sandstone	Shallow marine
12. Carnegie Formation	c. 0.005	0.5–5	1–6	+epi	?	?	?	?	Sandstone	?
13. Central Mount Stuart Formation	?	?	?	?	?	?	?	Yes	Sandstone	Emergent
14. Erudina Silstone Member	?	?	?	?	?	?	?	No	Mudstone–siltstone	Emergent
Europe and Russia										
15. Aisha Formation	?	?	?	?	?	?	?	No	?	?
16. Basa Formation	?	?	?	?	?	?	?	?	Sandstone	?
17. Booley Bay Formation	< 0.008	1	0.5–0.75	+hypo	Low	Parallel	No	No	Siltstone–sandstone	Deep marine
18. Chernyi Kamen Formation	?	0.5–2	3–4	+epi, +hypo	Low	Parallel	Yes	No	Shale–sandstone	Emergent
19. Diabaig Formation	< 0.006	< 0.5–5	2–10	+epi, –epi	High	?	Yes	No	Mudstone–sandstone	Lacustrine

(Continued)

Table 1. (Continued)

20. Erquy Formation	?	?	?	?	?	?	?	?	?	Emergent
21. Hornelen Old Red Sandstone	?	?	?	?	?	?	?	?	Sandstone	Lacustrine-fan delta
22. Lightspout Formation	c. 0.008	0.5–1.5	0.5–3	+epi, –hypo	Low	?	Yes	Yes	Mudstone–siltstone	Alluvial plain/fluviol/deltaic
23. Lopata Formation	?	?	?	?	?	?	?	?	?	?
24. Mogyliv Formation	?	3–5	?	+hypo	Low	?	Yes	No	Sandstone	?
25. Moshakov Formation	?	1–1.5	1–5	–hypo	Low	?	Yes	Yes	Sandstone	Shallow marine
26. Ostrov Formation	?	?	?	?	?	?	?	?	Sandstone	Shallow water
27. Port Lazo Formation Lower Member	c. 300	0.5–1.5	1–3	+epi, +hypo	Low	Perpendicular	Yes	Yes	Mudstone–sandstone	Emergent
28. Port Lazo Formation Upper Member	< 5	0.5–3	1–5	+epi	Low	Perpendicular	Yes	Yes	Mudstone–sandstone	Nearshore marine
29. Portway Formation	?	0.5–1.5	0.5–3	+epi, +hypo	Low	?	?	Yes	Siltstone–sandstone	Alluvial floodplain
30. Rozel Conglomerate	?	?	?	?	?	?	?	?	Shale	Terrestrial
31. Synalds Formation	7	0.5–3	0.5–3	+epi, +hypo	Low	Perpendicular?	Yes	Yes	Mudstone–siltstone	Emergent
32. Visingsö Formation	?	< 0.5–1	2–5	–epi	Low	?	Yes	No	Sandstone	Terrestrial
33. Zigan Formation	> 0.005	0.5–2	3–4	+epi, –hypo	Low	Parallel	Yes	No	Sandstone	Emergent
North America										
34. Crown Hill Formation	?	0.3–1.5	1–3	+epi	Low	Parallel	Yes	Yes	Mudstone–sandstone	Emergent
35. Ferryland Head Formation	< 9	0.6–1.5	2–8	+epi	Low	Parallel	Yes	No	Mudstone–sandstone	Emergent
36. Gibbett Hill Formation	< 12	0.5–1	1–5	+epi	Low	Perpendicular	Yes	Yes	Sandstone	Shallow water
37. Maturin Ponds Formation	< 0.005	0.1–1.5	0.1–5	+epi	Low	Perpendicular	Yes	No	Mudstone–sandstone	Emergent
South America										
38. Bom Jardim Allogroup	?	?	?	?	?	?	?	Yes	Sandstone	Braidplain delta
39. Cerro Negro Formation	?	1–3	0.25–1	+epi	Low	Perpendicular	Yes	No	Mudstone–sandstone	Emergent
40. Itajai Group	?	0.5–3	2–10	+epi	Low	Parallel	Yes	Yes	Mudstone–siltstone	Distal delta-front/upper shoreface

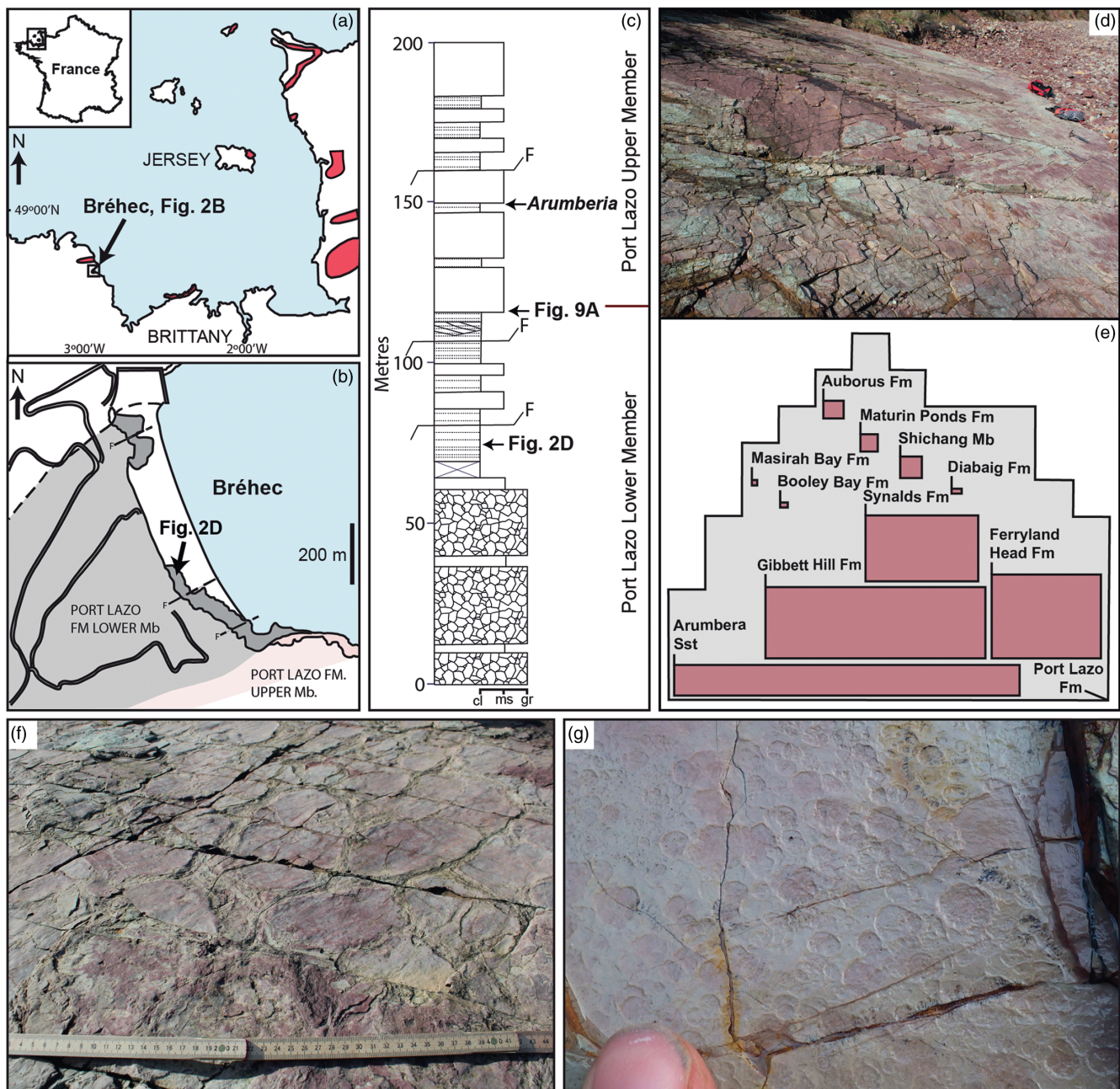


Fig. 2. (Colour online) Geographic, stratigraphic and spatial occurrence of *Arumberia* in the Port Lazo Formation, France. (a) Red outline marks outcrop locations of the Series Rouge (McMahon *et al.* 2017; Went, 2021) that hosts the *Arumberia*-bearing Port Lazo Formation. (b) Location of *Arumberia* bedding plane at Bréhec Bay (amended from Went, 2017). (c) Measured section through the Port Lazo Formation indicating the position of the studied *Arumberia*-bedding plane. Cl – clay; ms – medium-grained sandstone; gr – granular sandstone/pebbly conglomerate (amended from Went, 2017). (d) The *Arumberia*-bearing bedding plane located at Bréhec Bay. (e) Grey outline illustrates the greater dimension of the analysed Port Lazo bedding plane in comparison to other previous *Arumberia* reports (drawn to scale, as red rectangles inset to the mapped grey outline). The total size of the Port Lazo bedding plane is c. 300 m², but the graphic illustration is limited to the spatial coverage (86 m²) within which *Arumberia* was subjected by the authors to detailed scrutiny (measurements of line width, length, spacing, sinuosity and orientation). References detailing bedding plane dimensions of other *Arumberia* locations are listed in Table 2. (f) Desiccation cracks and (g) circular raindrop impressions identified on the studied red mudstone bed.

