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# The Ediacara Biota of the Wood Canyon formation: Latest Precambrian macrofossils and sedimentary structures from the southern Great Basin

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## ABSTRACT

Fossils of the Ediacara Biota preserve the oldest indisputable evidence of macroscopic animal life. Although new finds continue to expand the near global distribution of such organisms, relatively abundant and diverse populations of these primarily soft-bodied taxa are known from just a handful of localities. More commonly, reports of late Precambrian fossils consist of comparably lower diversity assemblages (less than ~10 genera), with a limited number of total specimens (less than ~1000 reported macrofossils over a broad geographic area). Determining the factors responsible for such differences can help to fully appreciate preserved patterns of Ediacaran biodiversity.

The lower member of the Wood Canyon Formation in the Death Valley region of the southern Great Basin, USA contains fossils of the Ediacara Biota. Here we redescribe previously recovered specimens based on new data from 3D surface scans and report several new finds from this unit. Although this allows the addition of two Ediacara taxa (*Pteridinium* and *Charnia*?) to the known diversity in the region, most potential macrofauna consist of amorphous, irregular forms with minimal preserved structures wherein an abiotic origin cannot be ruled out. A combination of factors – including variable taphonomic conditions, difficulty of identification and an original depauperate community – contribute to the observed diversity of this assemblage. Many biases that impact this record are either common (e.g., age, preservation requirements, difficulty of recognition) or comparable (e.g., paleoenvironmental and taphonomic controls) to known occurrences of Ediacara macrofauna. Thus, we argue this fossil record at least partially reflects the original community composition, suggesting that fossils of the lower Wood Canyon record a signal of relatively low diversity of the Ediacara Biota in the lead up to the Ediacaran-Cambrian boundary.

## 1. Introduction

Numerous characteristics of the fossil record result in assemblages with preserved diversity that does not match the original ecosystem (e.g., Allison and Briggs, 1993; Behrensmeier and Kidwell, 1985). Well known biases that affect the fossil record include a tendency for small, less robust taxa that degrade rapidly on geologic timescales to have an incomplete fossil record relative to their more resilient counterparts (Plotnick, 1986; Allison and Briggs, 1993; Cherns and Wright, 2000; Hendy, 2011). The age, geologic history, paleoenvironment, paleogeography and sampling intensity of a deposit all contribute to the uneven probabilities of reliably preserving the living assemblage (Behrensmeier

et al., 2000). However, numerous studies demonstrate that if such factors can be accounted for, primary signals of abundance and diversity can be recovered to examine ecological and evolutionary change in deep time (e.g., Alroy et al., 2001; Powell and Kowalewski, 2002; Smith et al., 2012; Benson et al., 2021).

The Ediacara Biota (~575–538 Ma; Matthews et al., 2021; Nelson et al., 2022) records the oldest fossils of complex, macroscopic communities, including animals (e.g., Xiao and Laflamme, 2009; Erwin et al., 2011; Droser and Gehling, 2015). These early metazoans were almost exclusively soft-bodied. Thus, they required exceptional conditions for fossilization, undoubtedly contributing to the rarity of such forms (Gehling, 1999; Narbonne, 2005). Ediacaran environmental

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conditions uniquely promoted the exceptional taphonomic pathway(s) through which they were preserved (Tarhan et al., 2016; Slagter et al., 2021). Organic mats, common during the end Ediacaran and essential for this preservational style (Gehling, 1999; Tarhan et al., 2016; Slagter et al., 2021) can produce biotic sedimentary structures that may be mistaken for macrofauna (Jensen et al., 2002; McIlroy et al., 2005; Seilacher et al., 2005; Davies et al., 2016; Nelson and Smith, 2019; Okubo et al., 2023). Difficulties of identification arise from the fact that these fossils are often subtle impressions of highly enigmatic forms, largely distinct from typical Phanerozoic fossil taxa.

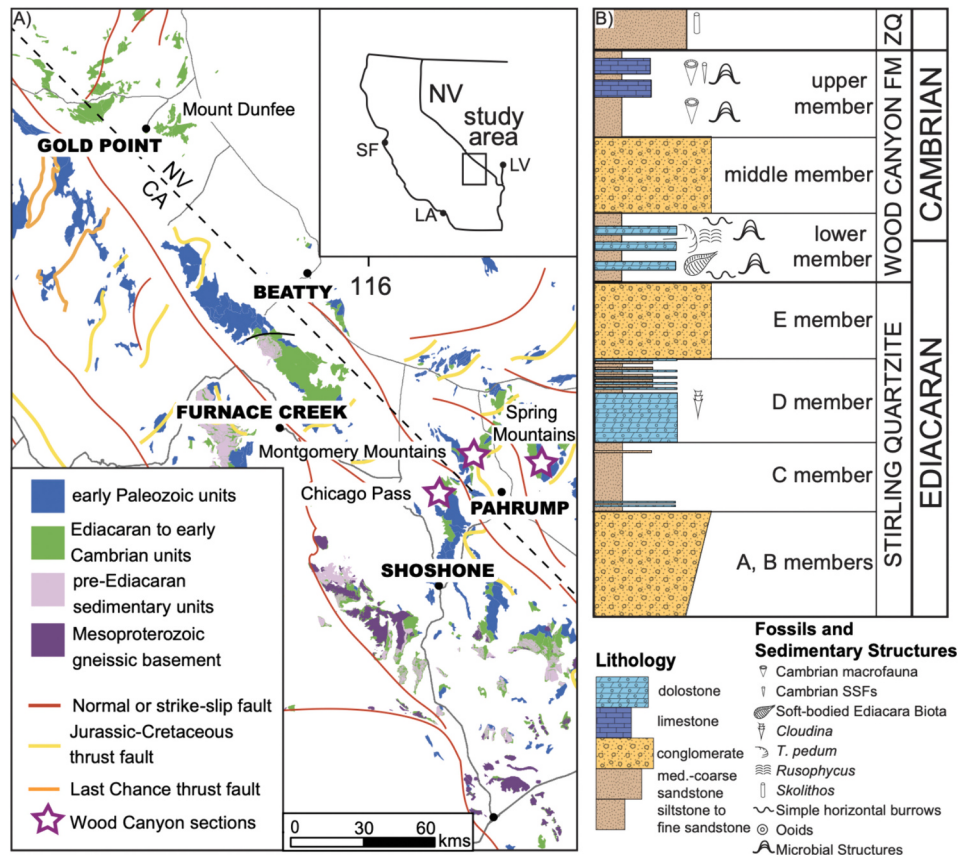
There are relatively few localities of mid- to late Ediacaran age containing low metamorphic grade sedimentary strata from suitable facies required to preserve the Ediacara Biota. Thus, interpretations are biased in favor of a few well-known sites (e.g., Mistaken Point, Namibia, South Australia, South China, and the White Sea; Narbonne, 2005; Xiao et al., 2021). Other Ediacaran aged fossil-bearing regions such as Charnwood Forest (Wilby et al., 2011), Northern and Central Australia (Hall et al., 2020a), and the Canadian Rockies (Hofmann and Mountjoy, 2010; Narbonne et al., 2014) are recognized around the world but contain significantly fewer, commonly endemic genera (e.g., Glaessner and Walter, 1975; Shen et al., 2007). Determining the factors responsible for such variable abundance and diversity is critical to understanding the lens through which we observe the earliest fossil animals.

Several studies accounting for taphonomic biases demonstrate evolutionary patterns in the rise and subsequent fall of the Ediacara Biota (Waggoner, 2003; Shen et al., 2008; Gehling and Droser, 2013; Laflamme et al., 2013; Boag et al., 2016; Darroch et al., 2018b; Tarhan et al., 2018; Evans et al., 2022). Biotic turnover is evident, and three temporally distinct faunal assemblages have been identified: the oldest

Avalon, middle White Sea and youngest Nama (Waggoner, 2003). These trends necessarily place significant weight on reports of abundant fossils from well-known and intensely studied sites. Further details in the trajectory of early metazoan evolution are likely to be revealed if more records can be incorporated into such analysis and quantitatively methods can be employed to evaluate the significance of inferred changes (e.g., Muscente et al., 2018; Tarhan et al., 2018).

Fossils of the Ediacara Biota are identified from Neoproterozoic deposits in the southern Great Basin, USA (e.g., Smith et al., 2017, 2023). Well-known sections in the region span the Precambrian-Cambrian boundary (Corsetti and Hagadorn, 2000) and are accessible – with multiple roadside localities just a short drive from major population centers, such as Las Vegas, NV and Los Angeles, CA. As such, these units have been the focus of many field excursions over several decades (e.g., Nelson and Durham, 1966; Diehl, 1974; Smith and Nelson, 2018; Smith et al., 2019) and numerous sedimentological, geochemical and paleontological studies (see Smith et al., 2023 and references therein). Despite this, the diversity and abundance of fossils remain low compared with Ediacaran fossil-rich sites, with most finds representing tubular forms (Hagadorn and Waggoner, 2000; Hagadorn et al., 2000; Smith et al., 2017; Schiffbauer et al., 2020; Selly et al., 2020).

