

## Original Article

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**Author for correspondence:**

Jennifer F. Hoyal Cuthill,  
Email: [j.hoyal-cuthill@essex.ac.uk](mailto:j.hoyal-cuthill@essex.ac.uk)

# Ediacaran survivors in the Cambrian: suspicions, denials and a smoking gun

Jennifer F Hoyal Cuthill 

Institute for Analytics and Data Science and School of Life Sciences, University of Essex, Wivenhoe Park, Colchester CO4 3SQ, UK

**Abstract**

The relative timing of extinctions and originations is a foundation for reconstructing evolutionary causes. However, there has been a tendency to dismiss reported Ediacaran holdovers in favour of effective extinction around the Cambrian boundary. Here, focusing on the classically Ediacaran frondose biota (Petalonamae), I suggest four main reasons why proposed Ediacaran survivors have previously been denied the acceptance they deserve: denials based on mistaken identity, doppelgängers, a last gasp or dead clades walking. I then point to the lower Cambrian species *Stromatoveris psymoglena* as a key example which simultaneously meets these objections. Collectively, Cambrian survivors are a ‘smoking gun’ showing that extinction of the classically Ediacaran frondose biota did not occur until at least 30 Ma after the end of the Ediacaran period, registered by phylogenetic petalonamid *Thaumaptilon* from the Burgess Shale. Therefore, to paraphrase Mark Twain, reports of their earlier demise have been greatly exaggerated. Causes of their ultimate extinction should instead be sought in their total range and diversity dynamics. Overall, the Ediacaran–Cambrian transition shows extremely low numbers of recorded survivors, but diversity dynamics are dominated by the Cambrian explosion. In this context, recorded occurrences for the classically Ediacaran frondose biota are compatible with at least two extinction events, one within a possible mass extinction near the Cambrian boundary, and later, their ultimate extinction in, or after, the middle Cambrian (Miaolingian Series, Wuliuan Stage). There is, however, no correlative basis for a causal link between the Cambrian transition and the effective or final demise of the classically Ediacaran soft-bodied biota.

**1. Introduction**

In 1897 Mark Twain wrote a now famous letter noting that reports of his death had been greatly exaggerated. While he eventually died in 1910, it is obvious that this inevitable event did not validate its earlier reports: if survival beyond a reported date can be demonstrated beyond reasonable doubt, contrary preconceptions must be updated. With regard to the fossil record, this matters, not least, because the relative timing of extinctions and originations is a foundation for the reconstruction of evolutionary causality, for which correlation represents necessary primary evidence.

Recently, a range of Ediacaran to Cambrian workers have suggested that the evolutionary transition between these periods is more complex and less sharp than once thought (Martin *et al.* 2000; Budd & Jensen, 2017; Muscente *et al.* 2018; Cribb *et al.* 2019; Wood *et al.* 2019). Two key lines of evidence can be identified among recent studies, which argue for a shift in perspective on prior views of early animal evolution. The first is that new fossil finds have pushed back into the Ediacaran the origin of taxonomic groups, traits and behaviours known previously from the Cambrian (Budd & Jensen, 2017; Cribb *et al.* 2019; Wood *et al.* 2019). Individual fossil blocks which preserve both classic Ediacaran morphologies and bilaterian-style trace fossils strikingly demonstrate that these were contemporaneous (Jensen *et al.* 1998; Wood *et al.* 2019). Further reports of early trace fossils range from simple, backfilled and vertical burrows described from the White Sea of Russia and radiometrically dated to  $555.3 \pm 0.3$  Ma (Martin *et al.* 2000), to surface scratch traces associated with the proposed bilaterian *Kimberella* (Gehling *et al.* 2014) reported to  $555.3 \pm 0.3$  Ma (Martin *et al.* 2000), comparatively large and complex, segmented traces, including approximate-spiral traces dated to  $539.4 \pm 1$  Ma (Jensen & Runnegar, 2005) and *Treptichnus*-type traces from close to the Cambrian boundary (Jensen *et al.* 2000), with the Ediacaran–Cambrian boundary dated in the 2020 Geological Timescale to *c.* 539 Ma ( $538.8 \pm 0.6$  Ma) (Peng *et al.* 2020) based on U–Pb radiometric dating from the Spitskop Member in southern Namibia (Linnemann *et al.* 2019). Such finds suggest that while bilaterians may have been rarer before the Cambrian, they were present in the Ediacaran (Jensen & Runnegar, 2005; Gehling *et al.* 2014; Cribb *et al.* 2019). The second line of evidence, on which this paper will focus, concerns Ediacaran ‘survivors’ or ‘holdovers’ in the Cambrian, to-date including records from at least four countries (Australia, the USA, China and

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Canada) and extending from the Cambrian boundary (Jensen *et al.* 1998) to at least the middle Cambrian (Conway Morris, 1993) at *c.* 508 Ma (Aria & Caron, 2017) to 505 Ma (Saleh *et al.* 2020) Ma.

Despite these straws in the wind, however, many, if not most, recent papers still describe an effective extinction of the Ediacaran soft-bodied macro-biota by, or at, the beginning of the Cambrian. For example, Narbonne (2005) stated, 'a handful of possible "Ediacaran survivors" have been described from Cambrian strata ..., but all diverse occurrences of the Ediacara biota ... predate the base of the Cambrian'. Similarly, Cribb *et al.* (2019) stated, 'the overwhelming majority of soft-bodied Ediacaran groups ... decline in the latest Ediacaran Nama interval and disappear entirely at the Ediacaran–Cambrian boundary'. While acknowledging evidence for at least some Ediacaran survivors in the Cambrian, Muscente *et al.* (2018) stated, 'for all intents and purposes, however, the fossil record of Ediacara biota broadly terminates at the Precambrian–Cambrian boundary'.

Furthermore, a number of papers (my own included (Hoyal Cuthill & Conway Morris, 2014)) have discussed potential causal connections between extinctions of, or within, the Ediacaran biota and evolutionary and environmental events around the Cambrian boundary, including the diversification of bilaterians (Seilacher, 1992; Narbonne, 2005), consequent increases in bioturbation, reductions in microbial mat-grounds and possible changes in sediment and ocean chemistry (Hoyal Cuthill & Conway Morris, 2014; Muscente *et al.* 2018; Cribb *et al.* 2019).

There is now extensive evidence for morphological, phylogenetic and taxonomic links between the Ediacaran and Cambrian frondose biotas (Conway Morris, 1993; Jensen *et al.* 1998; Hagadorn *et al.* 2000; Hagadorn & Waggoner, 2000; Shu *et al.* 2006; Hoyal Cuthill, 2022), notably including locally abundant *Stromatoveris* of the lower Cambrian Chengjiang biota (Hoyal Cuthill & Han, 2018a, b) and middle Cambrian *Thaumaptilon* from the Burgess Shale (Conway Morris, 1993; Hoyal Cuthill, 2022). This paper will explore three consequent questions, should such linking evidence be accepted. First, what are the objections that have previously been raised to proposed Ediacaran survivors and do these hold up in the light of recent evidence? Second, if we go on to accept the prolonged existence of at least some Ediacaran survivors, which of the things once thought about the Ediacaran to Cambrian transition must we actually do away with? Third, which new conclusions and questions does this prompt?