(1) *Preservation and ease of observation*: it is challenging to describe individual specimens of *Arumberia* because the lateral margins of the texture are commonly either indistinct, or incomplete at the scale of observation. This makes it difficult to accurately define its areal extent. Additionally, while sub-parallel to parallel lines constitute all reported *Arumberia* (Fig. 1), the morphology and relief of these can be highly variable even over short distances, with spatially

patchy expressions of branching, spacing, curvature and reticulation. Compounding these practical issues of description, *Arumberia* frequently has a topographic relief of < 1 mm, meaning that its visibility in natural outcrops can be hampered by poor light conditions, a lack of magnification and degradation through weathering.

(2) *Changing diagnostic criteria and loaded terminology*: the original type material of *Arumberia* (Glaessner & Walter, 1975,

Table 2. Geographic and stratigraphic distribution of globally recognized *Arumberia* forms.

	Location	Age (Ma)	Key reference	Age reference
Africa				
1. Auborus Formation	Namibia	1265–1000	Bland (1984)	Hunter (1981)
2. Kuibis Subgroup	Namibia, South Africa	550–541	Almond & Pether (2008)	Grotzinger <i>et al.</i> (1995), Waggoner (2003)
3. Nudaus Formation	South Africa	548–545	Almond & Pether (2008)	Grotzinger <i>et al.</i> (1995)
Asia				
4. Bhima and Kaladgi–Badami Sequence	India	Poorly constrained	Raha <i>et al.</i> (1991)	Pandey <i>et al.</i> (2009)
5. Bundi Hill Sandstone	India	650–550	Srivastava (2012)	Srivastava (2012)
6. Jodhpur Sandstone	India	681–541	Kumar & Pandey (2009)	Kumar & Pandey (2009)
7. Maihar Sandstone	India	570–544	Kumar & Pandey (2009)	Maithy & Kumar (2007)
8. Masirah Bay Formation	Oman	630–590	Allen & Leather (2006)	Allen & Leather (2006)
9. Shichang Member	China	700–680	Liu (1981)	Liu (1981)
Australia				
10. Arumbera Sandstone	Australia	580–541	Glaessner & Walter (1975)	Mitchell <i>et al.</i> (2010)
11. Bonney Sandstone	Australia	556±24	Bland (1984)	Australian Stratigraphic Lexicon
12. Carnegie Formation	Australia	580–541	Haines <i>et al.</i> (2008)	Mitchell <i>et al.</i> (2010)
13. Central Mount Stuart Formation	Australia	c. 541	Bland (1984)	Australian Stratigraphic Lexicon
14. Erudina Siltstone Member	Australia	522.8±1.8	Bland (1984)	Australian Stratigraphic Lexicon
Europe and Russia				
15. Aisha Formation	Siberia, Russia	620–541	Sovetov (2006)	Sovetov (2006)
16. Basa Formation	South Urals, Russia	< 573±2.3	Razumovskiy <i>et al.</i> (2020)	Razumovskiy <i>et al.</i> (2020)
17. Booley Bay Formation	Ireland	515–497	MacGabhann <i>et al.</i> (2007)	Vanguetaine & Brück (2008)
18. Chernyi Kamen Formation	Central Urals, Russia	557±13	Kolesnikov <i>et al.</i> (2012)	Maslov <i>et al.</i> (2013), Puchkov <i>et al.</i> (2016)
19. Diabaig Formation	Scotland	944±48	Callow <i>et al.</i> (2011)	Turnbull <i>et al.</i> (1996)
20. Erquy Formation	France	541–520	Bland (1984)	Went (2021)
21. Hornelen Old Red Sandstone	Norway	393–382	Bland (1984)	Commonly cited Middle Devonian
22. Lightspout Formation	England	555.9±3.5	McIlroy <i>et al.</i> (2005)	Compston <i>et al.</i> (2002)
23. Lopata Formation	Siberia, Russia	555–541	Shatsillo <i>et al.</i> (2015)	Shatsillo <i>et al.</i> (2015)
24. Mogyliiv Formation	Ukraine	580–545	Nesterovsky <i>et al.</i> (2018)	Elming <i>et al.</i> (2007)
25. Moshakov Formation	Siberia, Russia	< 567	Liu <i>et al.</i> (2013)	Kochnev <i>et al.</i> (2020)

(Continued)

Table 2. (Continued)

	Location	Age (Ma)	Key reference	Age reference
26. Ostrov Formation	Siberia, Russia	635–541 ^a	Bogolepova <i>et al.</i> (2010)	Bogolepova <i>et al.</i> (2010)
27. Port Lazo Formation Lower Member	France	540–520	This study	Went (2021)
28. Port Lazo Formation Upper Member	France	540–520	This study	Went (2021)
29. Portway Formation	England	< 555.9±3.5	McIlroy <i>et al.</i> (2005)	Compston <i>et al.</i> (2002)
30. Rozel Conglomerate	UK Channel Islands	583–487	Bland (1984)	Went (2005)
31. Synalds Formation	England	(555.9±3.5)–(566±2.9)	JC Pauley, unpubl. Ph.D. thesis, University of Liverpool, 1986; Liu (2011)	Compston <i>et al.</i> (2002)
32. Visingsö Formation	Sweden	(706±14)–(663±7)	Bland (1984)	Samuelsson & Strauss (1999)
33. Zigan Formation	South Urals, Russia	547.6±3.8	Kolesnikov <i>et al.</i> (2012)	Levashova <i>et al.</i> (2013)
North America				
34. Crown Hill Formation	Canada	560–541	Bland (1984), this study	O'Brien <i>et al.</i> (2006)
35. Ferryland Head Formation	Canada	560–541	Bland (1984), RA Sala Toledo, unpub. Ph.D. thesis, Memorial University of Newfoundland, 2004	O'Brien <i>et al.</i> (2006)
36. Gibbett Hill Formation	Canada	560–541	Bland (1984)	O'Brien <i>et al.</i> (2006)
37. Maturin Ponds Formation	Canada	560–541	Bland (1984), this study	O'Brien <i>et al.</i> (2006)
South America				
38. Bom Jardim Allogroup	Brazil	592–573	Netto (2012)	Netto (2012)
39. Cerro Negro Formation	Argentina	580–542	Arrouy <i>et al.</i> (2016)	Arrouy <i>et al.</i> (2016)
40. Itajaí Group	Brazil	563±3.3	Becker-Kerber <i>et al.</i> (2020)	Becker-Kerber <i>et al.</i> (2020)

^aAge assumed by the original authors based on presence of *Arumberia*.

redescribed by Retallack & Broz, 2020) lacks the full range of characteristics and spatial extents that have been revealed and incorporated into taxonomic diagnoses by later discoveries. Furthermore, some characteristics originally thought to be universal (e.g. conical forms with blunt apices, regular radial patterns of lines) are now known to be ancillary features, present in only a subset of instances. *Arumberia* has been reinterpreted several times as a body fossil (e.g. Retallack & Broz, 2020) or a pseudofossil (e.g. McIlroy *et al.* 2005), with resultant emended diagnoses changing to reflect those interpretations through the addition or removal of diagnostic features. As a result, some of these criteria employ terminology that is loaded with an implication of biogenicity, rather than passive descriptive terms (e.g. description of the constituent lines as ‘rugae’; Kolesnikov *et al.* 2015, 2017; McMahon *et al.* 2017), further hindering objective interpretation.

- (3) ‘*Arumberia*’ as a bucket-term: the most frequently observed characteristic of *Arumberia* is a set of closely spaced

sub-parallel to parallel lines on a bedding plane (Fig. 1). Interpreting such a simple form in isolation encounters the challenge of equifinality: such phenomena may have plural potential explanations, both biotic and abiotic, and the cause behind a specific feature may be underdetermined by available evidence (e.g. Davies *et al.* 2016, 2020). There appear to be instances in existing literature where the term ‘*Arumberia*’ has been liberally used to describe any observations of (sub) parallel lines: in some of these instances, the forms share no further characteristics in common with other described *Arumberia* (e.g. in terms of physical dimensions, accessory characteristics or host facies) (Table 1).

Below, we attempt to redress these outstanding issues by presenting observations of exceptionally extensive *Arumberia* from a newly discovered bedding plane in the lower Cambrian Port Lazo Formation in France, augmented with observations of well-preserved examples from elsewhere in the rock record. We

Table 3. Previous interpretations of *Arumberia*.

Reference	Interpretation
Salter (1856)	Lines of mineral structure and ripple marks
Glaessner & Walter (1975)	Cup-shaped metazoan
Brasier (1979)	Abiogenic hydraulic structures caused by turbulent flow
Bland (1984)	Substrate-attached, mat-like organism
JC Pauley, unpubl. Ph.D. thesis, University of Liverpool, 1986	Tectonic lineation randomly superimposed on genetically unrelated pit and blister-like features
Mcllroy & Walter (1997)	Physical sedimentary structure formed by the action of currents over a microbially bound substrate
Callow <i>et al.</i> (2011)	Large, benthic microbial filaments (differs from both the original and revised diagnoses of <i>Arumberia</i> ; Section 6)
Kolesnikov <i>et al.</i> (2017)	Microbial mat morphotype
Retallack & Broz (2020)	A genus within the class Vendobionta

use these observations to amend the diagnostic criteria of Glaessner & Walter (1975) in light of those characteristics that are universal, common or infrequent attributes of *Arumberia*, and highlight previously reported instances of '*Arumberia*' that can be considered doubtful. Our reassessment shows that the least equivocal instances of *Arumberia* exhibit a narrow stratigraphic and palaeoenvironmental range (cf. Bland, 1984).