Here we describe new late Ediacaran soft-bodied fossils from the lower member of the Wood Canyon Formation at the Montgomery Mountains, NV and Chicago Pass, CA (Fig. 1). Three-dimensional scans allow a revised taxonomic description of previously collected specimens (Smith et al., 2017) and examination of new material, demonstrating the presence of two previously unrecognized Ediacara taxa. Despite these advances, all specimens recovered appear incomplete, the majority cannot be classified, and, in some instances, an abiotic origin (e.g., load



**Fig. 1.** Geological map and stratigraphic column. (A) Geologic map of study region with main lower Wood Canyon localities Chicago Pass 36.142457 N 116.1518775 W, Montgomery 36.391944 N 116.101667 W and Spring Mountains 36.3425549 N 115.9181938 W marked with purple stars. (B) Generalized stratigraphy of the Wood Canyon Formation and related units. After Smith et al., 2023. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structures) remains possible. We explore the implications of this material and how it might fit within global patterns of change for the Ediacara Biota.

## 2. Materials and methods

### 2.1. Geologic setting

Extensive Mesoproterozoic through Phanerozoic sedimentary packages, including well-known Ediacaran strata, outcrop in the southern Great Basin (e.g., Smith et al., 2023). During the late Ediacaran and early Cambrian, episodic deposition was associated with the transition from active rifting to passive margin sedimentation (Stewart, 1966; Bond et al., 1985; Fedo and Cooper, 2001). Ediacaran-Cambrian successions in the region exhibit a general deepening trend to the west-northwest, with localities in the southeast Death Valley region recording deposition in the proximal part of this paleo-basin (Stewart, 1970; Corsetti and Hagadorn, 2000; Fedo and Cooper, 2001). This study focuses on the Wood Canyon Formation exposed at Chicago Pass, CA as well as the Montgomery and Spring Mountains, NV (Fig. 1A).

The Wood Canyon Formation is divided into lower, middle and upper members (see Smith et al., 2023 and references therein; Fig. 1B). Fine-grained siliciclastic rocks of the lower and upper members predominantly record shallow, subtidal settings, with the coarser middle member representing fluvial deposition (e.g., Stewart, 1970). However, both marine and transitional/terrestrial strata are recognized throughout, likely the result of sedimentation on the edge of a braided deltaic system (Fedo and Cooper, 2001; Smith et al., 2023). In most localities in the Death Valley region, including at Chicago Pass and the Montgomery Mountains, the lower member consists of three well-defined shallowing upward parasequences of predominantly shale, siltstone and fine- to medium-grained sandstone, each capped by a distinct m-scale orange-weathering dolostone unit (Fig. 1B; Stewart, 1966; Corsetti and Hagadorn, 2000; Smith et al., 2017). In the Montgomery Mountains the lower member is expanded, with additional thinner interbedded dolostone horizons compared with Chicago Pass (m-scale or less), however, the thicker dolostone marker beds can still be identified.

The Precambrian-Cambrian boundary is placed within the third parasequence of the lower Wood Canyon (above the second dolostone marker bed) based on identification of the Cambrian index fossil *Treptichnus pedum* (Corsetti and Hagadorn, 2000; Jensen et al., 2002). This is supported by negative  $\delta^{13}\text{C}$  values that have been correlated to the Basal Cambrian Excursion (BACE) within the second dolomite marker bed (Corsetti and Hagadorn, 2000; Smith et al., 2023). U–Pb CA-ID-TIMS ages on zircon grains from a reworked tuffaceous horizon in Sonora, Mexico suggest that the nadir of the BACE there has a maximum depositional age of  $539.40 \pm 0.23$  Ma (Hodgin et al., 2021). More recently, the five youngest detrital zircon grains from a siltstone within the second dolostone marker beds of the lower Wood Canyon yielded a CA-ID-TIMS maximum depositional age of  $532.83 \pm 0.98$  Ma (Nelson et al., 2023). This age constrains the end of the BACE and the first appearance of *T. pedum*, suggesting that the base of the Cambrian in this region may be younger than  $\sim 533$  Ma.

Wrinkle structures and other textured organic surfaces indicating the presence of organic mats are present throughout much of the Wood Canyon Formation (Hagadorn and Bottjer, 1999; Smith et al., 2023). This unit also hosts abundant trace fossils, exhibiting the progression from simple, horizontal burrows of the late Ediacaran (e.g., *Helminthoidichnites*) to more complex and vertical burrowing behaviors (e.g., *Cruziana/Rusophycus*, *Psammichnites*, *Treptichnus*, *Rhizocorallium*) characteristic of the early Cambrian (Jensen et al., 2002; O'Neil et al., 2022). The lower Wood Canyon contains rare macrofossils below the second marker bed, representing some of the youngest known members of the Ediacara Biota (Fig. 1B; Hagadorn and Waggoner, 2000; Hagadorn et al., 2000; Smith et al., 2017, 2023; Schiffbauer et al., 2020; Selly et al.,

2020; Runnegar, 2022; O'Neil et al., 2022). Consistent with other localities attributed to the Nama assemblage, these are dominated by tubular taxa (Hagadorn and Waggoner, 2000; Smith et al., 2017; Selly et al., 2020; Surprenant and Droser, 2024). Computed tomography of pyritized tubes reveal internal structures, which have been suggested as potential evidence for through-guts (Schiffbauer et al., 2020). Erniettomorphs, including *Ernietta* and *Swartpuntia*, as well as enigmatic disks, namely *Aspidella* and *Nimbia*, have been recovered from the lower member (Hagadorn and Waggoner, 2000; Hagadorn et al., 2000; Smith et al., 2017; Runnegar, 2022; O'Neil et al., 2022). There are also reports of load casts and taphomorphs of Ediacaran macrofauna associated with more definitive biotic remains (Hall et al., 2020b; Smith et al., 2023). A recent study presented evidence that at least some of these structures represent poorly preserved erniettomorphs, with variable preservation attributed to differences in grain size and clay content (Hall et al., 2020b).

Correlative units of the more carbonate-rich Deep Spring Formation are found to the northwest, representing more distal deposition (Stewart et al., 1970). These units exhibit a similar record of abundant mat textures, trace fossils and rare Ediacara taxa (Corsetti and Hagadorn, 2003; Smith et al., 2016, 2023; Tarhan et al., 2020). Macrofossils include tubular forms (Smith et al., 2016; Selly et al., 2020) and the possible erniettomorph *Pteridinium* (Cloud Jr and Nelson, 1966). However, the latter was recently reinterpreted as an organosedimentary structure attributed to differential compaction of microbial mat-bound heterolithic, rippled strata (Nelson and Smith, 2019).

### 2.2. Fossil examination

Excursions to the three sites highlighted in Fig. 1A were conducted over multiple field seasons from 2021 to 2023. Although strata above and below were examined, searches for macrofossils, textured organic surfaces and trace fossils focused on outcrops of the lower Wood Canyon following previous descriptions (Hagadorn and Waggoner, 2000; Hagadorn et al., 2000; Smith et al., 2017, 2023; Schiffbauer et al., 2020; Selly et al., 2020; Runnegar, 2022; O'Neil et al., 2022). Digital photographs of sedimentary structures were recovered during fieldwork. Potential Ediacara macrofauna were collected and photographed under controlled light and measured using digital calipers. Although rare possible biological structures were recognized *in situ*, all unambiguous fossils are from float. Despite this, all potential macrofauna were found alongside strata of the lower Wood Canyon, below the second dolomite marker bed, and so we interpret their stratigraphic position as above the Sterling Quartzite and below the Ediacaran-Cambrian boundary, following previous authors (Smith et al., 2017; Fig. 1B). No sections were measured and we rely on previous stratigraphic descriptions of these localities (Smith et al., 2017).

New specimens are housed at the Las Vegas Natural History Museum (LVNHM) designated by BLM.2024.001.01–0.19, and the Los Angeles County Museum of Natural History Museum (LACNHM) designated by LACMIP localities 43365 and 43366 (catalogue numbers 43365.1 and 43366.1). Additional specimens (both figured and unfigured) remain in the field.

Due to unique three-dimensional preservation, we re-examined a previously discovered slab containing multiple erniettomorphs and other potential Ediacara Biota (Smith et al., 2017; Hall et al., 2020b), collecting surface scans of the 12 individual pieces of rock that make up this entire slab using an Artec Space Spider. We also used this scanner to generate 3D models of new specimens recovered from fieldwork in the current study. Scans were processed and fossil images were isolated using the zbrush program, available through pixologic. All scan files are available as Supplementary Material.

### 2.3. Global diversity and abundance

To compare the record from the Great Basin with global Ediacaran

fossil localities, we used diversity data from a recently published compilation (Evans et al., 2022). This database is limited to soft-bodied organisms and excludes all trace fossils as well as body fossils that have not been classically aligned with the Ediacara Biota (e.g., those interpreted as algae or bacteria; see supplementary text of Evans et al., 2022). The database includes stratigraphic, lithologic, paleoenvironmental and preservational information, allowing comparisons between similar taphonomic modes. Occurrence data were grouped into broadly similar regions, with localities combined if the same stratigraphic nomenclature is applicable (e.g., the Blueflower Formation in the Mackenzie and Wernecke Mountains united as ‘NW Canada’; Pyle et al., 2004; Macdonald et al., 2013) or if they are from broadly similar geographic regions, typically within 10s of kms of each other (e.g., the Ediacara Member found throughout the Flinders Ranges and surrounding region all considered ‘South Australia’).