## 2. Ediacaran survivors in the Cambrian

Since Ediacaran soft-bodied macro-fossils were definitively identified as such, at least 19 genera have been described that can broadly be described as frondose (with frondose here broadly referring to any taxon with a proposed frond or 'petaloid' (Pflug, 1972) regardless of its inferred inclination to the sediment, e.g. upright or reclining). This count (which is considered minimal rather than exhaustive) includes 'rangeomorphs' such as *Rangaea* (with Liu *et al.* (2015) listing 12 Avalonian genera), arboreomorphs such as *Arboreal/Charniodiscus* (Laflamme *et al.* 2018), another proposed frondose taxon from Avalonia, *Parviscopa* (Liu *et al.* 2015), *Ernietta*, *Pteridinium* and *Swartpuntia* (Hoyal Cuthill & Han, 2018a). Albeit more controversially, due to frequently suggested bilaterian affinities (Gold *et al.* 2015), dickinsoniomorphs (exemplified by *Dickinsonia*) should also be considered alongside the frondose, or petalonamid (Hoyal Cuthill & Han, 2018a),

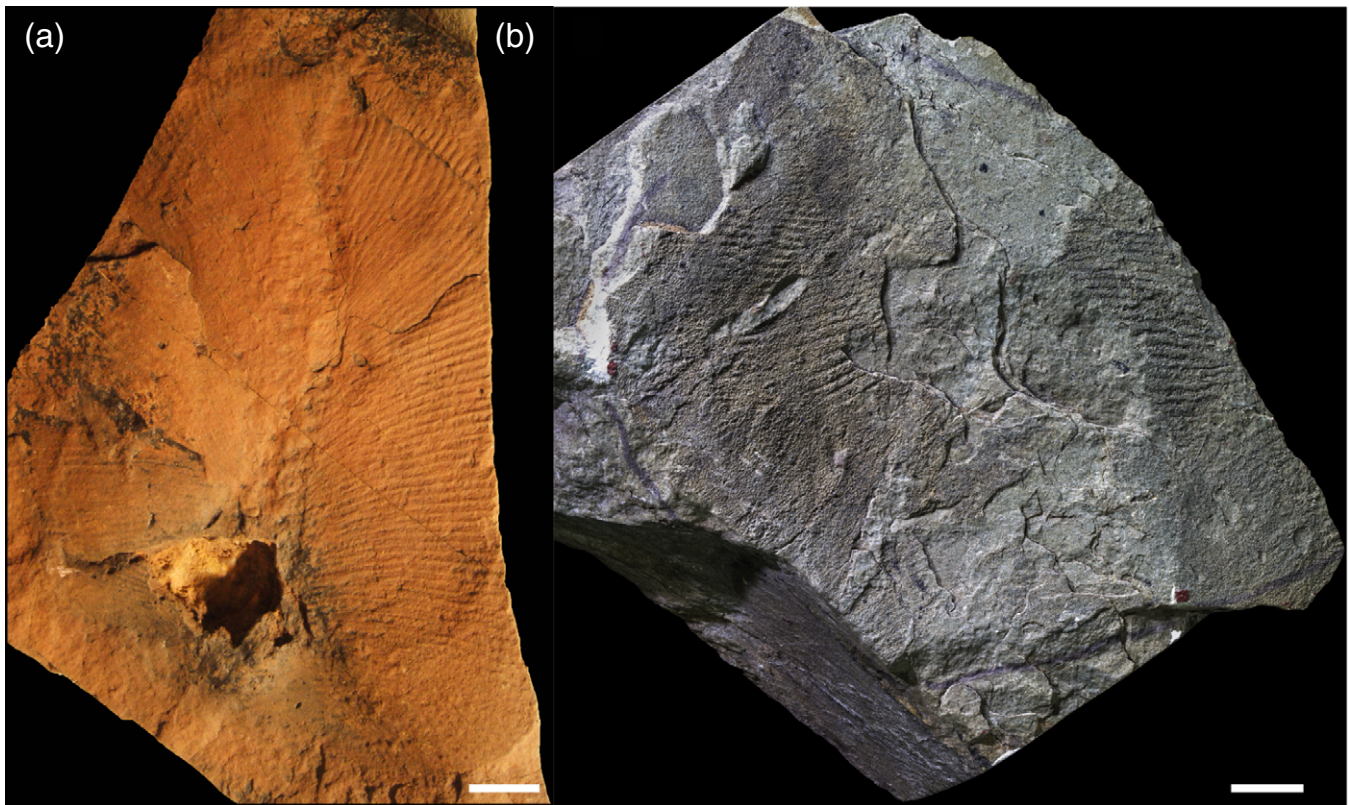
soft-bodied Ediacaran biota. In particular, at least some authors have previously grouped dickinsoniomorphs with other Ediacaran biota, based on argued morphological similarities such as a serially subdivided body unit, alternate branching observed in at least some specimens and axial and apical branch growth (Seilacher, 1992; Brasier & Antcliffe, 2008; Hoyal Cuthill & Han, 2018a).

While many of these Ediacaran genera have not been recorded from younger rocks, at least one has (Jensen *et al.* 1998; Hagadorn *et al.* 2000) and there are several additional reported occurrences of morphologically similar, frondose genera from the lower to middle Cambrian (Conway Morris, 1993; Hagadorn *et al.* 2000; Shu *et al.* 2006; Hoyal Cuthill & Han, 2018a). These records notably include fossils described as *Swartpuntia*, or *Swartpuntia*-like, from the lower Cambrian (e.g. Fig. 1; Jensen *et al.* 1998; Hagadorn *et al.* 2000), locally abundant *Stromatoveris* from the Chengjiang biota (Shu *et al.* 2006; Hoyal Cuthill & Han, 2018a) of the lower Cambrian (Series 2, Stage 3, >~514 Ma (Walker *et al.* 2018; Landing *et al.* 2020; Saleh *et al.* 2020)) and *Thaumaptilon* from the Burgess Shale (Conway Morris, 1993) of the middle Cambrian (Miaolingian Series, Wuliuan Stage, ~508–505 Ma (Aria & Caron, 2017; Landing *et al.* 2020; Saleh *et al.* 2020)). Here, I suggest, in particular, that previous objections which have been used to dismiss individual Ediacaran holdover taxa are simultaneously met by *Stromatoveris* and are therefore inadequate to negate the collective evidence the holdovers represent.