3. *Arumberia* in the Port Lazo Formation

Previous reports of *Arumberia* from the Port Lazo Formation in Brittany, France (Bland, 1984; Davies *et al.* 2016; McMahon *et al.* 2017; Went, 2017, 2021) have not described the feature in detail. The Port Lazo Formation is a constituent of the 'Series Rouge', a predominantly red-bed succession that crops out in coastal exposures across NW France and the neighbouring Channel Islands (Fig. 2a) (McMahon *et al.* 2017). Multiple potential ages have been suggested for the Port Lazo Formation. The French Geological Survey maps it as Early Ordovician in age, based on correlation to stratigraphy at Crozon that lies 125 km to the south across the North Armorican Shear Zone in the central Armorican domain (Egal *et al.* 1995). This correlation is consistent with the Port Lazo Formation being bounded by underlying Brioverian metasediments, which have recently yielded zircon U–Pb radiometric dates of 551 ± 7 Ma and 540 ± 5 Ma (Gougeon *et al.* 2021), and a 472 ± 5 Ma age from overlying andesites (Fig. 2a) (Auvray *et al.* 1980). However, regional variability in tectonic setting and sedimentary environments favours an early Cambrian age for the Port Lazo Formation, with deposition having commenced in extensional basins shortly after the Cadomian orogenic climax *c.* 540 Ma (Peucat, 1986). Three lines of evidence support this contention. (1) The strata had a source area to the west (McMahon *et al.* 2017), which is consistent with regional palaeogeography during the Cambrian Period (Went & McMahon, 2018; Went, 2021), but unlikely during the Early Ordovician Epoch when surrounding areas witnessed the deposition of the well dated marine 'Grès Armoricaïn' (Paris *et al.* 1999; Dabard *et al.* 2007). (2) Red-bed sequences in Normandy, which may be correlated

with the Port Lazo Formation (Went, 2021), underlie Cambrian Stage 3 (521–514 Ma) limestones (dated by the presence of the trilobite *Bigotina* Pillola, 1993) and Cambrian Stage 2 (529–521 Ma) siliciclastic strata. (3) Radiometric ages from overlying andesites (Auvray *et al.* 1980), which provide crucial support for a posited Ordovician age, are reliant on the igneous bodies being extrusive; however, the andesites have more recently been demonstrated to be a mixture of disconformable lavas and intrusive bodies (Went, 2017). Furthermore, the presence of *Arumberia* itself may provide circumstantial evidence for a Cambrian age once the global stratigraphic record of this feature is considered (see Section 5).

The majority of Series Rouge outcrops are exposed within the limbs of basin-wide synclines (Fig. 2a), but the studied section of the Port Lazo Formation occurs as an outlier to these, cropping out at Bréhec Bay (Fig. 2b). Sedimentological observations made over the course of this study, and previously, have shown that Port Lazo Formation specimens of *Arumberia* are restricted to very shallow-water facies that were intermittently subject to sub-aerial exposure (Davies *et al.* 2016; McMahon *et al.* 2017; Went, 2017, 2021).

The Port Lazo Formation is separated into two distinct members (Went, 2017), with the bedding plane central to this study occurring in the Port Lazo Lower Member (Fig. 2c, d). The surface has a pervasive covering of polygonal mud cracks (Fig. 2f), in addition to raindrop impressions and wave-ripple marks (Fig. 2g). These characteristics indicate that *Arumberia* occurs on a true substrate, that is, a bedding plane that faithfully records a synoptic topography that formed at the interface of sediment and water or air (Davies & Shillito, 2018, 2021). Its *c.* 300 m² surface area provides an opportunity to assess *Arumberia* morphology across a far larger area than has previously proved possible (Fig. 2e). Approximately 50% of the bedding plane is covered by *Arumberia* (although contiguous individual *Arumberia* are likely less extensive than this, due to their occurrence within multiple successive < 1 mm thick clay laminae that are impractical to correlate across the entire surface). Additional surfaces bearing *Arumberia* are also present at higher stratigraphic levels in the Port Lazo Formation Upper Member (Fig. 2c). These examples, which are far more limited in spatial extent, were preserved in shallow subaqueous, nearshore marine settings (Went, 2017; Table 2).

3.a. *Arumberia* lines

The Port Lazo *Arumberia* consist of a series of parallel or sub-parallel lines, usually < 2 mm in relief, 0.5–1.5 mm wide and spaced 1–3 mm apart (Fig. 3). Line relief and spacing can be variable even across individual specimens. The lines are most frequently low sinuosity and can exhibit intermittent bifurcations (Fig. 3a–d, g, h). A subordinate expression is present where *Arumberia* specimens are radially arranged, curving gently away from a single apex through an angle of up to 40° (Fig. 3e, f). *Arumberia* lines can sometimes be seen to transition along their length into a reticulated pattern (Fig. 3i, j). Reticulated patterns cover areas of up to 30 cm² and consist of intersecting lines that form irregularly shaped, sharp-edged polygons < 1 cm in diameter.

Arumberia lines frequently exhibit three-dimensionality to their preservation, implying that they originally had a cord-like form (in agreement with Bland, 1984; Becker-Kerber *et al.* 2021; see also Fig. 1h). On bedding surfaces, lines can occur in both positive epirelief (ridges) and negative epirelief (grooves), and both expressions of this relief can be seen along an individual line (a 'ridge–groove' transition) (Fig. 4). With magnification, they can

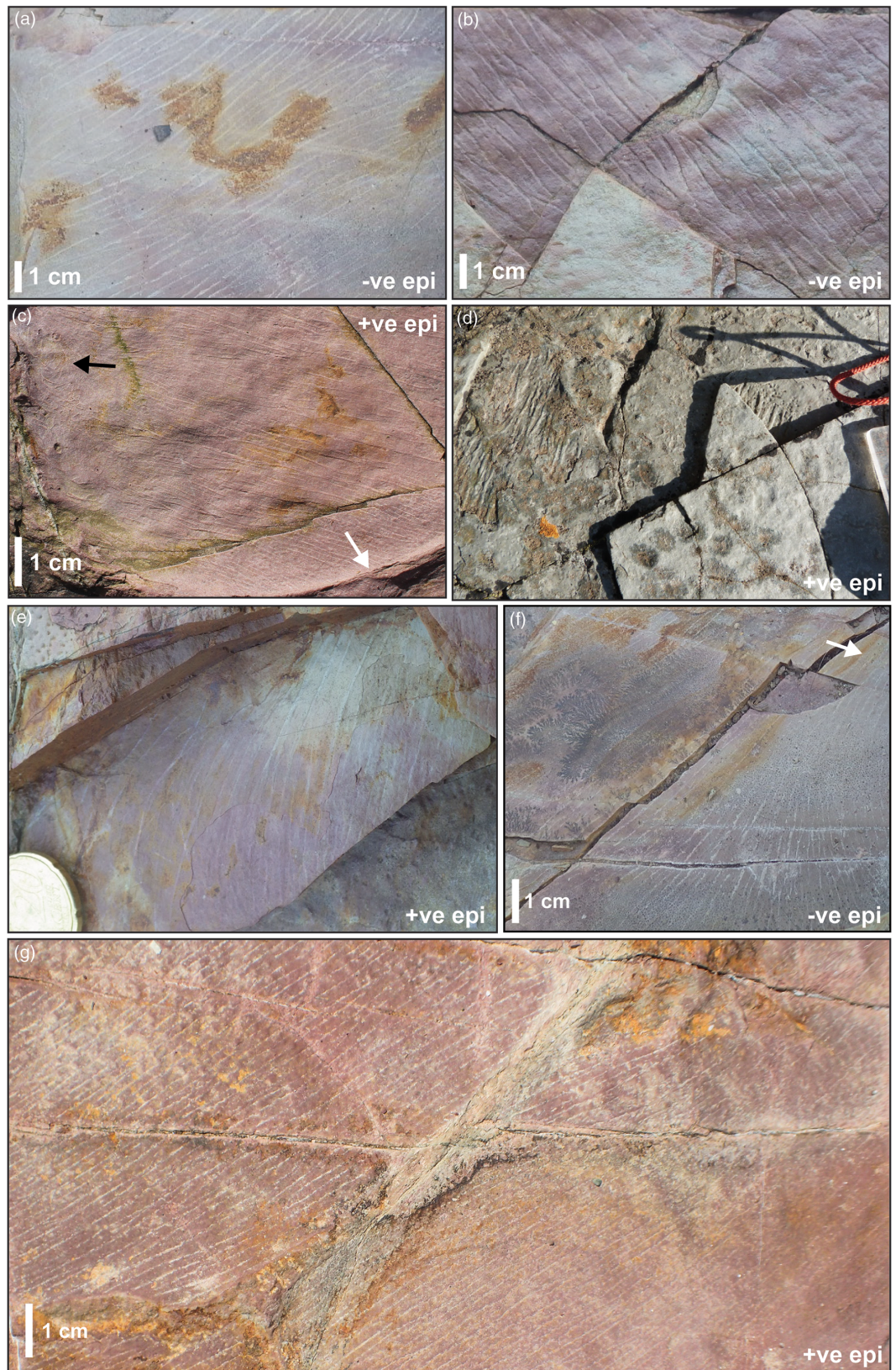


Fig. 3. (Colour online) *Arumberia* from the Port Lazo Formation. (a) *Arumberia* lines with intermittent bifurcations and reliefs of < 1 mm. (b) *Arumberia* lines with reliefs of approximately 2 mm. (c) *Arumberia* lines superimposed on a desiccated plate margin (white arrow). Black arrow depicts small ruptured domes shown in Figure 5f. (d) *Arumberia* lines in the Port Lazo Formation Upper Member. (e) Gently curved *Arumberia* that likely meet at a central node in the subcrop. Coin is 23.25 mm in diameter. (f) White arrow marks the approximate apex from which *Arumberia* lines in the bottom right of the image radiate. (g) *Arumberia* lines cross-cutting multiple desiccated polygons with no apparent deformation. (h) *Arumberia* positive epirelief lines superimposed by millimetre-wide negative epirelief 'dimples' (Section 3.c). Coin is 23.25 mm in diameter. (i) Sub-parallel *Arumberia* lines transition laterally into a reticulated pattern. No change in line relief or thickness occurs across the transition. (j) Line drawing of Figure 3i.