Generic diversity for the Great Basin was updated based on new results (Supplementary Dataset 1) including both maximum (with one rangeomorph and multiple erniettomorph genera present and considering all potential biotic structures identified here as Ediacara macrofauna) and conservative estimates (based largely on previously published results and assuming most enigmatic structures do not represent macrofossils). We also compiled estimates of abundance based on published literature for all unique fossil occurrences in the previous database. The reporting of such information is highly variable, ranging from exact counts to subjective descriptions (e.g., as “abundant” or “rare”). Exact counts were identified for approximately 75% of total occurrences, partially due to recent paleoecological descriptions of classic localities (e.g., Gehling and Droser, 2013; Zakrevskaya, 2014; Mitchell et al., 2015). While such counts are preferred, they represent underestimates of the total number of taxa identified at any given locality. For example, an author of this manuscript has previously reported the number of *Dickinsonia* specimens from both the Nilpena Ediacara National Park (NENP) and those housed at the South Australia Museum (SAM; Evans et al., 2017). However, a significant, but undetermined number of specimens now housed at the SAM were collected from NENP, and more specimens have been recovered in subsequent field seasons from this locality. Thus, we default to the lower number reported exclusively from NENP. At other localities (e.g., Mistaken Point), specimen counts are only available for a subset of the total described fossiliferous bedding surfaces (e.g., Darroch et al., 2013; Mitchell et al., 2015; Vixseboxse et al., 2021), again representing an underestimate of total abundance. Beyond these data-rich sources, original systematic paleontological descriptions from initial naming of taxa are the most common source of exact specimen counts. These are often outdated and/or contain total specimen counts that combine multiple localities. In other cases, exact numbers were inferred from the number of figured and/or described specimens.

When the same genus is reported from multiple localities in one region, we default to the highest abundance value (number) reported from a single locality. This is an attempt to minimize differences between well-studied areas, where abundance data are reported for multiple discrete localities, and those where abundance data may be available for relatively few localities. Further, different authors may refer to the same locality by different names, and this method reduces overcounting abundance data from such regions/localities.

Based on the variability of reporting and high likelihood that many entries represent an underestimate of the total number of known specimens, we report both exact and normalized abundance data based on four logarithmic categories (single specimen = 1; rare = 10; common = 100; abundant = 1000). If exact numbers are available, we normalize to the next highest category. For example, in recent descriptions of new genera, seven specimens of *Kuckaraukia* from the Urals (Razumovskiy et al., 2015) and 120 specimens of *Obamus* from South Australia (Dzaugis et al., 2020; Boan et al., 2023) were reported. Thus, *Kuckaraukia* is considered rare and *Obamus* abundant, with values of 10 entered for the former and 1000 for the latter. Other reported fossil

abundances are more ambiguous, for example *Ernietta* and *Rangea* from Farm Aar in southern Namibia are reported as having “more than 100 specimens” (Elliott, 2016; Vickers-Rich et al., 2013). This leaves significant uncertainty as to whether using the exact value (100) is more or less accurate than a normalized value (1000). Three reported abundances in the database (*Fractofusus* from Mistaken Point, *Shaanxilithes* from North and South China; Mitchell et al., 2015; Wang et al., 2021) totaled >1000 specimens, and so exact numbers were used to avoid artificial inflation. In addition, the number of *Funisia* reported from South Australia is “>999” (Gehling and Droser, 2013) but this number is likely a major underestimate (Surprenant et al., 2020). It is difficult to assign a numeric value with any accuracy for such abundant fossil and *Funisia* is unlikely to be the only taxa for which such data are highly inaccurate. Thus, though the actual abundance is likely >10,000 specimens, we use a normalized value of 1000 based on the published record.

This method is undoubtedly biased in numerous ways (e.g., Dunhill et al., 2018 and references therein) and future analyses are required to better understand these patterns. However, this provides a practical and consistent method to compare diversity and abundance dynamics between global Ediacaran localities based on the current available literature. Estimates of outcrop area and unit thicknesses were obtained from Macrostrat (Peters et al., 2018), for sections in North America (Table 1; Douglas, 1970; Childs, 1985; Gabrielse and Brookfield, 1988; Stott, 1995). Where available, these are compared with generic richness and abundance estimates obtained here.

### 3. Results

Rare body fossils were identified in the lower member of the Wood Canyon Formation, and no unambiguous, non-tubular Ediacara Biota were found in situ at either locality. Most potential macrofauna were recovered from the Montgomery Mountains, with rare specimens also found at Chicago Pass and the Spring Mountains, preserved as casts and molds in siltstone and fine- to medium-grained sandstone. We also examined a slab with several possible erniettomorphs, repositated at the Smithsonian Institution, USNM 624300. Although most are difficult to confidently interpret, newly recovered specimens include potential erniettomorphs (Fig. 3), possible rangeomorph petaloids and related structures (Fig. 4), textured surfaces indicative of organic mats as well as macroscopic sedimentary features described below (Fig. 5). Pyritized tubes (e.g., Smith et al., 2017; Schiffbauer et al., 2020) and trace fossils (Jensen et al., 2002; O’Neil et al., 2022) were observed but not collected. Unless otherwise indicated, all specimens and sedimentary structures described below were found in float, as loose slabs, below the second dolomite marker bed of the lower Wood Canyon in the Montgomery Mountains.

#### 3.1. Erniettomorpha

Surface scans of previously described erniettomorph specimens from a single slab (Smith et al., 2017) allow visualization of the spatial relationships between fossils (Fig. 2B, Supplementary File 1) and comparison with newly recovered specimens described below. The slab consists of five distinct erniettomorphs (e.g., Fig. 2C, D) and several smooth, round structures lacking any internal morphology (Fig. 2E). A sixth erniettomorph was previously removed to make thin sections for detailed taphonomic investigation (Hall et al., 2020b). Because the entire slab was recovered from float, the orientation of fossils is not known, but most specimens appear to occur near a single horizon (the “top” of the slab represented in Fig. 2A, B). At least one erniettomorph (Fig. 2C) is preserved on a distinct layer from the others. Vanes of individual erniettomorphs are mostly parallel to bedding, with others oblique to perpendicular, and no preferred orientation is recognized between specimens (Fig. 2B). A cross hatched structure was also described without taxonomic assignment, which appears to exist on a separate plane from all other fossils (Fig. 2B, light blue). Reexamination

**Table 1**  
Comparison of fossil metrics (data from Evans et al., 2022) with estimates of rock quantity where available in Macrostrat for rock units containing the Ediacara Biota.

| Locality       | Smallest unit(s) in Macrostrat | Diversity (no. of genera) | Abundance (no. of specimens) | Outcrop area (km <sup>2</sup> ) | Cumulative stratigraphic thickness (m) | No. of genera/ outcrop area (km <sup>2</sup> ) |
|----------------|--------------------------------|---------------------------|------------------------------|---------------------------------|----------------------------------------|------------------------------------------------|
| Great Basin    | Wood Canyon; Deep Spring       | 8                         | 510                          | 28,491                          | 1900                                   | 2.8•10 <sup>-4</sup>                           |
| Mistaken Point | Conception Group               | 20                        | 14,912                       | 30,126                          | 2134                                   | 6.6•10 <sup>-4</sup>                           |
| NW Canada      | Rackla Group                   | 7                         | 32                           | 24,527                          | 10,000                                 | 2.9•10 <sup>-4</sup>                           |
| SW Canada      | Miette Group                   | 3                         | 30                           | 22,522                          | 4590                                   | 1.3•10 <sup>-4</sup>                           |

did not reveal any new information regarding the likely classification of this specimen, although we note that the cross-hatched pattern (Smith et al., 2017) resembles the holotype of *Palaeophragmodictya* from Australia (Gehling and Rigby, 1996). However, other specimens of this genus from both Russia and Australia exhibit a bell-shaped morphology distinct from that described here, and this genus is currently known exclusively from strata interpreted as significantly older than the lower Wood Canyon (Gehling and Rigby, 1996; Serezhnikova, 2007).

Well-preserved erniettomorphs exhibit characteristic tubular body construction (Fig. 2C, D, G–K), expressed as ridges with regular spacing ranging from 1 to 4 mm, rarely visible in cross section (Fig. 2G). Sub mm-scale, transversely disposed corrugations are also observed within these larger, more distinct ridges (Fig. 2C, F, K white arrows). These have been described previously for erniettomorphs and may represent sediment infill during life (Elliott, 2016; Ivantsov et al., 2016; Gibson et al., 2019; Darroch et al., 2022). A general sac-like structure is not obvious, even with 3D scans (Fig. 2B) but is interpreted for most specimens (Fig. 2C, F). A suture line is visible for a single specimen, parallel to the long axis (Fig. 2H–K). This specimen consists of three discrete vanes, meeting at a suture that extends across the long axis and forming a semi-spheroidal or ‘boat’ shape (Fig. 2H). These characteristics are consistent with *Pteridinium*, although units do not appear to be offset or deflect at the suture line as is described for this genus (Elliott et al., 2011; Meyer et al., 2014; Elliott, 2016; Darroch et al., 2022). A second specimen composed of a single vane may be interpreted with a suture line where units thin perpendicular to the long axis (white arrow in Fig. 2C) consistent with *Ernietta* (Elliott et al., 2011; Ivantsov et al., 2016). Incompleteness precludes definitive classification, but we follow previous authors in considering most specimens as *Ernietta* based on a general sac-like shape and possible sutures perpendicular to the long-axis (Smith et al., 2017; Hall et al., 2020). Smooth structures within this same slab are distinct from erniettomorphs (Smith et al., 2017), but may represent poorly preserved fossils (Hall et al., 2020b). Ridges imparted from neighboring organisms (Fig. 2F) suggest that these features formed prior to fossilization. This is potentially inconsistent with load casts, but a variety of taphonomic scenarios remain possible (e.g., Owen, 2003).