## 3. Denials

### 3.1 Objection 1. Mistaken identity from fragmentary glimpses?

Some of the first-alleged Ediacaran survivors are represented by only small numbers of sometimes fragmentary fossils, which has contributed to expressed uncertainty regarding their identification and affinities. For example, specimens from the Ediacaran–Cambrian (Smith *et al.* 2017; Hall *et al.* 2020) Wood Canyon Formation and lower Cambrian (Muscente *et al.* 2018) Poleta Formation (Fig. 1b) were originally described by Hagadorn and colleagues in 2000 (Hagadorn *et al.* 2000) as *cf. Swartpuntia* (with *cf.*, Latin *conferre*, meaning comparable or similar to a referenced taxon but not attributable to it with complete certainty (Lucas, 1986)). Another Wood Canyon specimen was reported as *Swartpuntia c.f. germis* (Hagadorn & Waggoner, 2000). A later review (Narbonne, 2005) cited Cambrian *Swartpuntia*-type fossils from the USA as well as Australia (Jensen *et al.* 1998), alongside *Thaumaptilon* from the Burgess Shale (discussed further below), as 'possible Ediacaran survivors' (emphasis added). Smith *et al.* (2017) stated, 'fragments of sandstone with parallel structural elements were identified as *Swartpuntia*, but this is a problematic classification with no complete specimens or specimens preserving a basal stalk'. It is notable in this context, therefore, that the stalk originally described in *Swartpuntia* (Narbonne *et al.* 1997) is not clearly visible even in the classic Namibian material (Fig. 1a). Furthermore, while the Wood Canyon *Swartpuntia* fossils are rare and somewhat fragmentary, this is also the case for the classic Namibian material (Narbonne *et al.* 1997). The descriptions of *cf. Swartpuntia* from the Wood Canyon Formation figure two specimens (Hagadorn *et al.* 2000), and Hagadorn & Waggoner (2000) figure one more. The classic Namibian material (which includes the holotype) is represented by two specimens available in the type and figured collection of the National Earth Science Museum of Namibia (nos. F238-H, F245-p), neither of which shows the entire organism,



**Fig. 1.** Ediacaran holotype of *Swartpuntia germsi* (a) compared with Cambrian cf. *Swartpuntia* (b). (a) National Earth Sciences Museum of Namibia specimen no. F238-H. (b) University of California Museum of Paleontology specimen no. UCMP 37450, photo courtesy of Dave Strauss, originally described from the Poleta Formation, White Mountains, California (Hagadorn *et al.* 2000). The Cambrian specimen shows the broad aspect ratio typical of Ediacaran *Swartpuntia* and parallel lines compatible with characteristic petaloid sub-branching. Scale bars 1 cm.

due to breakage (although they are nonetheless exceptionally large and well-preserved Ediacaran fossil specimens). Most importantly, however, the Cambrian specimens do show several features consistent with taxonomic placement within genus *Swartpuntia* (Fig. 1), including large size, broad aspect ratio and parallel angled units, as generally seen in the sub-branched fronds or ‘petaloids’ of Ediacaran frondose taxa.

Further to this, the prior representation of Ediacaran survivors by small numbers of somewhat fragmentary specimens has been changed by the case of lower Cambrian *Stromatoveris psygmoglena*. Over 200 organically preserved specimens of *S. psygmoglena* have been found (Hoyal Cuthill & Han, 2018a) since initial description of the species (Shu *et al.* 2006). Collectively, these specimens preserve multiple views of the organism’s morphology, facilitating detailed comparisons with Ediacaran taxa, including those that are similarly represented by multiple specimens (which together give a comprehensive picture of external morphology). The correspondences such comparisons show thereby cover the macro-structural arrangement of multiple petaloids, petaloid substructure and presence and structure of the basal holdfast region (Hoyal Cuthill & Han, 2018a). The abundance of morphological information that these new specimens provide (Hoyal Cuthill & Han, 2018a, b) therefore means that Ediacaran holdovers can no longer be collectively dismissed on grounds of potential mistaken identity from a fragmentary view.

### 3.2 Objection 2. *Doppelgängers?*

Another related objection to potential Ediacaran holdovers has been the possibility of evolutionary convergence on a broadly

analogous morphology, particularly an anchored frondose body-plan. For example, with subsequent reference to *Stromatoveris*, the objection had been made (Antcliffe & Brasier, 2007) that ‘if affinities between . . . groups are to be put forward and sustained, then we recommend that developmental homologies between them be demonstrated’. Similarly, with reference to Cambrian, Uratanna Formation *Swartpuntia*-type fronds (Jensen *et al.* 1998) and Chengjiang *Stromatoveris* (Shu *et al.* 2006), Muscente *et al.* (2018) opined that these fossils ‘do not closely resemble classic Ediacaran genera’, although they also noted that, ‘in cases of compression-type frond-like fossils, this apparent difference may be a result of differential taphonomy’.

Objections to broad similarity as a basis for taxonomic affinity are certainly noteworthy, not least because some kind of anchored structure which is itself elaborated (e.g. in an approximately fractal manner) is found across macro-organisms such as plants, fungi and animals (e.g. octocorals). There are likely strong functional reasons for this extensive convergence. Fractal structures represent space-filling forms which can be generated by repetition of very simple rules of growth (Hoyal Cuthill & Conway Morris, 2014). They are therefore encountered across diverse space-filling structures, both biotic and abiotic (e.g. river systems or mineral growths). Biologically, fractals are common to many interface systems, for example for exposure to light (e.g. leaves), the uptake of gases (whether dissolved in water (e.g. gills) or aerial (e.g. lungs)) or dissolved organic nutrients (e.g. projections of animal gut walls), for filter feeding on larger organic particles (e.g. in crinoids) or the dispersal of propagules (e.g. fungal spores). For entirely or partially sessile organisms that possess some kind of frond-like

structure, some kind of anchor is a likely necessity (e.g. crinoids, octocorals, fungi, algae, plants etc.).

While convergence, therefore, remains a general possibility, especially when only limited anatomical information is available, the likelihood of convergence as opposed to homology resulting from close relation declines as more morphological characters are shared. In *Stromatoveris*, the extensive anatomical information available from the large number of exceptionally preserved specimens has facilitated formal phylogenetic testing of hypotheses of convergence across a wide range of outgroups. This analysis strongly supported a direct phylogenetic and taxonomic affinity between *Stromatoveris* and Ediacaran frondose genera (grouped within an extension of proposed animal phylum Petalonamae, Pflug) (Hoyal Cuthill & Han, 2018a).