be seen to be an artefact of partial weathering: the ridges record positive epirelief on the upper surface of the line-hosting lamina, and the grooves reflect casts of positive hyporelief in an underlying lamina (Fig. 4b). Ridge–groove transitions may reflect instances

where *Arumberia* lines have been preserved in full relief between successive, very thin (*c.* 0.3 mm) clay laminae, or they may reflect moulding by sub-millimetre-thick laminae. In order to preserve the original three-dimensional (3D) morphology, *Arumberia*

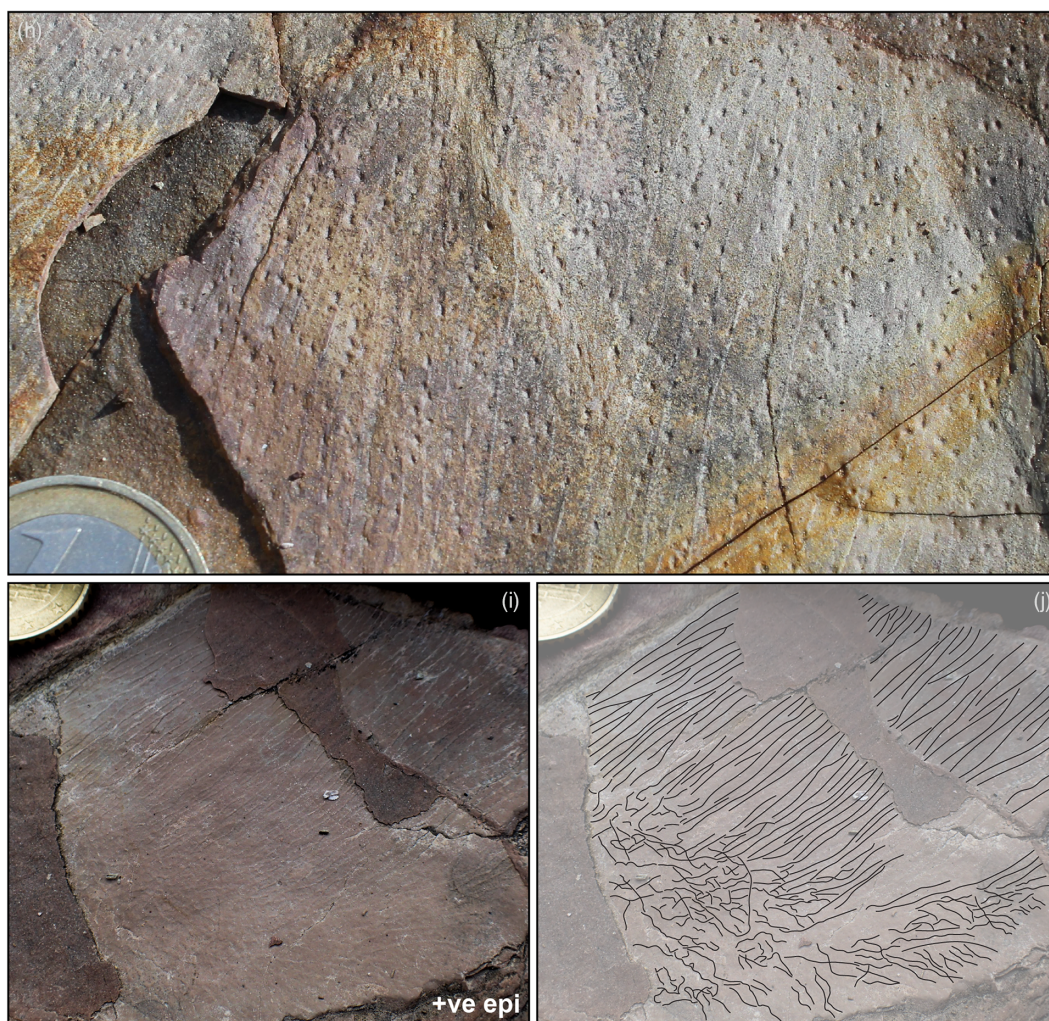


Fig. 3. Continued

colonized the substrate during a net interval of sedimentary stasis, with subsequent deposition (in this instance of clay) covering *Arumberia*'s external surface, preceded by little or no scour (e.g. Davies & Shillito, 2021).

The three-dimensionality of the lines, and transitions from directed linearity to reticulated patterns, contradict previous assertions that *Arumberia* could be a physical sedimentary structure arising from unidirectional flow (i.e. a surficial texture registered on the substrate, such as current rills or flute marks: Brasier, 1979; Jenkins *et al.* 1981; McIlroy & Walter, 1997; Seilacher, 2007). Instead, these combined characteristics indicate the prior existence of a feature that was external to the sediment in which it is now hosted, and which responded variably along its length. The reticulation bears similarities to the patterning that emerges when buoyant filaments of bacteria or algae become entangled in standing or draining water (Shepard & Sumner, 2010; Davies *et al.* 2016; Cuadrado & Pan, 2018).

On the large bedding plane exhibiting *Arumberia* (Fig. 2d), the drainage of water and associated drying and emergence is indicated by the presence of polygonal mud cracks and raindrop impressions (Fig. 2f, g). The occurrence of raindrop impressions overprinted on *Arumberia* implies that *Arumberia* was an ineffective buffer against droplet impact (Davies *et al.* 2016) (see also Fig. 1j). When in proximity to a desiccated plate margin, *Arumberia* can

be seen to have deformed alongside the shrinking cohesive muds, and individual lines are seen to curl to form irregular, broadly concentric circles (Fig. 5). These instances demonstrate that *Arumberia* was already present on the muddy surface before desiccation. Small positive epirelief 'blisters' were observed at the margins of the deformed *Arumberia* (Fig. 5f), which potentially also formed during emergence as water escaped from the surficial clay veneer or a microbial mat, producing transient bubbles that subsequently ruptured at the surface. That *Arumberia* ridges and grooves document discrete 3D forms is further supported by late Ediacaran specimens from Newfoundland, Canada, in which individual *Arumberia* lines are seen to consist of multiple, finer lines that can appear to be superimposed upon one another (Fig. 1d, h).

3.b. *Arumberia* orientation

Directional measurements of *Arumberia* lines have a tight spread of WNW–ESE orientations over the total area of 300 m² and through < 0.1 m of vertical succession (Fig. 6). Palaeocurrent measurements taken throughout the succession indicate that dominant current flow was near perpendicular to this axial orientation ($n = 61$), and symmetrical ripple mark crest lines on overlying beds have near-identical strikes ($n = 14$). The evident spatial arrangement of *Arumberia* lines with respect to measured palaeoflow implies a hydrodynamic role in morphogenesis.

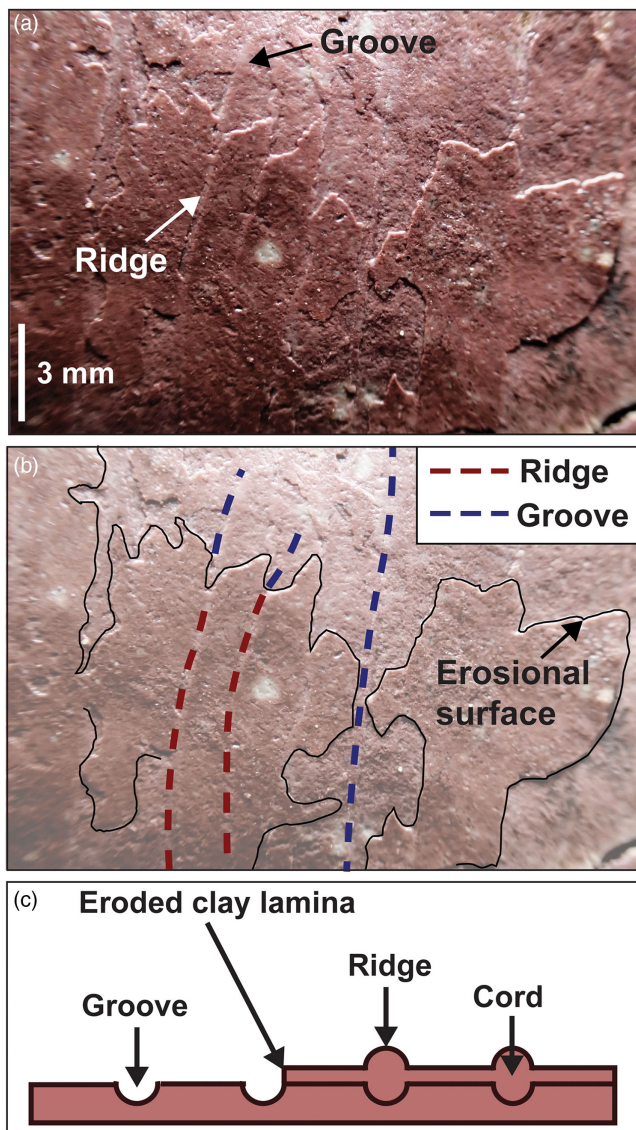


Fig. 4. (Colour online) 3D form of *Arumberia* in the Port Lazo Formation. (a) Clay veneers containing both positive epirelief lines on the top and positive hyporelief lines on the bottom. The hyporelief lines compress negative epirelief forms into the underlying bed, and changes in relief along individual lines occur at points where clay laminae have eroded from the outcrop. (b) Line drawing of Figure 4a. (c) Schematic depicting observed relief of 3D *Arumberia* ‘cords’ and the terminology used in this manuscript.