We found several additional specimens from the Montgomery Mountains (Fig. 3) that are consistent with the morphology of Erniettomorpha (Elliott et al., 2011; Meyer et al., 2014; Ivantsov et al., 2016; Smith et al., 2017; Gibson et al., 2019; Darroch et al., 2022). None are as well preserved as examples in the slab presented in Fig. 2 and observed morphology is highly variable, commonly overlapping with features of loading (e.g., Owen, 2003) and mat-bound structures (Nelson and Smith, 2019). Comparison with erniettomorphs, including those described from the lower Wood Canyon above (Fig. 2), suggests that at least some may represent body fossils, but this remains equivocal.

Positive endorelief, cm-scale spherical forms surrounded by matrix of similar lithology (Fig. 3) match observations of *Ernietta* from Namibia (Elliott et al., 2011; Ivantsov et al., 2016). Similarities include sub mm-scale lineation (Fig. 3A, B white arrows) rarely visible within these forms, exhibiting orientations that do not match bedding of the host rock, if bedding is discernable. Additionally, repeated, mm-scale tubular structures, match the biserially quilted, tubular body construction characteristic of the Erniettomorpha, but lack an overall morphology

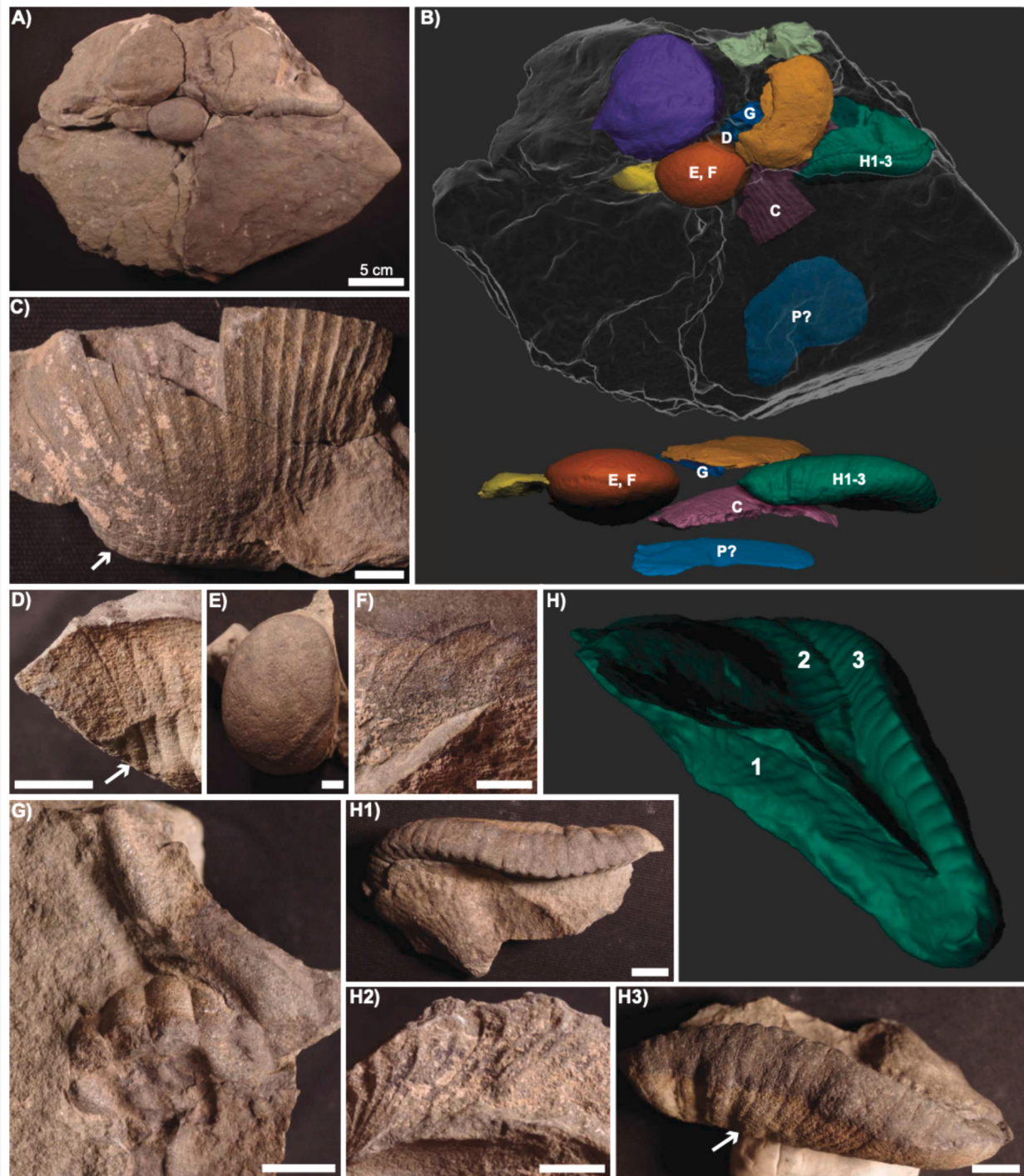
consistent with any previously described members of this group (Fig. 3C, D; Supplemental File 2, 3). Perpendicular corrugations (sub-mm) are also visible within and between larger tubular elements (white arrows Fig. 3C, D) consistent with observation of *Ernietta* and *Pteridinium* (Elliott, 2016; Ivantsov et al., 2016; Gibson et al., 2019; Darroch et al., 2022).

In rare cases, potential erniettomorphs were found in situ both above and below the first dolomite marker bed at the Montgomery Mountains (Fig. 3E, F). These almost exclusively consist of multiple spherical to ovoid structures of similar size on the same bedding plane, with rare examples exhibiting potential evidence for a tubular body construction (Fig. 3G). Commonly, such structures are expressed in positive epirelief (Fig. 3E, F), with positive endorelief (Fig. 3H) and hyporelief (Fig. 3I) also observed. At Chicago Pass, a single possible erniettomorph (Fig. 3J, Supplementary File 4) was identified in float, approximately 20 m above the first dolomite marker bed. This specimen is incomplete, but the overall shape, three-dimensional preservation and orientation of units perpendicular to the long axis are consistent with *Pteridinium*. A likely erniettomorph was also recovered from the Spring Mountains approximately 20 m below the first dolomite marker bed (Fig. 3K; Nelson et al., 2023). Similar to other examples reported here, mm-scale, sub-parallel ridges are consistent with the repeated tubular morphology diagnostic of the Erniettomorpha, but no features provide evidence for further classification within this group.

3.2. Rangeomorpha and related structures

We identify four possible frond petaloids from the Montgomery Mountains. Most are poorly preserved and incomplete. A single, fragmentary specimen (Fig. 4A, Supplementary File 5) exhibits unambiguous evidence for multiple orders of branching (Fig. 4B, C), consistent with rangeomorph body construction and distinct from other Ediacaran frondose taxa belonging to Arboreomorpha and *Swartpuntia* (Lafamme and Narbonne, 2008; Brasier et al., 2012; Hoyal-Cuthill and Conway-Morris, 2014; Dunn et al., 2019). The highly incomplete nature of this specimen leaves several diagnostic characters unresolvable (polarity, growth dynamics, presence/absence of a stalk or stem, etc.). However, observed characters include at least three orders of subparallel branching and furled primary branches (sensu Brasier et al., 2012). These features are consistent with several rangeomorph species. We conservatively assign this to *Charnia*? as this genus exhibits the features described, has recently been reported from deposits of similar age from the Yangtze Gorges area, South China (Wu et al., 2022) and is paleogeographically widespread in deposits correlative with both the White Sea and Nama assemblages.

Less detailed specimens exhibit 1–2 possible orders of branching (Fig. 4D, E, black arrows), as well as structures that resemble stalks and/or smooth membranes (Fig. 4D, E, white arrows). Poor preservation yields little taxonomic information, and these could represent rangeomorphs or other frondose taxa, including arboreomorphs or the erniettomorph genus *Swartpuntia*. Smooth membranous features are possibly analogous to “amorphous sheet-like structures” found in association with likely transported Ediacaran fronds from South Australia (Droser et al., 2020). Similar structures were also found in the absence of frond petaloids at the Montgomery Mountains and Chicago Pass (e.g., Fig. 4F).