Of the three described specimens of *Thaumaptilon walcottii* from the Burgess Shale (Conway Morris, 1993), all show the highly compressed carbon-film preservation typical of Burgess Shale-type Lagerstätten and two of the specimens are comparatively small. Therefore, these collectively present less morphological evidence than the >200 specimens of *Stromatoveris*, for example. However, the holotype of *Thaumaptilon* (Fig. 2) is a large and exceptionally well-preserved specimen. This specimen shows, first, the overall sub-branched frondose morphology with basal holdfast typical of Ediacaran genera (Conway Morris, 1993) that have been placed phylogenetically within Petalonamae (Hoyal Cuthill & Han, 2018a). It also shows a number of additional, detailed morphological similarities to Ediacaran petalonamid specimens compatible with placement within this clade. These include the presence of a demarked central region, interpretable as an inter-axial band (Hoyal Cuthill & Han, 2018a), within which primary branching can be seen to occur but which is demarked from the outer lateral regions of the specimen by strong overprinted vertical lines (Fig. 2c). The holotype of *Thaumaptilon* also shows continuation of the surface texture similar to that of the upper frond within the basal, inferred holdfast, region (which in the case of *Thaumaptilon* combines small-scale striations with a pustular appearance, as can sometimes also be observed in *Stromatoveris*). Phylogenetic character coding for *Thaumaptilon* in a new photo-referenced character matrix (MophoBank Project 3868 (Hoyal Cuthill, 2022)) extended from that of Hoyal Cuthill & Han (2018a) enables phylogenetic analysis alongside previously proposed Ediacaran to Cambrian petalonamids and a wide range of outgroups. This supports phylogenetic placement of middle Cambrian Burgess Shale *Thaumaptilon* within Petalonamae (Fig. 2d).

### 3.3 Objection 3. A last gasp

Ediacaran-style, frondose impression fossils found alongside dense and complex trace-fossils were described from the lower Cambrian Uratanna Formation of Australia in 1998 (Jensen *et al.* 1998). Their morphology shows similarities to Namibian *Swartpuntia* specimens (Jensen *et al.* 1998) as well as other Ediacaran genera known from the Ediacaran of Australia. The fact that these specimens are found relatively close to the Cambrian boundary left open possibilities that they represented closure of a taphonomic window for mouldic preservation, particularly in sandstone (Jensen *et al.* 1998) (though see also Tarhan *et al.* 2018), or a last gasp of an Ediacaran biota and ecology recently overrun by bilaterian invaders in a 'biotic replacement' (Laflamme *et al.* 2013; Muscente *et al.* 2018). For example, given Palaeozoic examples of siliceous preservation, Tarhan *et al.* (2018) suggested, 'that the preservational window for Ediacara-style fossilization clearly did not close at the end

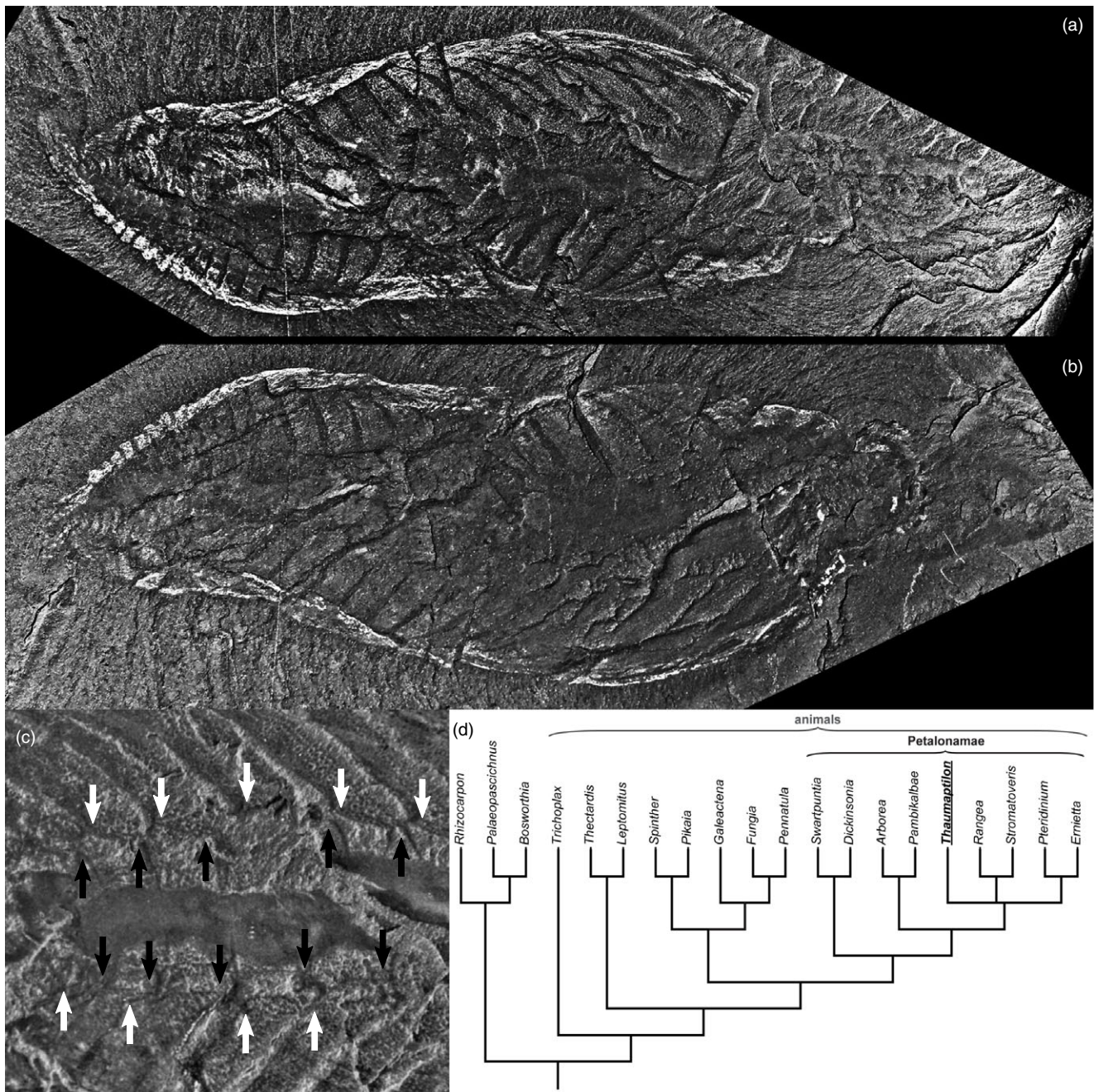
of the Ediacaran, but in fact remained open for over a hundred million additional years suggests that the disappearance of Ediacara Biota fossils cannot be attributed to taphonomic bias'. A key point is therefore that organically preserved Cambrian fronds including *Stromatoveris* and *Thaumaptilon* can be phylogenetically placed as surviving representatives of a classically Ediacaran biota (Fig. 2d; Hoyal Cuthill & Han, 2018a, b; Hoyal Cuthill, 2022). Consequently, they demonstrate that the classically Ediacaran biota did not disappear from the fossil record at the end of the Ediacaran Period, but instead increasingly appeared in a different preservational mode, typical of the changing time. General replacement of a mouldic preservational mode (Jensen *et al.* 1998) by organic preservation (as seen in Chengjiang *Stromatoveris* (Shu *et al.* 2006; Hoyal Cuthill & Han, 2018a) and also some earlier Ediacaran fossils, e.g. White Sea *Dickinsonia* (Bobrovskiy *et al.* 2018)) is precisely the pattern which would be predicted by a progressive shift away from the dominant (though not exclusive (Bobrovskiy *et al.* 2018)) mouldic mode of Ediacaran fossilization, towards increasing carbonaceous Lagerstätten preservation in the Cambrian (Sperling *et al.* 2018), combined with survival of at least some of the classically Ediacaran soft-bodied biota throughout this interval. The place to look for Ediacaran survivors or close relatives higher up in the Australian succession might then be carbonaceous Lagerstätten such as the Emu Bay Shale, with enigmatic soft-bodied fauna such as 'petalloid' problematica (Paterson *et al.* 2016) providing contenders for further comparative analysis. Globally, an organically preserved record of classically Ediacaran frondose morphologies continues through the lower Cambrian *Stromatoveris* from the Chengjiang biota up to the middle Cambrian *Thaumaptilon* from the Burgess Shale.