3.c. Association with dimple-pimple marks

Arumberia lines may be associated with 0.5–1.5 mm diameter circular features that lack internal structure (Figs 3d, h, 7). These features have reliefs of < 1 mm and can occur in dense populations consisting of hundreds of examples. They are generally found in negative epirelief (dimples) and positive epirelief (pimples) within < 1 mm thick clay veneers (reflecting full relief orbs, in the same way that *Arumberia* lines reflect full relief cords). One surface shows surficial dimples and basal pimples, effectively recording impression of clay laminae from above and below by two opposing hemispheres (Fig. 7d). Elsewhere, at least 10 fully illustrated and described global occurrences of *Arumberia* exhibit similar features (Table 1), which have variably been suggested to be resting cysts of *Arumberia* (Bland, 1984), structures which mark a distinct stage in the development of *Arumberia* (Becker-Kerber

et al. 2020), independent body fossils assigned to the taxon ‘*Beltanelliformis minutae*’ (McIlroy *et al.* 2005), pseudofossils associated with the perforation of microbial matgrounds (Menon *et al.* 2016) or volcanic lapilli (McIlroy & Walter, 1997). While the features remain enigmatic, the local palaeogeographic context of the Port Lazo specimens eliminates the possibility of volcanic lapilli.

4. Emended diagnostic criteria for identifying *Arumberia*

The original diagnosis of *Arumberia* provided by Glaessner & Walter (1975) was based on specimens from the Arumbera Sandstone, but 39 additional *Arumberia* reports from around the globe (Tables 1, 2), in addition to key characteristics recognized in the Port Lazo examples, necessitate modification of its diagnosis.

Arumberia: Glaessner & Walter 1975 (figs 6a–c, 7a–c, 8).

Emended diagnosis: Surface texture comprising parallel, sub-parallel or radiating lines 0.4–4.0 mm wide and spaced 0.25–30.0 mm apart. Lines can present in both positive and negative epirelief and hyporelief, with total line relief rarely exceeding 2.0 mm. Lines are commonly several centimetres long but may continue for tens of centimetres. Lines may bifurcate, but typically maintain constant width along their lateral extent. Edges are indistinct. Lines rarely overlap, but can transition laterally into reticulated networks.

Distribution: *Arumberia* has been described from every continent except Antarctica (see full list of localities in Table 2). Its temporal range is discussed in Section 5.

Discussion: Emended diagnoses for *Arumberia* and *Arumberia banksi* were recently presented by Retallack & Broz (2020), following re-examination of the type material of *Arumberia banksi* and other specimens from Central Australia. They interpreted features including septae, chambers and radiating ribs within their studied material, and included these within their emended diagnosis. We find no evidence of septae or chambers in any of the *Arumberia* specimens we have studied, and also find no reason to consider the radiating pattern of ribs to be a diagnostic feature. As such, we do not include these features in our emended diagnosis.

There has been disagreement regarding whether *Arumberia* should be considered a genus (Glaessner & Walter, 1975), arising from the uncertainty regarding its origin (see Section 6) and the absence of sufficient fossil material to permit more than a subjective hierarchical context. Recent formalization within the class Vendobionta (Seilacher, 1992; Retallack & Broz, 2020) is not followed here, since: (1) a discrete macroorganism interpretation for *Arumberia* is seemingly incompatible with its ability to express quite different morphological forms (e.g. linear, Fig. 3a–h; reticulated, Fig. 3i, j; curled, Fig. 5) dependent on the prevailing environmental conditions; and (2) we do not consider Vendobionta to be a valid clade (Dunn & Liu, 2019). McIlroy *et al.* (2005) opted to classify it as a pseudofossil under ‘microbially modified sedimentary structures’. While we agree that there is the potential for a microbial role in the formation of this surface structure, we argue that the 3D morphology of individual lines indicates that they preserve casts of fossil organisms, rather than modifications of sedimentary surfaces. Our interpretation of *Arumberia* as the remains of a distinct organism or population of organisms requires that it retains its Linnaean terminology.

Glaessner & Walter’s (1975) type material was given the species name *Arumberia banksi*. Five additional *Arumberia* species have

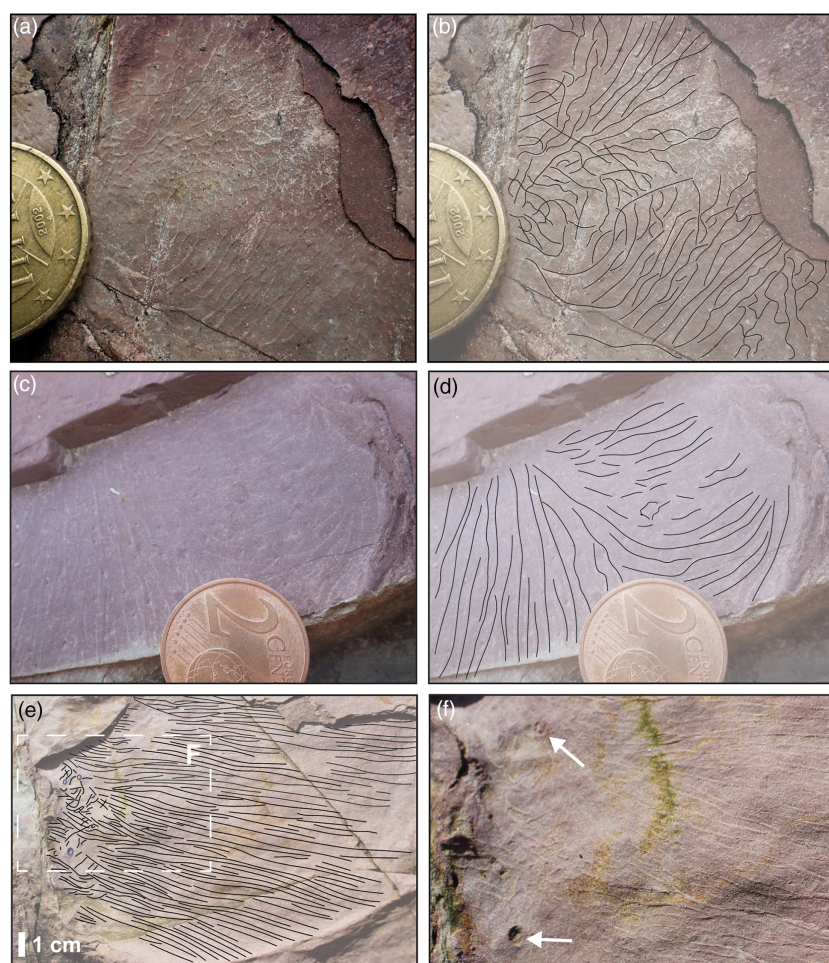


Fig. 5. (Colour online) Response to emergence displayed on *Arumberia*-bearing bedding planes in the Port Lazo Formation Lower Member. (a, c) Curled *Arumberia* lines in proximity to and in contact with desiccated plate margins. (b, d) Line drawings of Figures 5a and c, respectively. (e) Line drawing of linear *Arumberia* lines transitioning laterally into curled, discontinuous forms in proximity to a desiccated plate margin (original figure shown in Fig. 3c). (f) Inset of Figure 5e showing possible ruptured domes ('blister structures') occurring alongside deformed *Arumberia* adjacent to a desiccated plate margin. Similar discoidal ring-shaped bulges, no more than 30 mm in diameter and 3 mm in height, are present across the bedding plane. Coin in Figure 5a is 22.25 mm in diameter. Coin in Figure 5c is 18.75 mm in diameter.

since been proposed (*A. vindhyanensis*, '*A. usvaensis*', '*A. multykensis*', '*A. beckeri*' and '*A. olli*': Kumar & Pandey, 2008; Kolesnikov *et al.* 2012). Presently, only *A. banksi* and *A. vindhyanensis* are considered valid (Kolesnikov *et al.* 2017), and these are differentiated by the frequency of line bifurcation. *Arumberia banksi* was most recently re-described by Retallack & Broz (2020), while the systematic description of *Arumberia vindhyanensis* can be found in Kumar & Pandey (2008). In the Port Lazo Formation, specimens that could be attributed to both of these species can be seen to grade into one another (compare Fig. 3a and Fig. 3g), suggesting that subdivision to species level may have limited biological meaning (see Section 6.d). Morphological differences between forms may instead stem from external hydrodynamic or environmental factors.