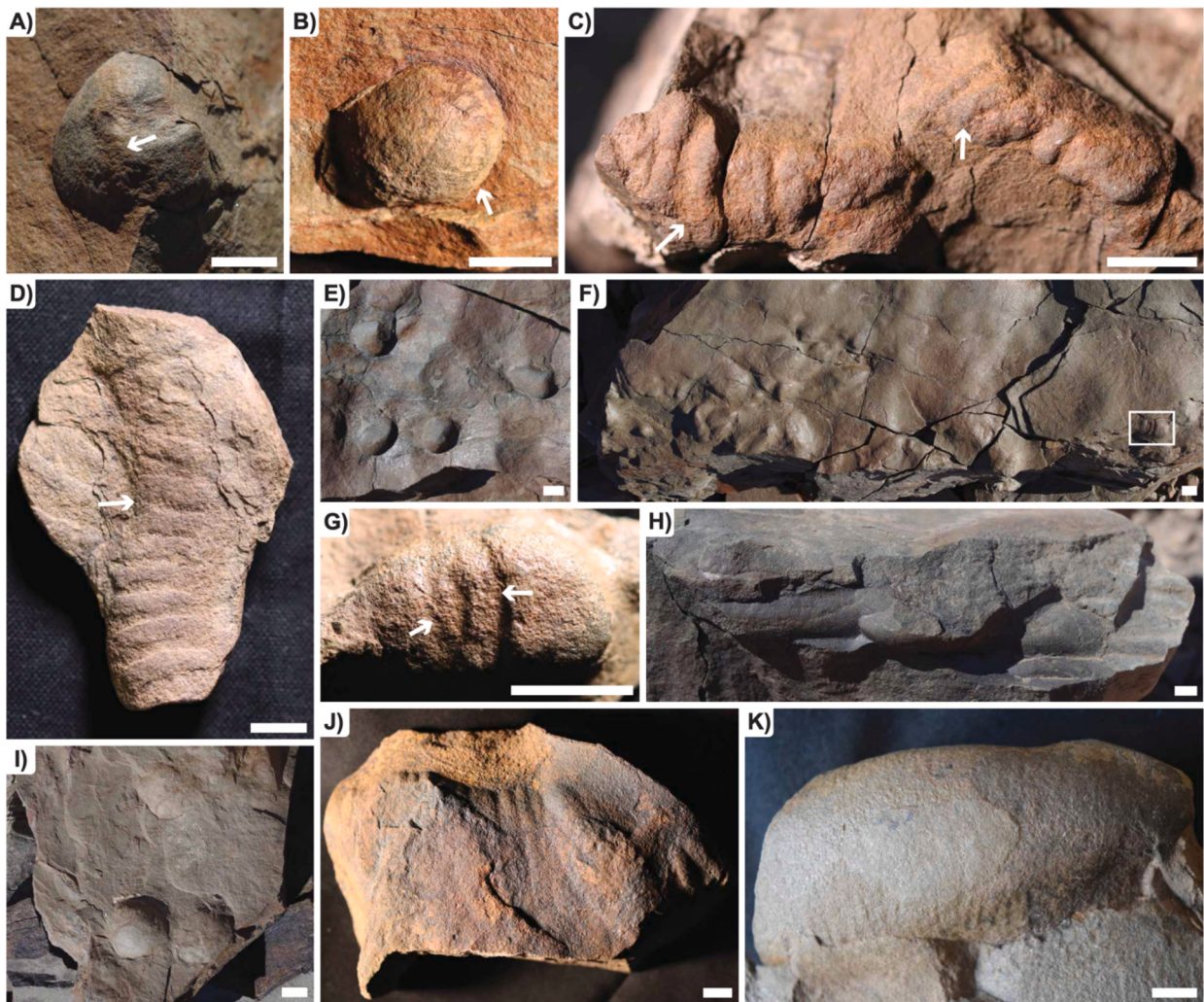


**Fig. 2.** Photos and three-dimensional scans of probable erniettomorphs and other possible biogenic structures from the Montgomery Mountains described by [Smith et al. \(2017\)](#). (A) Photograph and (B) 3D scan of the entire slab with definitive fossils and smooth, rounded structures highlighted and surrounding matrix transparent (top panel in B) or entirely removed (bottom panel in B, tilted 90 degrees from A). Specimens highlighted include possible *Palaeophragmadictya* (light blue, labelled with “P?”), erniettomorphs (dark blue, pink, light and dark green) and rounded structures (purple, yellow, orange). Letters in B refer to photographs in subsequent panels. (C, D) Well-preserved, incomplete probable *Ernietta*. (E) Rounded structure with (F) erniettomorph morphology imprinted on exterior. (G) Incomplete probable *Ernietta* with cross sectional view exhibiting double-walled tubular body. (H) Scan and (H1–3) photographs of probable *Pteridium*. Numbers in (H) refer to three distinct vanes, with 2 and 3 shown in (H1), vane 1 in (H2) and vane 3 in (H3). White arrows indicate sub mm-scale transverse corrugations and potential location of suture in panel C. USNM 624300. Scale bars in C–G and H1–3 = 10 mm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

These are recognized based on a markedly smooth texture compared with the more irregular surrounding matrix ([Fig. 4D, F](#)) suggesting an organic origin, however it remains possible that they represent the onlapping of finer sediments over a felled frondose organism. As with

possible erniettomorphs described above, morphologies overlap with those of non-Ediacara Biota, primarily rippled mat-bound sedimentary structures ([Nelson and Smith, 2019](#)).

More common, but still rare discoidal features were also observed at



**Fig. 3.** Possible erniettomorphs from the lower Wood Canyon. (A, B) Spherical, positive endorelief structures resembling *Ernietta*. (C, D) Potential fossils with regular, mm-scale tubular body construction similar to other erniettomorphs from the lower Wood Canyon. (E, F) Bedding planes with multiple rounded structures preserved in positive epirelief. White box in (F) indicates specimen in (G) with possible tubular body. (H) Endorelief structures of uncertain origin. (I) Structures without internal morphology but gross outline matching erniettomorphs from this section. (J) Potential *Pteridinium*. (K) Probable *Erniettomorph* reported by Nelson et al. (2023). White arrows (A–D, G) indicate sub mm-scale corrugations perpendicular to primary body divisions. (A–I) From the Montgomery Mountains, catalogue numbers BLM.2024.001 (A) 0.04; (B) 0.16; (C) 0.14; (D) 0.01; (F, G) 0.17; (H, I) remain in the field. (J) LACMIP 43365.1 from Chicago Pass; (K) from Spring Mountains. Scale bars 10 mm.

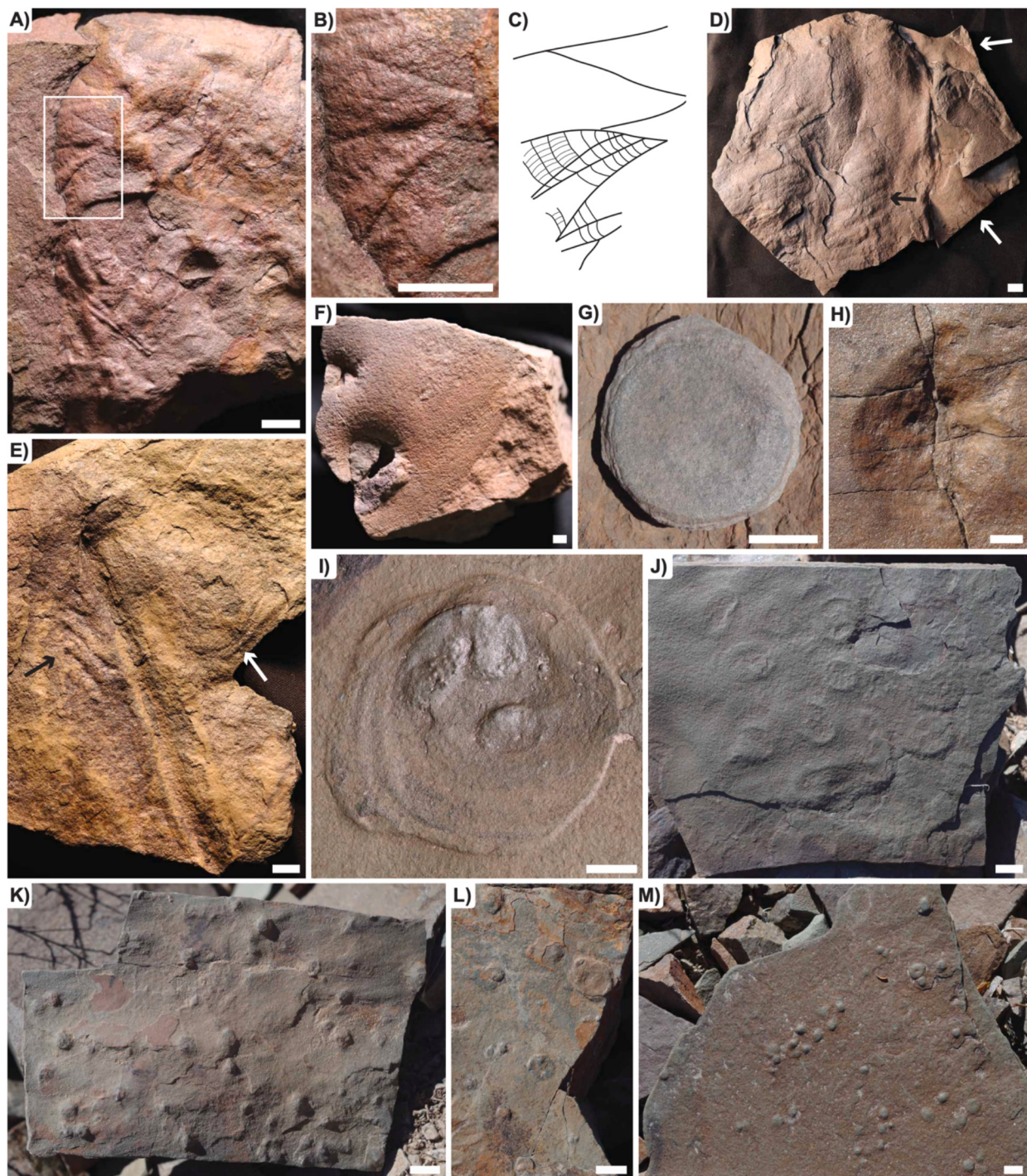
both localities (Fig. 4G–M). The largest of these structures (Fig. 4G–I) resemble *Aspidella*, a form genus likely representing the holdfasts of frond petaloids of various morphology/taxonomy (Gehling et al., 2000; Tarhan et al., 2015b). Consistent with descriptions elsewhere, these are mostly expressed in positive relief, although negative relief is also observed (Fig. 4H). Lack of in situ examples prevents determination of epi- vs hypo-relief. Rare specimens exhibit features such as concentric wrinkles, a central boss, or an outer rim (Fig. 4I).