### 3.4 Objection 4. A dead clade walking

Prior to the discovery of a large number of specimens of *Stromatoveris*, the recorded Ediacaran survivors were all represented by small numbers of specimens per taxon and locality. The total number of Cambrian occurrences of Ediacaran survivors has also been considered comparatively low (Narbonne, 2005). Some have apparently interpreted this literally, as an indication that Ediacaran survivors represented a dead clade walking (in the sense of Jablonski, 2001): a minority component being edged out of the new Cambrian ecology. For example, Narbonne (2005) stated, 'changing taphonomic conditions ... [do] not fully account for the extreme scarcity of Ediacara-type fossils in Lower Cambrian Lagerstätten, such as at Sirius Passet and Chengjiang'.

Despite extensive work on Burgess Shale-type Lagerstätten, no further specimens of *Thaumaptilon* have been described to supplement the three originally known (Conway Morris, 1993). This picture of uniformly low local abundance was changed in the case of *Stromatoveris psygmoglena*, however, by the discovery (within the hyper-productive Chengjiang Lagerstätte) of at least 200 specimens. This demonstrates that this species, with its typically Ediacaran frondose morphology, was at least locally abundant within an advanced Cambrian ecology, which included recent phyla and life habits such as active filter feeding (Hou *et al.* 2017; Hoyal Cuthill & Han, 2018a).

Overall, therefore, recorded occurrences indicate: First, that Ediacaran survivors are represented across the major Cambrian Lagerstätten types from the early to mid-Cambrian, covering mouldic style-preservation (Hagadorn *et al.* 2000) (previously common in the Ediacaran (Narbonne, 2005)); Burgess Shale



**Fig. 2.** Cambrian *Thaumaptilon walcottii* (Conway Morris, 1993) and reconstructed phylogenetic position within the extended Petalonamae. (a, b) Part (a) and counterpart (b) of holotype. Specimen USNM 468028 held in the collections of the National Museum of Natural History, Smithsonian Institution. Specimen from the Stephen Formation, Burgess Shale (Conway Morris, 1993). Images courtesy of S. Conway Morris. Photograph of dry specimen under direct light, uniform digital contrast enhancement applied. Specimen length 212 mm (Caron, 2011). (c) Detail of basal section of part showing evidence of petaloid overprinting including offset primary lines (adjacent white and black arrows) separated by a strong perpendicular line, and an inter-axial band (central region between two rows of white–black arrow pairs). (d) Phylogenetic reconstruction based on a photo-referenced character matrix (Hoyal Cuthill, 2022) extended to include *Thaumaptilon*, from Hoyal Cuthill & Han (2018a). Strict consensus of two most parsimonious trees based on 42 characters, two parsimony uninformative, with tree length = 67, consistency index CI = 0.64, retention index RI = 0.85.

carbon films (Conway Morris, 1993); and Chengjiang, moderately three-dimensional, carbonaceous compressions (Shu *et al.* 2006; Hoyal Cuthill & Han, 2018a). Second, Ediacaran holdovers retain a global occurrence record into the Cambrian (Budd & Jensen, 2017). Third, despite a low overall preservation potential implied by infrequent, Lagerstätte-restricted occurrences (Budd & Jensen, 2017), *Stromatoveris* provides evidence of at least local abundance up to the middle Cambrian. Fourth, *Thaumaptilon* from the

Burgess Shale marks survival (Budd & Jensen, 2017) at least four stages into the Cambrian period (Walker *et al.* 2018) and 30 million years after their previously suggested effective extinction at the end-Ediacaran (Narbonne, 2005; Hoyal Cuthill & Conway Morris, 2014; Muscente *et al.* 2018; Cribb *et al.* 2019). Thus, while Cambrian frondose survivors do not appear to have recovered to their Ediacaran diversity, their Cambrian range exceeds the short extinction survival range (e.g. at the single geological stage

scale (Jablonski, 2001)) previously suggested for typical ‘dead clades walking’, and the numerous specimens of *Stromatoveris* demonstrate continued local abundance in Cambrian ecosystems.

#### 4. Implications

Arguably, previous objections to proposed Ediacaran survivors which portrayed them as mistaken glimpses, doppelgängers, a last gasp or dead clades walking have formed a basis for continued focus on the Cambrian transition in discussions of potential extinction causes. In other words, prior dismissals of Ediacaran survivors in the Cambrian as fragmentary and taxonomically uncertain (mistaken identities), potential convergences (doppelgängers), transitional (a last gasp) or short-lived and ecologically unimportant (dead clades walking) have facilitated presentations of an effective extinction of this biota at the Cambrian boundary (Narbonne, 2005; Muscente *et al.* 2018; Cribb *et al.* 2019). Some of these prior arguments were, however, formulated when the recorded tally of Ediacaran holdovers was limited to small numbers of specimens, some of which were fragmentary and/or found close to the Cambrian boundary. This situation has been changed by the discovery of hundreds of specimens of *Stromatoveris* (linked to frondose Ediacaran ‘petalonamids’ by morphological phylogenetic analysis (Hoyal Cuthill & Han, 2018a)). These locally abundant fossils from the Cambrian Chengjiang biota provide direct evidence against mistaken glimpse, doppelgänger, last gasp, or dead clade walking scenarios (as outlined above).

If the, now extensive, morphological evidence for Ediacaran survivors (Conway Morris, 1993; Jensen *et al.* 1998; Hagadorn & Waggoner, 2000; Hagadorn *et al.* 2000; Shu *et al.* 2006; Hoyal Cuthill & Han, 2018a, b; Hoyal Cuthill, 2022) to at least the middle Cambrian (Conway Morris, 1993) at c. 508 Ma (Aria & Caron, 2017) to 505 Ma (Landing *et al.* 2020; Saleh *et al.* 2020) is given the recognition it deserves (as also advocated by Budd & Jensen, 2017), what are the consequent implications for the pattern and causes of their eventual extinction?