5. Global stratigraphic range of true *Arumberia*

Arumberia has a narrow stratigraphic range, spanning the Neoproterozoic to lowermost Cambrian strata (Table 2), a trend that becomes particularly pronounced when equivocal reports of the surface texture are omitted (Fig. 8). These equivocal reports include 14 records where *Arumberia* is reported but not figured or described in a paper (i.e. with no evidence presented to verify or falsify the claim), and the following six instances that are here rejected as being *Arumberia* because they are either markedly dissimilar to both the original (Glaessner & Walter, 1975) and

emended diagnoses (Section 4), or are insufficiently well preserved to confirm their identification as *Arumberia*.

- (1) Bland (1984) proposed that a sedimentary surface texture illustrated by Miller (1975, fig. 2) from the Mesoproterozoic Auborus Formation of Namibia may be *Arumberia*. However, the original figure lacks the definition to confirm this, and Miller (1975) interpreted the texture as forming abiotically due to aeolian adhesion on a mudflat.
- (2) Bland (1984) suggested that a specimen illustrated by Kaudern (1932, fig. 5) from the Neoproterozoic Visingsö Formation of Sweden may represent poorly preserved casts of *Arumberia*. Kaudern's (1932) original figure shows only a small hand specimen with no sedimentological context, and the sample is therefore an unconvincing example of *Arumberia* given its poor preservation.
- (3) Callow *et al.* (2011, fig. 10) reported and figured surface textures described as *Arumberia* from the early Neoproterozoic Diabaig Formation of Scotland. However, these surface textures differ from both the original and revised diagnoses of *Arumberia*, with lines being sporadically spaced, changing width along their lateral extent and showing a wide disparity of orientations even across small bedding planes. The interpretation of these specific structures by Callow *et al.* (2011) as forming due to the moulding of entwined microbial filaments appears robust, but they are dissimilar to classic *Arumberia*.

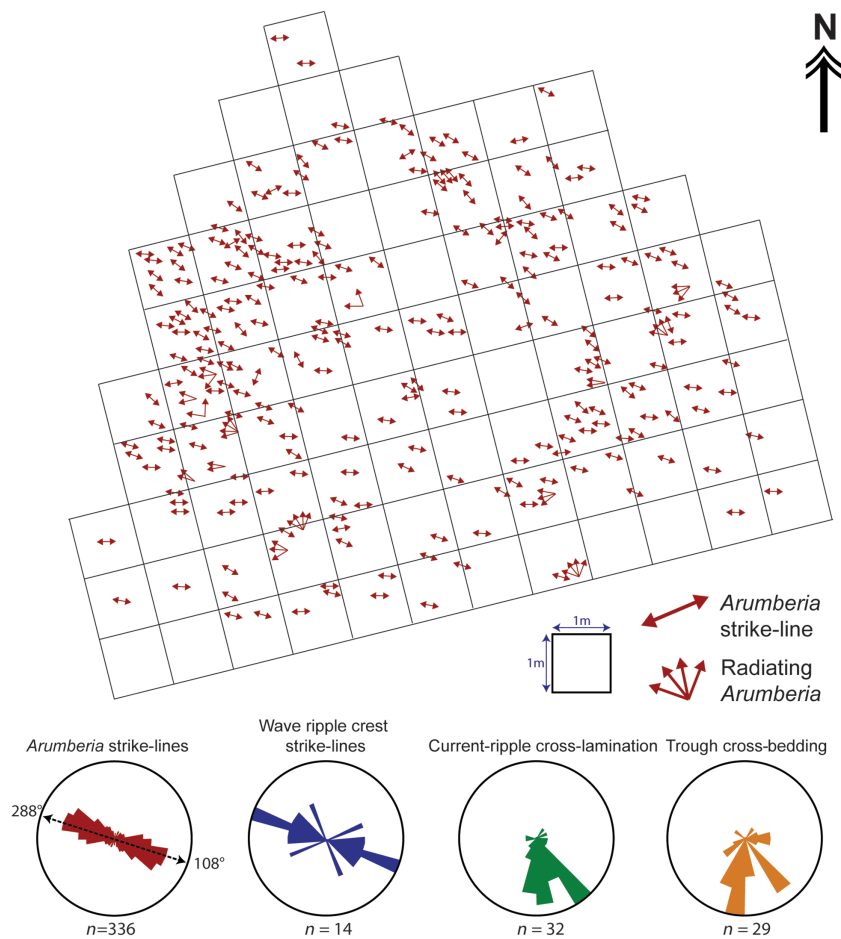


Fig. 6. (Colour online) Map of *Arumberia* line orientations on a 300 m² bedding plane in the Port Lazo Formation. Rose diagrams indicate predominant palaeoflow is approximately perpendicular to line orientation. Total mapped area 86 m².

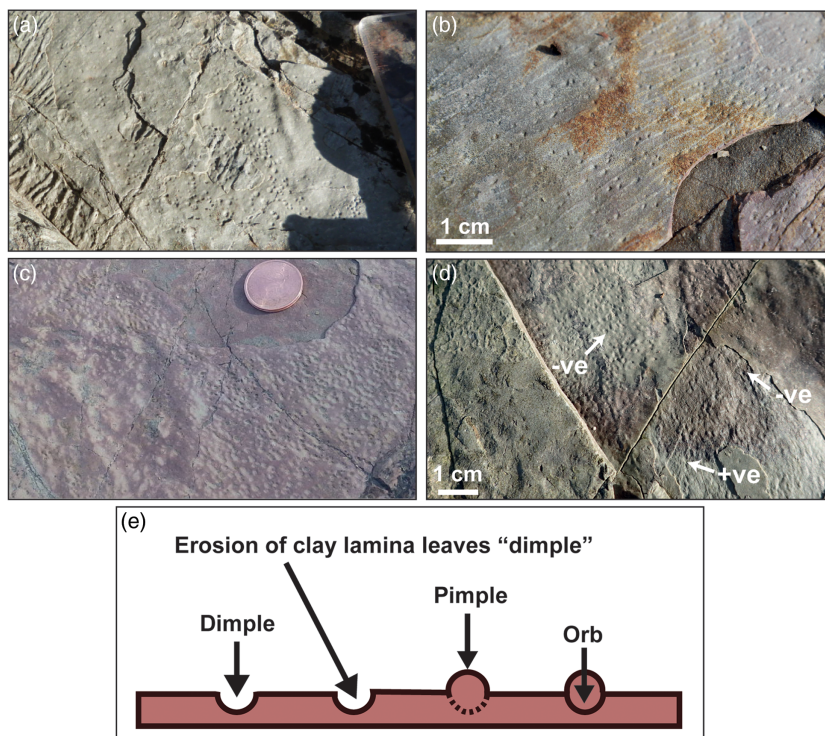


Fig. 7. (Colour online) ‘Dimple-pimple’ marks associated with *Arumberia* in the Port Lazo Formation. (a) Population of negative epirelief dimples on a plane directly underlying clay laminae hosting *Arumberia* lines. (b) Positive epirelief *Arumberia* lines superimposed by negative epirelief dimples. (c) Subcircular negative epirelief dimples occurring independently of *Arumberia*. Coin is 23.25 mm in diameter. (d) Positive epirelief pimples immediately overlain by negative epirelief dimples. (e) Interpretative sketch of 3D spheroidal orbs, and regularly viewed two-dimensional dimples and pimples.