Other discoidal structures (Fig. 4J–M) are more ambiguous with respect to holdfast interpretations. Of these, positive relief disks with a raised outer rim match descriptions of *Nimbia* (Fig. 4J), although they are smaller (1–3 mm) than the type-material (4–15 mm) of *Nimbia occlusa* (Fedonkin, 1980; Hagadorn and Waggoner, 2000). This genus was previously identified from the lower Wood Canyon and underlying Stirling Quartzite (Hagadorn and Waggoner, 2000) and is known from Precambrian sections globally, including Cryogenian-aged units from NW Canada (Hofmann et al., 1990), Mesoproterozoic deposits from Siberia (Liu et al., 2013) as well as Cambrian strata (Crimes et al., 1995). As is typical for Ediacaran disks, these were initially considered to represent medusoids (Fedonkin, 1980) but have been more recently

attributed to microbial colonies (Liu et al., 2013) or *Aspidella*-type holdfasts (Burzynski et al., 2020). Other structures exhibit no obvious morphology beyond a discoidal outline, the size of which broadly overlaps with the inferred cyanobacterial colonies united under the genus *Beltanelliformis* (Ivantsov et al., 2014; Bobrovskiy et al., 2018). Morphologies of all disks identified also match observations of gas and/or fluid escape structures (e.g., “sand-volcanoes”; Owen, 1996; Menon et al., 2016) as well as trace fossil ‘plugs’ (*Berguria/Conichnus*) known from late Ediacaran deposits (e.g., Darroch et al., 2021). Although *Aspidella* and *Nimbia* have been previously documented in the lower Wood Canyon (Hagadorn and Waggoner, 2000; Hagadorn et al., 2000; Smith et al., 2017; Runnegar, 2022; O’Neil et al., 2022), we did not observe definitive features to distinguish these from other hypotheses and so their affinities and biogenicity remain equivocal.

### 3.3. Mats and other problematic structures

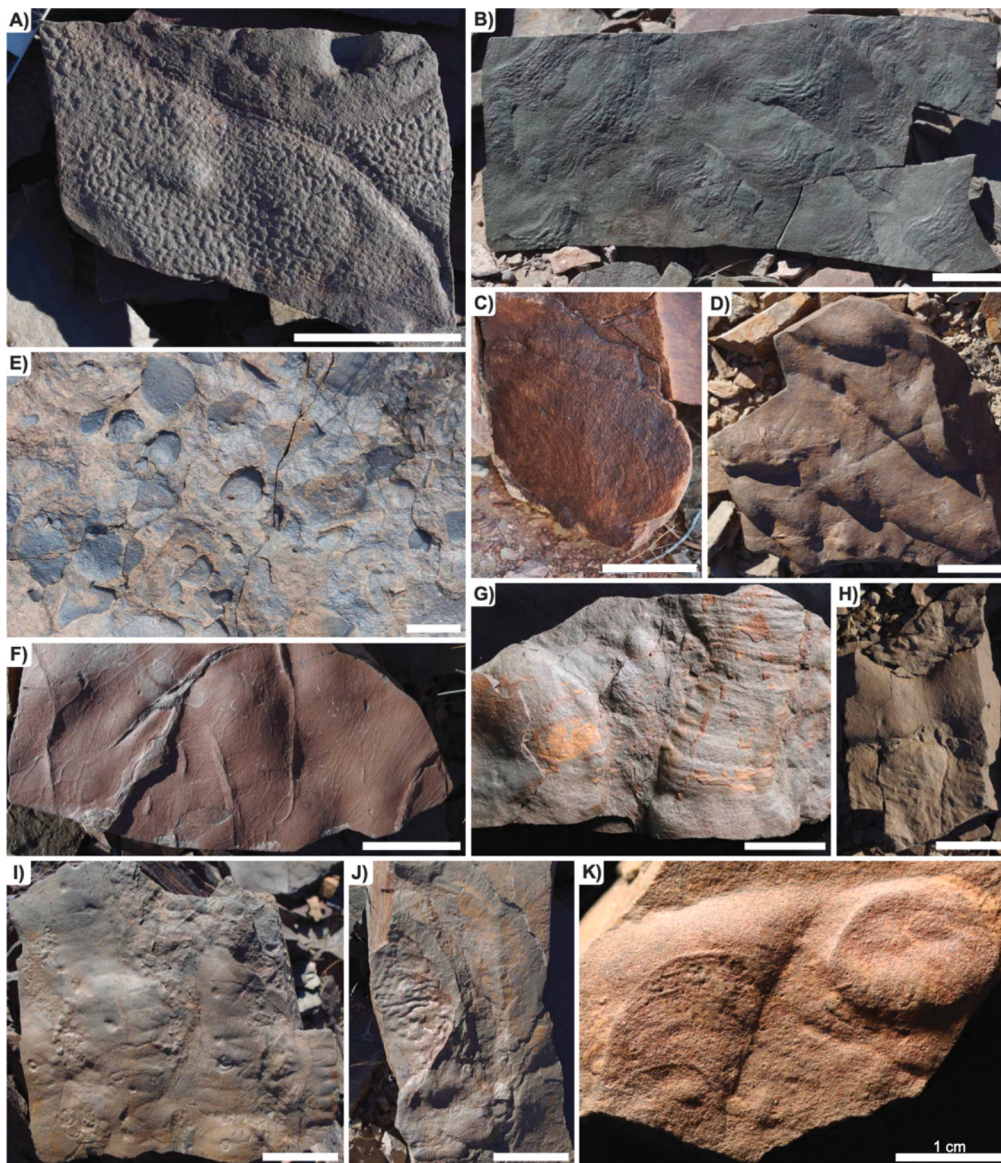
Abundant textures likely indicative of organic mats (e.g., Fig. 5A, B) and trace fossils were identified throughout the lower and upper Wood Canyon Formation, consistent with previous reports (Jensen et al., 2002;



**Fig. 4.** Potential rangeomorphs and discoidal structures from the lower Wood Canyon. (A) Specimen tentatively assigned to *Charnia*?, white box corresponds to panel (B) with three orders of branching outlined in (C). (D, E) Poorly preserved potential fronds with primary branching (black arrows) and associated 'amorphous sheet-like' structures (white arrows). (F) Potential 'amorphous-sheet' found in isolation (i.e., absent associated fronds). (G–M) discoidal structures of varying morphologies. (A–E, H–M) From the Montgomery Mountains, catalogue numbers BLM.2024.01 (A, B) 0.12; (D) 0.18; (E) 0.06; (I) 0.19; (H, J–M) remain in the field; (F, G) from Chicago Pass; (F) LACMIP 43366.1; (G) remains in the field. Scale bars 10 mm.

Smith et al., 2017; O'Neil et al., 2022), although some morphologies of the former overlap with abiotic wrinkle structures (Pratt, 2021). Definitive sedimentary structures also match previous descriptions (e.g., Smith et al., 2017, 2023) and include loading structures (Fig. 5C), flute casts (Fig. 5D), mud chips (Fig. 5E), sandstone intraclasts, syneresis cracks (Fig. 5F), symmetric ripples and cross bedding. Various specimens with a more problematic origin were also observed in these sections. Several (Fig. 5G–I) are comparable to the corrugated tubular forms

described from the correlative Esmerelda Member of the Deep Spring Formation (Nelson and Smith, 2019). In the lower Wood Canyon, observed morphologies include forms with regular to irregularly spaced ridges oriented perpendicular to the long axes (Fig. 5G, I). Other structures range from almost entirely amorphous (Fig. 5J) to well-defined (Fig. 5K), with evidence of wrinkling. Although a variety of biotic and abiotic processes may be responsible for these forms, we suggest the most likely interpretation is that at least some of the



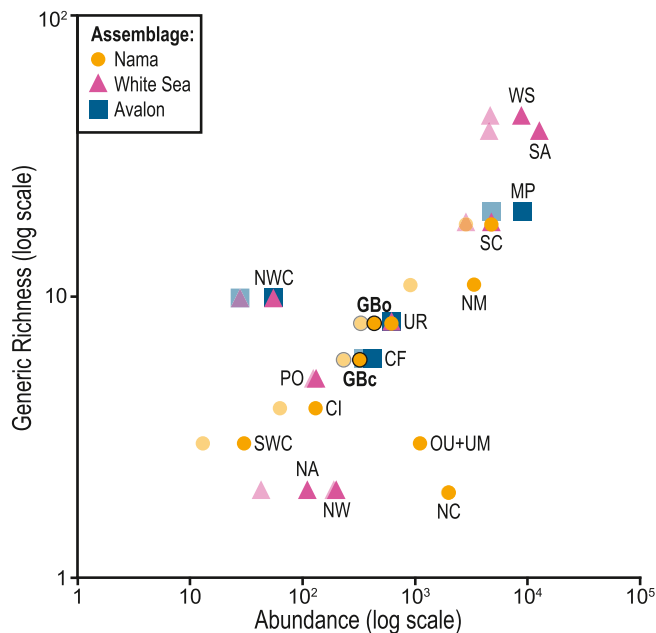
**Fig. 5.** Textures indicative of mats and other structures from the lower Wood Canyon, including: (A, B) textured organic surfaces, (C) load structures, (D) flute casts, (E) mud-chips, (F) syneresis cracks and possibly mat related wrinkle marks, and (G–K) Possible organic mat related organosedimentary structures of varying morphology. (C, E) From Chicago Pass; all others are from the Montgomery Mountains. (G) BLM.2024.001.11; (K) BLM.2024.001.09; all others remain in the field. Scale bars 50 mm.

specimens in Fig. 5 represent organosedimentary structures resulting from various forces acting upon heterogeneous organic mats (Nelson and Smith, 2019). The regularity of the resultant structures (corrugations) can overlap with the morphology of the repeated tubular elements of erniettomorphs and the branching architecture of rangeomorphs, including those described here (e.g. Fig. 3C, D; 4D, E). Such interpretations are complicated by the incomplete and fragmentary nature of Ediacaran macrofauna from the lower Wood Canyon (see discussion below).