##### 4.1 Bilateral diversification supplemented rather than replaced the Ediacaran biota

Without positing a major, unevincenced change in life habits between the Ediacaran and Cambrian frondose taxa, the implication is, first, that a classically Ediacaran morphology and its associated life habits (including feeding mode, predator defences and sediment anchoring mechanisms etc.) was capable of withstanding a time overlap with bilaterians of at least 47 million years (Budd & Jensen, 2017), from the appearance of trace fossils attributed to bilaterians by 555 Ma (e.g. Martin *et al.* 2000) to the occurrence of *Thaumaptilon* (Conway Morris, 1993) at ~508–505 Ma (Aria & Caron, 2017; Landing *et al.* 2020; Saleh *et al.* 2020). This time overlap is therefore of greater duration than their known Ediacaran time range of 35 Ma, from 574.17 ± 0.66 Ma (Matthews *et al.* 2021) to 539 Ma (Budd & Jensen, 2017). Second, the classically Ediacaran frondose morphology retained locally abundance (Hoyal Cuthill & Han, 2018a) within the comparatively advanced Cambrian ecology evident among the Chengjiang biota (Hou *et al.* 2017). This demonstrates that, in the case of the frondose soft-bodied biota, diversification of taxa and associated ecologies at the start of the Cambrian did not replace, but instead supplemented, those of the Ediacaran.

##### 4.2 The onset of the Cambrian explosion did not cause the elimination of the Ediacaran biota

The recorded occurrences of the Ediacaran to Cambrian frondose soft-bodied biota indicate no correlation between the start of the Cambrian explosion and the extinction of this classically Ediacaran clade, morphology or ecology as a whole (Budd & Jensen, 2017). Consequently, the Ediacaran survivors in the Cambrian tell us something important about the potential causes of their ultimate demise. The Cambrian boundary does not represent an extinction that was total or effectively total, with dead clade walking or last gasp scenarios ruled out by local abundance of *Stromatoveris* among the Changjiang biota. At a minimum, therefore, previous reports of an end-Ediacaran total (Seilacher, 1992), or effective (Narbonne, 2005; Hoyal Cuthill & Conway Morris, 2014; Muscente *et al.* 2018; Cribb *et al.* 2019), extinction of the classically Ediacaran soft-bodied biota are arguably greatly exaggerated.

To explain the extinction of the Ediacaran biota, there have been a number of previously proposed variations on models of ‘biotic replacement’, which link the extinction of classically Ediacaran groups to changes associated with the Cambrian explosion of bilaterian diversity (Muscente *et al.* 2018), including direct competition or indirect environmental or geochemical disturbance (Seilacher, 1992; Laflamme *et al.* 2013; Muscente *et al.* 2018). However, no such proposal accounts adequately for Ediacaran holdovers in the Cambrian with a survival range as long as their known Ediacaran duration and continued local abundance. Rather, this provides evidence directly contradicting a biotic replacement extinction model for the Ediacaran biota, at least in its strongest form of total or effective elimination of classic Ediacaran taxa as a causal consequence of bilaterian diversification at the Ediacaran–Cambrian transition (Seilacher, 1992; Laflamme *et al.* 2013; Muscente *et al.* 2018, 2019).

##### 4.3 Occurrences of Ediacaran–Cambrian biotas show a significant but partial diversity loss at this boundary

Partial extinction and consequent loss of diversity around the Cambrian boundary is supported by recorded occurrences, however, based on both qualitative and quantitative considerations. For instance, small to medium-sized, moderately elongate frondose taxa are represented in both the Ediacaran (e.g. *Rangea*, *Charnia*, *Arborea*) and the Cambrian (e.g. c.f. *Swartpuntia*, *Stromatoveris* and *Thaumaptilon*, the largest at up to 21 cm (Caron, 2011)). However, there remain highly distinctive Ediacaran taxa and associated morphologies (that should therefore stand a high chance of recognition even in very different preservational styles), which have no similar known representatives in the Cambrian. These include, for example, metre-scale specimens of *Dickinsonia rex* and large specimens of the rangeomorph *Bradgatia* which are fractally subdivided visibly (at the cm-to-mm scale) to at least four branching orders. The total number of Ediacaran survivors recorded from the Cambrian also remains comparatively low (Narbonne, 2005), with the number of reported finds indicating a maximum possible number of frondose species in the unit order. The three Cambrian frondose genera considered here (c.f. *Swartpuntia*, *Stromatoveris*, *Thaumaptilon*) comprise 16 % of the nineteen frondose genera counted for the Ediacaran, and only one of these Ediacaran genera (*Swartpuntia*) is also represented in the Cambrian, literally indicating an inter-period genus diversity loss of 95 %, with recovery to 16 % of prior diversity. Changes in the dominant mode of fossilization at the Cambrian

boundary remain a likely contributing factor (Jensen *et al.* 1998). However, as it stands, the fossil record of frondose soft-bodied taxa across the Ediacaran to Cambrian transition indicates a substantial, though partial, extinction event in the latest Ediacaran, close to the Cambrian boundary (Narbonne, 2005).

In this respect, the diversity dynamics of the Ediacaran biota are similar to those of some later clades (Budd & Mann, 2020b; Barnes *et al.* 2021) showing a long period of relative abundance, a partial extinction event and then another long period of survival at lower diversity before eventual extinction, apparently without descendants. Thus, potential causes of their total extinction should be sought, not solely in events around the Cambrian boundary, but in their overall diversity dynamics (taking into account their long Cambrian range) and their last occurrence record, which would be ~508–505 Ma (Aria & Caron, 2017; Landing *et al.* 2020; Saleh *et al.* 2020) based on *Thaumaptilon* from the Burgess Shale (though see Retallack (2018) for suggestions of a Devonian occurrence).

These diversity dynamics are potentially compatible with participation in a succession of at least (Muscente *et al.* 2019) two mass extinction events, one marked but partial extinction in the latest, or end, Ediacaran (often previously treated as the last appearance of the frondose Ediacaran macro-biota, as discussed above) and final extinction in, or after, the middle Cambrian. After 505 Ma, the next major extinction event apparent from Paleobiology Database (PBDB) occurrence records (specifically a top 30 event of species (Hoyal Cuthill *et al.* 2020) or genus (Fig. 3) extinction or radiation) is the extinction of Cambrian species recorded at the Ordovician boundary at 485 Ma (with  $\geq 42$  % species extinction recorded within a 1 Ma time window of the boundary). With regard to the true last occurrences of the Ediacaran soft-bodied biota, it is interesting, though unfortunate, that Ordovician discoveries in the Fezouata Shale, including arthropod taxa previously restricted to the Cambrian, have not, thus far (Saleh *et al.* 2020), extended to any entirely soft-bodied taxa, leading to suggestions of a comparative loss of the exceptional soft-tissue preservation seen in Cambrian (Saleh *et al.* 2020), as well as Ediacaran, Lagerstätten.