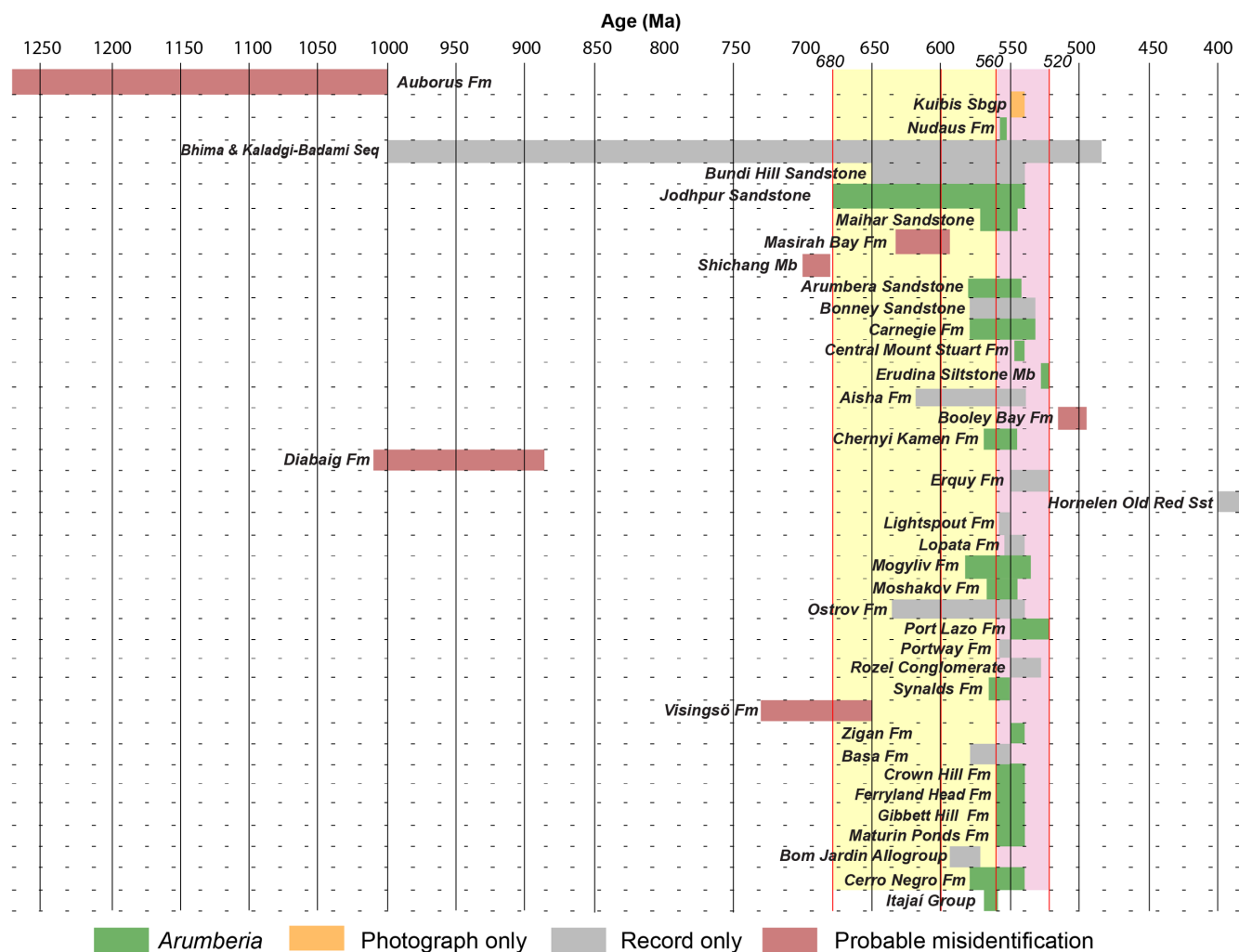


Fig. 8. (Colour online) Chronostratigraphic ranges of reported instances of *Arumberia*. Green bars mark *Arumberia* identifications that are fully described and photographed and shown to closely match either the original (Glaessner & Walter, 1975) or emended (this study) *Arumberia* diagnosis. Orange bars mark instances where *Arumberia* has been photographed, but no other sedimentological or morphological details have been provided. Grey bars denote formations in which *Arumberia* have been stated to occur, but no informative details of morphology have been provided. Red bars indicate formations where *Arumberia* has been described but, following scrutiny of form (Section 5), likely represent features not equivalent to *Arumberia* (as originally diagnosed by Glaessner & Walter, 1975). Yellow and purple columns indicate the chronostratigraphic restriction of *Arumberia* when dubious reports are excluded (680–520 Ma). Purple column alone shows a tighter stratigraphic range (560–520 Ma), evident when considering only overlapping ranges of posited ages.

- (4) Reported *Arumberia* from the Ediacaran Masirah Bay Formation of Oman were figured by Allen & Leather (2006, figs 14c, d) and Brasier *et al.* (2011, fig. 11b). Brasier *et al.* (2011) noted that the features extended for up to “hundreds of square kilometres” and suggested that they reflected the flow of bottom currents interacting with possible filamentous microbes or algae. In both publications the small dimensions of the figured specimens make an assured diagnosis difficult, but their apparent and regular intertwining of sinuous ridges is not present in any other known *Arumberia* specimens (Table 1).
- (5) *Arumberia* reported from the Upper Cambrian Booley Bay Formation of Ireland (MacGabhann *et al.* 2007, fig. 15) do not have a uniform line thickness across each bedding plane, unlike *Arumberia* examples described elsewhere (Table 1). Additionally, many individual lines exceed 0.5 cm in diameter, greater than any other previously described *Arumberia*.
- (6) Liu (1981) described *Arumberia* from a limestone bed of the Shichang Member in China, the only report from a carbonate

lithology. The small figured specimen makes confirmation difficult, but the positive epirelief lines appear to be an order of magnitude greater in size than any other *Arumberia* reports (Table 1).

When these examples are excluded, all remaining reports of *Arumberia*-hosting strata date to 520–680 Ma in age (Fig. 8). When considering the overlapping ranges of posited ages, the stratigraphic range can be further refined to 520–560 Ma in age (this is also true for 12 of the 14 instances of reported *Arumberia* that were not figured in their original reports).

6. Abiotic or biotic?

The limited range of consistently expressed morphological characteristics of ‘true’ *Arumberia*, and the inclusion of a wide variety of instances of clustered lines on bedding planes within the genus in the past, have resulted in ongoing debate regarding the biogenicity of this feature. Three lines of evidence are discussed here to interrogate these competing claims: similarity to abiotic forms, the tight

global stratigraphic range and the preferred orientation of specimens.

6.a. Similarity to abiotic forms

Features with a passing resemblance to some *Arumberia* specimens were created abiotically by Dżułyński & Walton (1965) in flume tank experiments devised to study sedimentary features associated with deep marine flysches. Brasier (1979) was the first to note this similarity, and it has subsequently been invoked to contend that *Arumberia* was, at least in part, hydrodynamic in origin (e.g. Kumar & Pandey, 2008; Callow *et al.* 2011; Menon *et al.* 2016). We note that the structures developed by Dżułyński & Walton (1965) occurred within turbidity-current-generated sand, while the majority of *Arumberia* worldwide come from mudstones and siltstones deposited in emergent and nearshore marine environments (Table 1; a notable exception is the Masirah Bay Formation '*Arumberia*' from lower shoreface/offshore facies (Allen & Leather, 2006) discussed in Section 5). Tangible characteristics of exposed *Arumberia* in the Port Lazo Formation (3D cord-like form, reticulated transitions, potential for cords to curl when subject to emergence) cannot, in concert, be explained by purely hydrodynamic mechanisms. Cohesive mud and granular sand have very different responses to hydrodynamic forces, and so the similarity to Dżułyński & Walton's (1965) sedimentary structures is most likely an artefact of equifinality. Furthermore, the observation that exceptionally well preserved specimens comprise finer linear structures (Fig. 1d, h) rules out abiotic formation mechanisms that produce only surface impressions. The bundling of these cords is consistent with them preserving discrete filamentous organisms such as bacteria or algae, and is inexplicable by fluid dynamics alone.

6.b. Stratigraphic range

McIlroy & Walter (1997) used the tight stratigraphic range of *Arumberia* to suggest that it is an anactualistic fabric on sedimentary surfaces resulting from the interplay of microbial mats with physical hydrodynamic processes. However, this interpretation cannot explain the absence of *Arumberia* from Phanerozoic or lower Precambrian strata. Both of these intervals host abundant sedimentary surface textures attributable to the interplay of fluids and microbial mats (Davies *et al.* 2016). *Arumberia* is absent from comparable Phanerozoic sedimentary facies where bedding planes have received intensive study: for example, there are no reports of *Arumberia* in voluminous desiccated red mudrocks of the Siluro-Devonian Old Red Sandstone and equivalent strata, despite detailed investigations of surficial trace fossils (e.g. Gordon, 1988; Smith *et al.* 2003; Shillito & Davies, 2017) and microbial sedimentary surface textures (Davies *et al.* 2006, 2016; Marriott *et al.* 2013) in littoral facies. Similarly, *Arumberia* is also unknown from pre-Ediacaran successions that have been interrogated for microbial sedimentary structures (e.g. Eriksson *et al.* 2012; Lan *et al.* 2013; Beraldi-Campesi *et al.* 2014).

Given that no physical hydrodynamic fluid processes are likely to have been unique to the Ediacaran–Cambrian transition, the most parsimonious explanation for the stratigraphic restriction of *Arumberia* (Fig. 8) is that there was a dominant biological component to its formation (Bland, 1984; Kumar & Pandey, 2008, 2009; Kolesnikov *et al.* 2012, 2015, 2017; Arrouy *et al.* 2016). This is also implied by the variability in individual *Arumberia* linearity (Fig. 5), reticulation (Fig. 3i, j) and spacing (Fig. 3a–h) observed within the large bedding plane studied at Port Lazo.

Such morphological diversity is challenging to account for solely through hydrodynamic processes, but can be explained as different manifestations of a living system.

Forms resembling *Arumberia* have been observed on the surface of biofilms in modern salterns, with radiating and curved macroscopic ridges interpreted to form as a microbial community responds to changing environmental pressures (Kolesnikov *et al.* 2017). While these extant 'arumberiamorph structures' demonstrate a further mechanism by which equifinal *Arumberia*-like morphologies can form, they are unlikely to be direct analogues for the ancient *Arumberia* described here, given the global abundance of such forms in Ediacaran–Cambrian strata and the total absence of verified instances in the post-Cambrian rock record. The absence of *Arumberia* in any Phanerozoic strata, despite directed searching of equivalent facies, is most prosaically explained as a faithful historic testimony of its disappearance. This is because a Cambrian to Recent gap in the record of any sedimentary or fossil feature is significant: the notion that it is explainable by a > 500 Ma duration failure of the sedimentary-stratigraphic record to archive a relatively mundane sedimentary environment is unsubstantiated.

6.c. Orientation of *Arumberia* lines

One consensus viewpoint regarding *Arumberia* is that there is a dominant directionality to its orientation on individual surfaces, which has been considered to result from either physical (e.g. Brasier, 1979; Jenkins *et al.* 1981; McIlroy & Walter, 1997; Seilacher, 2007) or biological (Glaessner & Walter, 1975; Bland, 1984) mechanisms of alignment. Of the 40 reports in Table 1, 17 consider *Arumberia* line orientations with respect to the local current (as measured by ripple mark strike-lines on bedding planes hosting *Arumberia*, or indirectly inferred from palaeoflow indicators measured throughout the host succession). These case studies reveal that *Arumberia* may in fact strike both parallel and perpendicular to the original flow direction (Fig. 9a–f; Table 1). Within the Port Lazo Formation studied here, a strong perpendicular arrangement is apparent (Section 3.b; Fig. 6).