### 3.4. Diversity and abundance of the Ediacara Biota from the Great Basin

Comparison of total generic richness and estimated abundance between Ediacaran fossil localities suggests a distinction between five fossil-rich regions (Mistaken Point, Namibia, South Australia, South China, and the White Sea) and all others, including those from the Great Basin (Fig. 6). Although there is a continuum between all regions investigated (especially given the logarithmic scale presented in

Fig. 6A), these five sites exhibit considerably greater diversity and abundance. Despite various taxonomic uncertainties, our results suggest the addition of two genera (*Pteridinium* and *Charnia*?) belonging to the Ediacara Biota from this region. Discoidal structures resembling the form genus *Aspidella* that represent holdfasts of frondose taxa, including *Charnia*? identified here, were excluded from the original dataset (Evans et al., 2022). Simple rounded structures, including *Beltanelliformis*, *Nimbia* and other possibly synonymous forms (see discussion in Ivantsov et al., 2014) were also excluded from the original dataset (Evans et al., 2022) based on their potential microbial origin (Ivantsov et al., 2014; Bobrovskiy et al., 2018). Even assuming all potential biotic structures examined here represent Ediacara macrobiota ('optimistic estimate'), total abundance would increase by <100 total specimens. Attempts to correct for available outcrop in North America (Table 1) match overall trends in diversity given similar estimates of outcrop area for these regions.



**Fig. 6.** Comparison of generic richness and abundance from major Ediacaran regions on logarithmic scales. Solid shapes represent normalized abundance values, transparent shapes based on exact counts if reported. Abbreviations: Charnwood Forest (CF); Central Iran (CI); Great Basin, conservative estimate (GBC); Great Basin, optimistic estimate (GBo); Mistaken Point (MP); North China (NC); Namibia (NM); Northern Australia (NA); Norway (NW); Northwest Canada (NWC); Olenek Uplift (OU); Podolia (PO); South Australia (SA); South China (SC); SW Canada (SWC); Uchar-Maya (UM); Urals (UR); White Sea (WS). Transparent points for OU, UM and NC are plotted, but are difficult to resolve based on overlap with solid shapes.

#### 4. Discussion

The diversity and abundance of taxa belonging to the Ediacara Biota from the Great Basin is less than other well-known, fossil-rich deposits from the Ediacaran. While this region plots relatively close in terms of diversity and abundance to occurrence data from Namibia in the log-scale diagram presented in Fig. 6, we note significant difference between the records. For example, half of the total genera described (encompassing all non-tubular Ediacara Biota) from the lower Wood Canyon and Deep Spring are represented by rare, incomplete specimens (*Erietta*, *Pteridium*, *Swartpuntia* and *Charnia*?) compared with hundreds of complete examples from the Nama Group (e.g., Elliott et al., 2011; Elliott, 2016; Vickers-Rich et al., 2013; Ivantsov et al., 2014; Gibson et al., 2019; Maloney et al., 2020). Further, the total abundance of Ediacara Biota from Namibia is roughly an order of magnitude greater than from the Great Basin. The reduced total specimen count may limit, for example, the amount of paleoecological information that can be gained from studies of the Wood Canyon Formation and correlative units. Understanding the potential factors responsible for the diversity and abundance of Ediacara taxa observed in the southwestern US may, however, be broadly applicable to various units globally.

##### 4.1. Preservation and sampling bias

We consider several first-order taphonomic factors responsible for the incompleteness of the fossil record (e.g., substantial age, paleo-environment, or preservational conditions) as unlikely to have biased the diversity of taxa currently recognized from the lower Wood Canyon compared with other Ediacaran sections globally. While these undoubtedly contribute to the rarity of Ediacaran fossil localities, our comparisons are restricted to similar aged deposits that all yield exceptional soft-bodied preservation and so these factors are not

applicable to comparisons here (Fig. 6). Specifically, the identification of Ediacara Biota fossils within the Wood Canyon Formation demonstrates that the necessary conditions were, at least occasionally, met to promote soft-bodied preservation in the cast and mold style typical of this group. Previous reports of abundant pyritized tubes (Smith et al., 2017; Schiffbauer et al., 2020; Selly et al., 2020) suggest that multiple taphonomic pathways existed for exceptional fossilization in these units. Textures indicative of microbial mats likely involved in such taphonomic pathways and commonly associated with Ediacaran fossils are abundant throughout these sections, extending well into Cambrian aged strata. This raises the possibility that the relative abundance and/or diversity of mat textures may provide a method for normalizing macrofossil diversity in the future (e.g., Tarhan et al., 2022; see further discussion below).

One possible explanation for differences between fossil communities of similar age is that these are the result of latitudinal diversity gradients, well-documented in both extant and Phanerozoic assemblages (e.g., Hillebrand, 2004; Jablonski et al., 2006). Paleogeographic reconstructions for the Ediacaran are highly variable (e.g., Robert et al., 2018), with projections typically placing the Great Basin at low latitudes (< 30 degrees) including near the equator (e.g., Merdith et al., 2021). Ediacaran sites correlative with the Nama assemblages with both greater (e.g., Namibia, South China) and reduced (e.g., Olenek Uplift, Central Iran) taxonomic richness are known from similar latitudes globally (e.g., Merdith et al., 2021). This is consistent with previous work suggesting that paleogeography does not play a significant role in our current perception of Ediacaran diversity patterns (Laflamme et al., 2013; Boddy et al., 2022; Evans et al., 2022).

No amount of searching prevents the next researcher from discovering a new productive horizon and sampling intensity is difficult to account for, although methods exist to correct for such inequalities in the fossil record (e.g., Signor et al., 1982; Smith et al., 2012; Dunhill et al., 2017; Benson et al., 2021). In regions with low reported diversity, it is often unclear how many excursions to these sites have yielded no specimens. This can be attributed to the typical lack of publishing null results; a search for fossils that yields no specimens will often go unreported. The variety of published field-guides (e.g., Nelson and Durham, 1966; Diehl, 1974; Smith and Nelson, 2018; Smith et al., 2019), journal articles (Corsetti and Hagadorn, 2000, 2003; Hagadorn et al., 2000; Hagadorn and Waggoner, 2000; Fedo and Cooper, 2001; Jensen et al., 2002; Smith et al., 2016, 2017, 2023; Nelson and Smith, 2019; Schiffbauer et al., 2020; Selly et al., 2020; O'Neil et al., 2022), and general accessibility of localities in the Great Basin suggests that generations of experienced geologists and paleontologists have searched over decades for Ediacaran fossils at these sites. This may indicate that limited sampling is unlikely responsible for the diversity of Ediacaran fossils recovered from the lower Wood Canyon. Statistical comparisons of the robustness of diversity trends from other well-known deposits in South Australia, the White Sea and Namibia further suggest that under sampling is unlikely to account for global diversity trends (Tarhan et al., 2018).

Comparing diversity and abundance to sampling proxies that attempt to account for the variability of the rock record, such as outcrop area and stratigraphic thickness, may help remove certain biases (e.g., Raup, 1976; Peters and Foote, 2001; Smith, 2001). Our ability to correct for the available outcrop of Ediacaran deposits globally is somewhat limited, as data regarding total outcrop area and stratigraphic thickness are not available for most units. Advances in the digital accessibility of such information through Macrostrat (Peters et al., 2018) do provide estimates for localities in North America. A recent study suggests that sedimentary rock quantity increases significantly across the Ediacaran-Cambrian boundary, which likely contributes to the major increase in diversity across this boundary (Segessenman and Peters, 2024). Units for which area and thickness are available vary considerably between localities and coverage of the Ediacara Biota. For example, the regions presented in Table 1 include the Conception Group of

Newfoundland, which consists of three units that contain Ediacara Biota (the Drook, Briscal and Mistaken Point formations) and two units for which we have no recorded occurrences in our dataset (the Mall Bay and Gaskiers Formation; Matthews et al., 2021). Reported diversity and abundance values for the region also include fossils from the overlying St. John's Formation for which rock area estimates are not currently available in Macrostrat. Thus, the cumulative area reported may represent an inaccurate estimate of all fossil-bearing Ediacaran strata from Newfoundland. On the other hand, the subject of this study, the Wood Canyon Formation, is dominated by Cambrian-aged strata, and so the cumulative outcrop area presented in Table 1 is likely overestimated compared to the total availability of Ediacaran fossil-bearing strata in the region. Further, the metamorphic grade at certain localities where the lower Wood Canyon Formation is exposed (e.g., the Funeral and Panamint Mountains) likely crosses important thresholds beyond which fossil preservation is unlikely. Given these uncertainties, it is unclear whether normalizing for areal extent removes sampling biases as intended.