Ultimate extinction within a wider, mass extinction event is, however, not the only possibility. It is notable that the diversity dynamics of the frondose soft-bodied biota are also similar to those of stem groups modelled mathematically by a birth–death process (Budd & Mann, 2020b) that experience only stochastic, background diversity declines. Within this model, solely stochastic versus externally driven stem-group extinctions are distinguished primarily by different probability distributions of durations (Budd & Mann, 2020b), meaning that the extinction of any given stem group might fit within either distribution (albeit with a higher or lower probability). Consequently, in the real fossil record, distinguishing potential causes of specific extinctions is likely to rely on wider tests: for example, for extinction correlation across different taxonomic groups or with independent evidence of environmental perturbation.

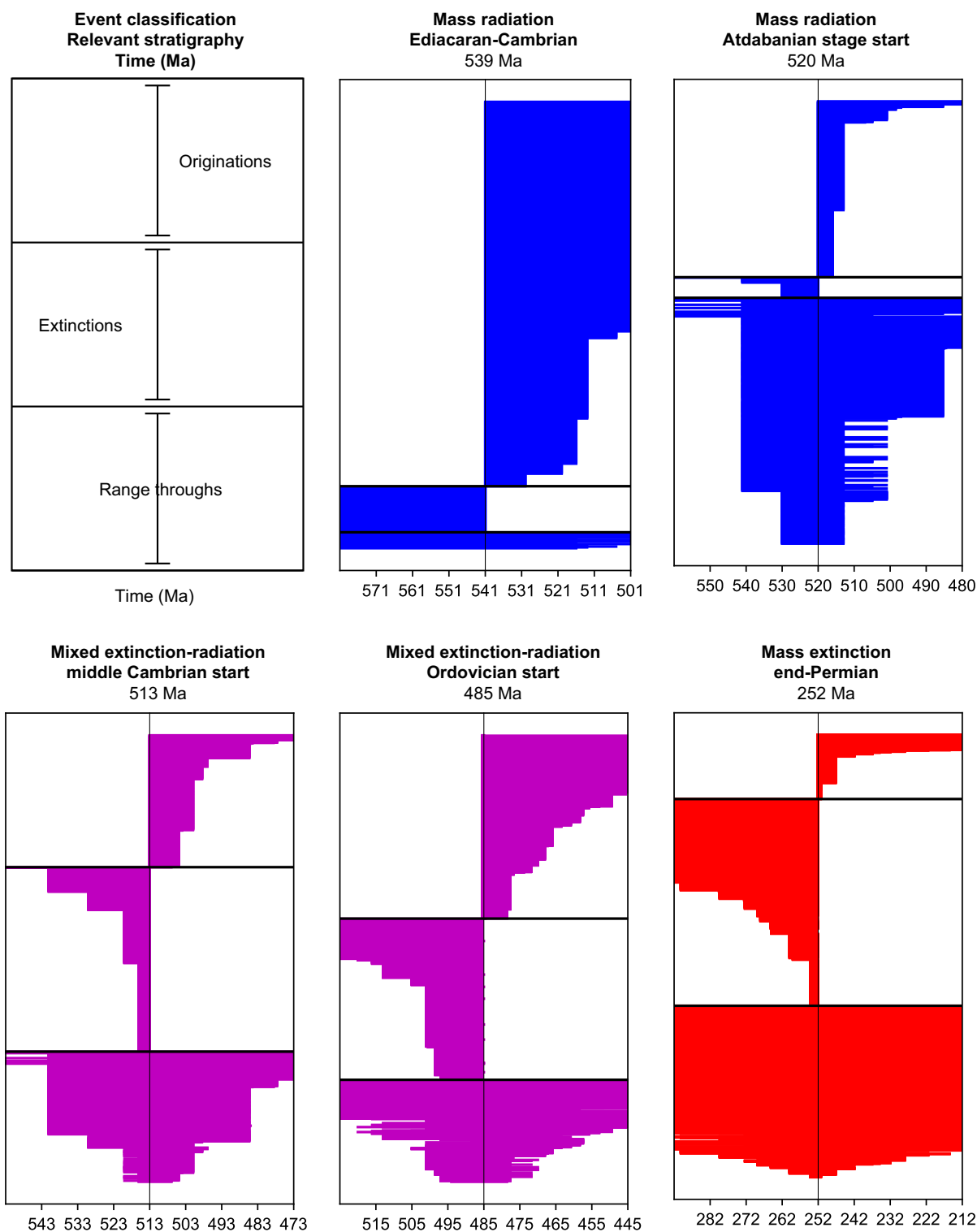
In the context of overall diversity as currently recorded in the PBDB (one of the most comprehensive compilations of comparative species ranges publicly available), the perception of extinction severity at the end-Ediacaran depends on the precise measurement context. The end-Ediacaran does not fall among the most significant mass extinctions in the sense of events dominated by extinction rather than radiation (Hoyal Cuthill *et al.* 2020), based on species extinction as a proportion of total diversity present at that time (with 12 % species extinction (Hoyal Cuthill *et al.* 2020) and 10 % at the genus level (Figure 3; Supplementary Computer Code in Supplementary Material

available online at <https://doi.org/10.1017/S0016756821001333>). This measure is designed to assess the balance of extinction and origination (Hoyal Cuthill *et al.* 2020) and calculates recorded species extinctions as a proportion of total diversity within a 1 Ma time window, where total diversity comprises all species either originating, going extinct or ranging through. Instead, here the dominant picture from overall diversity change (Fig. 3) is of the swamping of end-Ediacaran survivors, and extinctions, by diversification in the Cambrian explosion (86 % genus origination) (Hoyal Cuthill *et al.* 2020), a pattern potentially compatible with the early stages of rapid, non-linear diversification (e.g. see modelling of Budd & Mann, 2020a).

However, from a different measurement perspective, which sets aside originating species to consider extinction relative to survival (Fig. 4; Supplementary Computer Code in Supplementary Material available online at <https://doi.org/10.1017/S0016756821001333>), the beginning of the Cambrian period at 539 Ma shows the lowest proportion of recorded species survivals, relative to extinctions, for the Phanerozoic, at 7 %, compared with an overall mean of 92 %, and a mean of 28 % for these 15 events with lowest survivorship. This measure calculates (within each 1 Ma time window) the proportion of survivors, as range throughs/(range throughs + extinctions without originations), where range-through taxa have their minimum Ma and maximum Ma bracketing a time window, and taxa with extinctions without originations have minimum Ma but not maximum Ma within a time window. This is therefore similar to previously proposed per capita extinction measures (e.g. one measure of per capita extinction =  $-\ln[\text{range throughs}/(\text{range throughs} + \text{extinctions without originations})] \div \text{interval length}$  (Foote, 2000)). Based on extinction versus survival among PBDB occurrence records, the Ediacaran–Cambrian transition would therefore qualify as a mass extinction. Indeed among the data used in this analysis, it is the most severe recorded Phanerozoic mass extinction event. The time with the next-lowest proportion of species survivors relative to the number of extinctions is the end-Permian mass extinction at 9 % (Fig. 4a). Analysis at the genus level is required to capture, among the PBDB occurrence records, the Cambrian survival of *Swartpuntia* (Jensen *et al.* 1998; Hagadorn *et al.* 2000; Hagadorn & Waggoner, 2000), in particular, as well as other notable genera bridging the Ediacaran and Cambrian such as *Cloudina* and *Anabarites* (Yang *et al.* 2016). Considering PBDB occurrences recorded at the genus level, the lowest survivorship is also observed at the Ediacaran–Cambrian transition (which shows 26 % genus survival; Fig. 4b).