Kolesnikov *et al.* (2017) suggested that the organization of *Arumberia* lines may not necessarily be current-induced, but instead archive a trophic response of a microbial community in competition for sunlight. However, if this were the case, line orientation should be expected to be random relative to flow, rather than preferentially oriented with or normal to the prevailing current direction. We note that in several cases, *Arumberia* is aligned with flow in those environments where there was a unidirectional component (as shown by preserved linguoid ripple marks with superimposed, parallel *Arumberia* lines; Fig. 9b, c), but lies perpendicular to flow in settings with dominantly oscillatory flow conditions (as shown by *Arumberia* lines striking alongside preserved symmetrical wave-ripple marks; Fig. 9a, f). This would imply that *Arumberia* orientation could be in flux when 'active', and that the orientation of preserved *Arumberia* lines was dependent on external influences at the chance instant of burial. Lines aligned with ripple crests under gently oscillating flow, but were streamlined in the direction of a steady flow (e.g. see Davies *et al.* 2017). Reorganization in this way suggests that the *Arumberia* lines may record flexible cords that were pliant with hydrodynamic forcing. Such organization has analogue with extant marine algae, the flexible components of which reorganize and reorientate under increasing unidirectionality and discharge of water flow (e.g. Denny & Gaylord, 2002).

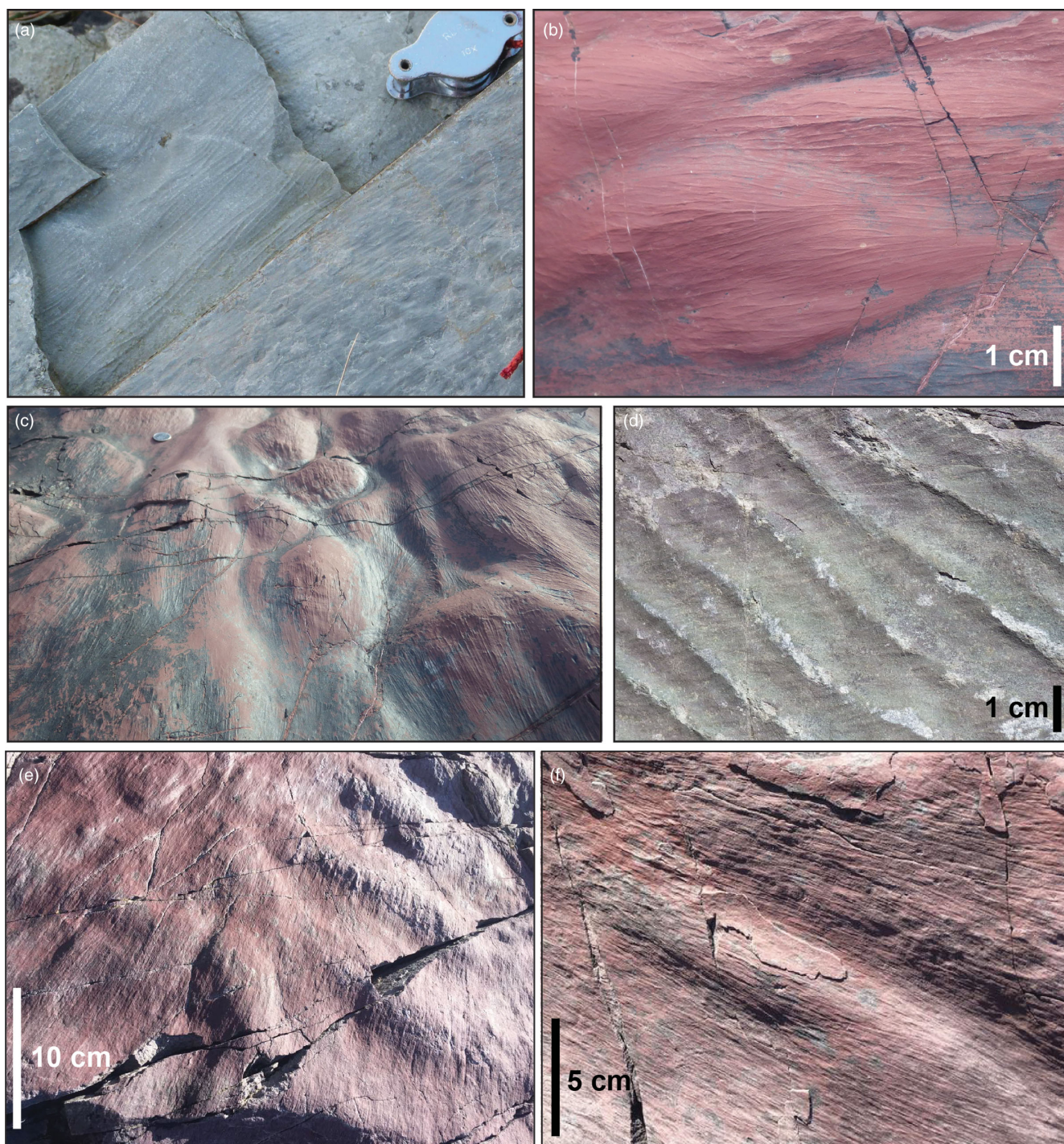


Fig. 9. (Colour online) Relationships between *Arumberia* lines and original flow. (a) Flow-perpendicular *Arumberia* superimposed on top of symmetrical wave-ripple marks. Port Lazo Formation Upper Member. (b, c) Flow-parallel *Arumberia* situated on top of unidirectional linguoid ripple marks. Crown Hill Formation, Newfoundland. (d) Flow-parallel to oblique *Arumberia* situated above symmetrical ripple marks. Ferryland Head Formation, Newfoundland. (e) Flow-parallel *Arumberia* situated above asymmetrical ripples marks. Crown Hill Formation, Newfoundland. (f) Flow-perpendicular *Arumberia* situated above poorly developed wave-ripple marks. Gibbett Hill Formation, Newfoundland. Hand lens is 4 cm wide. Coin is 16.25 mm in diameter.

Perpendicular arrangements with the prevailing current flow, observed in the Port Lazo Formation (Fig. 6) and elsewhere (Table 1), require that there was a secondary, weaker current that was strong enough to re-orientate *Arumberia* but insufficient to reorganize the sediment grains on the colonized surface. One potential scenario arises when a subordinate current drains water

away following an interval of elevated water level (e.g. in the receding waters of a tidal prism). Such conditions were likely frequently met in the deposition of *Arumberia*-bearing strata, which are composed of periodically emergent facies in the majority of unequivocal reports of the form (Table 1). In the Port Lazo Formation, evidence of water drainage and exposure is indicated

by the occurrence of raindrop impressions (Fig. 2g) and desiccation cracks (Fig. 2f) alongside *Arumberia*, and possibly also through the reticulated *Arumberia* forms (Fig. 3i, j).

6.d. *Arumberia* is most likely a fossil organism

The arguments above strongly suggest that *Arumberia* records an extinct, environmentally restricted and sessile biological entity that was composed of non-biomineralized, 3D, flexible cords (see also Bland, 1984, p. 630). The origins of some of its associated features (e.g. dimple-pimple marks) remain enigmatic, and its precise biological affinity remains uncertain, even though it is parsimonious to assume that it was algal or microbial. While this conclusion is similar to that reached by Kolesnikov *et al.* (2012), who suggested that *Arumberia* records extinct, highly organized microbial colonies capable of producing 3D 'rugae', we caution against splitting the texture into biological 'species' given the propensity of these to grade into one another (Section 4). Differences between these forms (e.g. *A. banksi*, *A. vindhyanensis* and also non-*Arumberia* linear morphologies) may stem from external hydrodynamic or environmental factors, reflecting the form that happened to be adopted at the instant of burial. Clear transitions between linear (Fig. 3a–h), reticulated (Fig. 3i, j) and curled (Fig. 5) *Arumberia* rule out a recent 'vendobiont' fossil hypothesis (Retallack & Broz, 2020), since discrete macroorganisms would not have been expected to reorganize their form during emergence.

7. Conclusions

Arumberia consists of parallel, sub-parallel or radiating lines that present in both positive and negative epirelief. A detailed examination of the most contiguous *Arumberia*-bearing bedding plane so far discovered, from the Port Lazo Formation (NW France), combined with a literature survey of all known *Arumberia* reports, indicates:

- the 3D morphology of *Arumberia* resemble cords or tubes distinct from the preserving sediment;
- linear *Arumberia* cords transition laterally into reticulated networks, morphologies that bear strong resemblance to modern instances of reticulate marks formed as buoyant filaments of bacteria or algae become tangled in standing or draining water;
- some *Arumberia* cords are demonstrably composed of finer, superimposed and overlapping threads;
- *Arumberia* cords curl in proximity to desiccated plate margins, an apparent response to shrinking cohesive sediment undergoing emergence;
- the orientation of *Arumberia* lines differs in different depositional settings, with lines apparently being streamlined in the direction of a unidirectional current, but oriented parallel to ripple crests when subject to oscillating flow; and
- the significant majority of *Arumberia* occurrences worldwide are recorded from rocks dated to 520–560 Ma in age.

Together, these observations discredit the possibility that *Arumberia* is a purely physical sedimentary structure, and strongly favour a biological origin as the impression of an extinct, sessile Ediacaran–Cambrian organism or population of organisms composed of 3D, flexible cords.

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