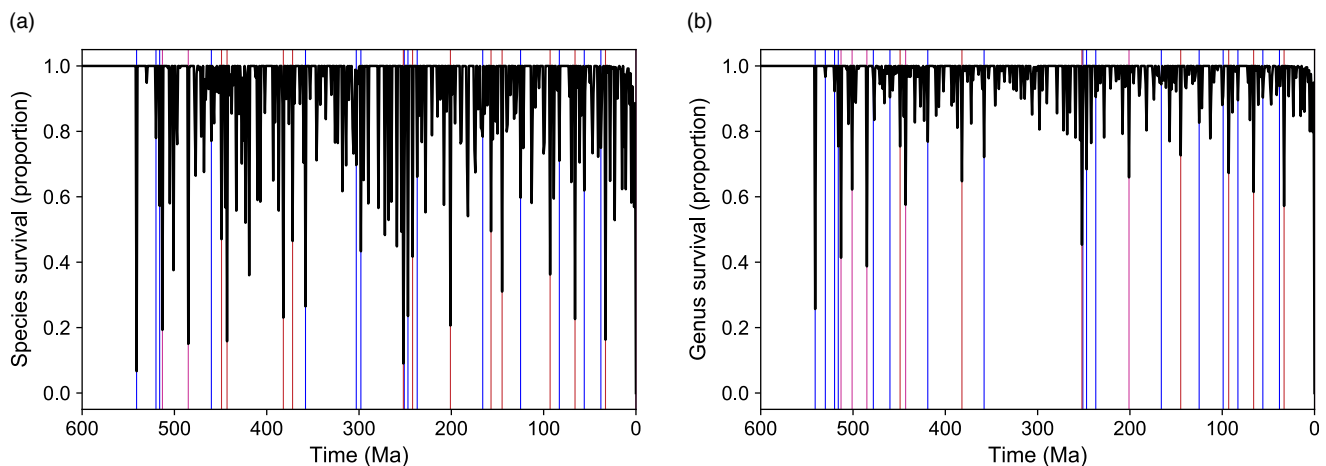
Based on comparative analysis across databased fossil occurrences, the end of the Ediacaran period is therefore notable for two reasons. First, this does show an extreme shortage of recorded survivors relative to extinctions. Second, however, the overall diversity dynamics around the boundary are dominated by the exceptional proportion of species and genus originations recorded at the onset of the Cambrian (Hoyal Cuthill *et al.* 2020); Figs 3–4). The frondose Ediacaran biota crossing the Cambrian boundary therefore experienced the most extreme influx of species evident in the databased fossil record and survived this, albeit at what appears to be markedly reduced diversity.

Coordinated extinctions across databased taxa are compatible with an environmentally forced mass extinction event at the Cambrian boundary (e.g. Narbonne, 2005; Smith *et al.* 2017). However, the PBDB data show signs of comparatively coarse stratigraphic coding for Ediacaran taxa (Figs 3–4), for example



**Fig. 3.** Number of Ediacaran–Cambrian genus survivors in context. ‘Drill plots’ (*sensu* Hoyal Cuthill, Guttenberg & Budd, 2020) showing genus time ranges for all genera recorded in the PBDB in a 1 Ma time window around a major event. Time ranges are vertically sorted into genera originating, going extinct or ranging through their time window (key, top left). Events shown are the five most extreme, based either on proportionate genus extinction or origination. Events are annotated and coloured according to whether a significance threshold (here 22 %) is passed by extinction only (mass extinction, colour, red), origination only (mass radiation, colour, blue) or both (mixed mass extinction–radiation, colour, magenta). For genera at the Ediacaran–Cambrian: extinctions without origination comprise 10 %, originations without extinction 86 %, and survivors 4 %. At both genus (figured) and species (Hoyal Cuthill *et al.* 2020) levels, the Ediacaran–Cambrian boundary shows the highest levels of origination measured, as a proportion of total diversity within a 1 Ma time window, across the Phanerozoic.





**Fig. 4.** Proportionate Ediacaran–Cambrian survival in context. (a) Species and (b) genus survival at 1 Ma increments calculated using occurrence records in the PBDB. Survival was measured (Supplementary Computer Code in Supplementary Material available online at <https://doi.org/10.1017/S0016756821001333>) as a proportion of standing diversity within a 1 Ma time window, setting aside origination: survival proportion = range throughs/(range throughs + extinctions without originations). At both species (a) and genus (b) levels, the Ediacaran–Cambrian transition shows the lowest proportion of survivors measured, relative to extinctions, across the Phanerozoic. Vertical lines indicate top 5% times of extinction (colour, red), radiation (colour, blue) or combined extinction–radiation (colour, magenta).

occurrences coded at period scale. Coarse coding of occurrences can be expected to exaggerate any correlation of extinction between taxa (e.g. by extending real time ranges to period boundaries). This therefore suggests the need for continued, finer-scale recording and analysis of taxon stratigraphic ranges over this crucial time interval (Smith *et al.* 2017; Wood *et al.* 2019).

## 5. Conclusion

Importantly, the Cambrian boundary is not correlated with a total, or effective, extinction of the classic frondose Ediacaran biota (the Petalonamae), and the causes of their ultimate demise should be sought at least 30 million years later, from the middle Cambrian. Ediacaran to middle Cambrian coexistence with bilaterians appears to rule out displacement by newly evolved competitors as a cause of the ultimate extinction of the frondose biota contrary to previous suggestions (Laflamme *et al.* 2013, though see also Budd & Jensen, 2017; Wood *et al.* 2019). Their recorded diversity dynamics are compatible with at least two widely separated extinction events (around the Ediacaran–Cambrian boundary then from the middle Cambrian). One or both of these may have been wider mass extinctions including other taxa, with exceptionally low genus and species survival at the Ediacaran–Cambrian boundary supported by PBDB occurrence records. However, it also remains possible that a role in the Cambrian explosion primarily as bystanders rather than participants in diversification was both a result of the background diversity dynamics of this clade (e.g. see Budd & Mann, 2020b; Barnes *et al.* 2021) and a cause of their eventual extinction.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0016756821001333>

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