Another possible explanation for the lack of abundant Ediacara taxa from the lower Wood Canyon is that, while the combination of factors needed for exceptional fossilization were met, they were exceedingly rare. Hall et al. (2020b) proposed that relatively coarse-grained, quartz-rich sand fill of fossils as well as a kaolinite and smectite rich matrix results in well-preserved erniettomorphs. This suggests that a specific set of depositional and mineralogical conditions were required for the preservation of soft-bodied taxa, undoubtedly contributing to the low total abundance of Ediacaran fossils throughout the region. It is unclear that this should impact total diversity and abundance when compared to contemporaneous localities, as these involve largely overlapping lithologies, preservational pathways and fossilized organisms. Further, the identification of fossils at multiple localities from discrete horizons (Smith et al., 2017), suggests that such conditions were met multiple times within these deposits. Mat textures and trace fossils found throughout the Wood Canyon Formation (Jensen et al., 2002; Smith et al., 2017; O'Neil et al., 2022) indicate that preservational conditions conducive to replicating non-mineralized structures were prevalent. Further petrographic study of both ambiguous and definitively biotic structures is needed to determine the commonality of sedimentary conditions required for exceptional preservation.

#### 4.2. Depositional environment

Fossil taxa of the Ediacara Biota can be restricted to particular depositional settings (see examples in Waggoner, 2003; Gehling and Droser, 2013; Boag et al., 2016) suggesting that certain organisms had a limited spatial distribution along the Ediacaran seafloor. Although alternatives have been proposed (see Retallack, 2013), the consensus among researchers is that this biota was mostly or entirely restricted to the marine realm (e.g., Wood et al., 2003; Xiao et al., 2013; Tarhan et al., 2015a; Smith et al., 2017; Maloney et al., 2020). The majority of sections studied display sedimentological evidence for deltaic to shallow marine, clastic dominated depositional settings (Fedo and Cooper, 2001). This is broadly consistent with strata containing fossils of the White Sea and Nama assemblages globally (Boag et al., 2016; Darroch et al., 2021; Evans et al., 2022), although shallow marine environments encompass a variety of parameters (e.g., energy, temperature, nutrient availability) that undoubtedly impact the distribution of macrofauna.

Uncertainty in any global comparison of localities yielding fossils of the Ediacara Biota arises from the difficulty of reconciling sedimentological descriptions by numerous authors spanning several decades, which can often include conflicting descriptions of the same units (see discussion in Evans et al., 2022, supplementary material). It is beyond the scope of this study to address all such inconsistencies, however, relevant parallels with fossiliferous units in Namibia and South Australia are instructive. Our sedimentological assessment of deltaic sandstones within mixed carbonate-siliciclastic units, likely representing shallow

marine environments that experienced periodic medium- to high-energy current activity match previous descriptions of the lower Wood Canyon (e.g., Hagadorn and Waggoner, 2000; Fedo and Cooper, 2001; Smith et al., 2023) as well as fossil bearing deposits of the Nama Group (Elliott et al., 2011; Meyer et al., 2014; Ivantsov et al., 2016; Gibson et al., 2019; Maloney et al., 2020) and Ediacara Member (Tarhan et al., 2017; Droser et al., 2020). Strata examined here also contain channelized sandstone beds interpreted as gutter casts, similar to those yielding fossils likely transported into submarine deltaic settings during storm events at localities such as Farm Aar, Namibia and NENP, South Australia (Elliott et al., 2011; Gehling and Droser, 2013; Vickers-Rich et al., 2013; Droser et al., 2020). Other sedimentary features observed, such as textured organic surfaces and sandstone intraclasts, are common to Ediacaran fossil-rich sites (e.g., Tarhan et al., 2017). Combined, these data suggest that the variable paleoenvironments recorded in heterolithic sections of the lower Wood Canyon at least partially overlap with those of more fossil-rich localities.

Other characters of exceptional deposits yielding abundant and diverse fossils of Ediacara Biota were not observed here. For example, palimpsest ripples and 'shims' are characteristic of facies containing some of highest diversity fossil communities globally from South Australia (Tarhan et al., 2017; Droser et al., 2020). These are unique features prevalent in sections where systematic excavation of individual bedding planes provides an unparalleled view of the White Sea assemblage (e.g., Droser et al., 2020). The lack of such features from the lower Wood Canyon could explain our inability to identify similar discreet bed surfaces with abundant fossils. However, we did observe distinct bed junctions between sandstones of matching lithologies. This lack of amalgamation, which is similarly observed in the Ediacara Member at NENP (e.g., Tarhan et al., 2017) is attributed to the presence of organic mats. Further, areas within both the Montgomery Mountains and Chicago Pass localities contain strata whose dip closely matches the slope of the hillside, and so meter scale bedding plane exposures are present, and excavation is possible. Preliminary attempts yielded mat textures and ripples but no definitive macrofauna. An important factor may be that the identification of productive horizons for excavation at NENP, as elsewhere, is guided by abundant fossils recovered in float (Droser et al., 2020), and so it is unclear whether the lack of such beds in the Great Basin is due to a general lack of fossils or minor paleoenvironmental differences. Further, it can be difficult to disentangle the effects of habitability and taphonomy on a depauperate assemblage, both of which are modulated by depositional setting.

Related to considerations of paleoenvironment is whether specimens are preserved in situ or experienced transport prior to burial, which affects biological interpretations and the preservational fidelity of fossils. In countless Phanerozoic and modern shallow-marine settings, the transport and accumulation of mineralized tissue yields time-averaged deposits, wherein the diversity and abundance of taxa is inflated relative to the total living biomass during any one period (e.g., Lawrence, 1968; Behrensmeier et al., 2000). In Cambrian Burgess Shale-type deposits, transport to areas of the seafloor with conditions conducive to soft-part preservation is likely a requirement for characteristic exceptional fossilization (e.g., Conway-Morris, 1979; Gaines, 2014). These high-energy processes can also lead to breakdown over time, preserving only the most recalcitrant tissues/organisms that died relatively close to the time of transport (e.g., Lawrence, 1968; Allison, 1986). At NENP, in situ fossil communities on individual bedding planes yield higher diversity, abundance and fidelity of the Ediacara Biota compared with transported specimens from mass-flow deposits (Gehling and Droser, 2013; Tarhan et al., 2017; Droser et al., 2020). Fossils in the latter setting are interpreted as the most resilient and abundant organisms from the original assemblage, including erniettomorphs and frondose taxa, which are commonly fragmented and/or distorted when associated with pre-burial transport (Droser et al., 2020; Evans et al., 2019).

The preponderance of fossils found in float from the lower Wood Canyon, despite an abundance of bedding planes with matching

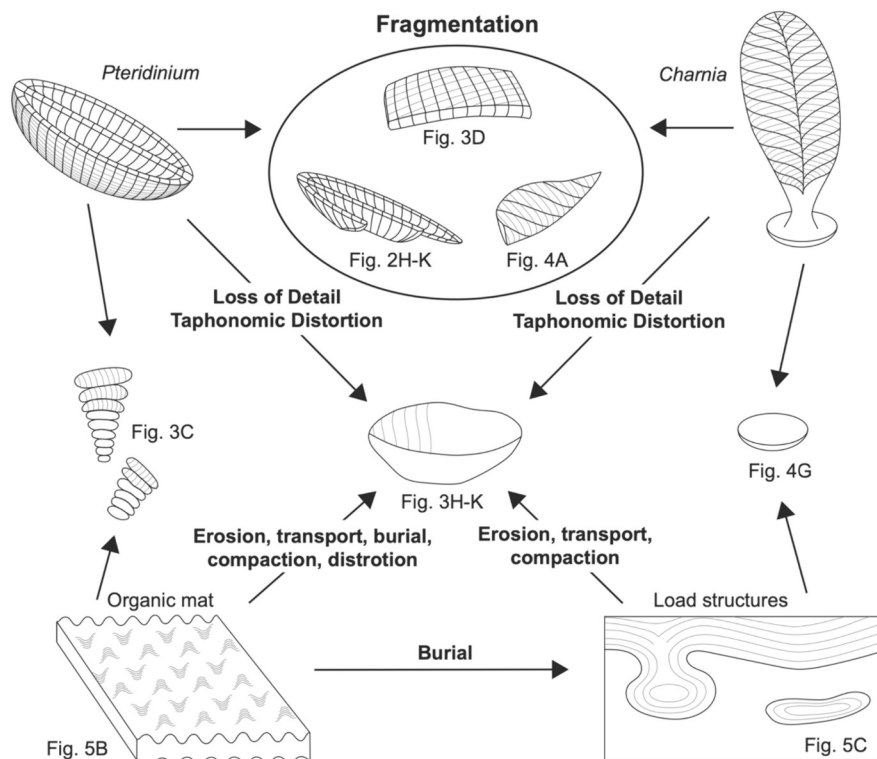
lithologies observed throughout these sections, precludes any definitive statements about the nature of preservation and/or transport prior to burial. However, erniettomorphs exhibit multiple vanes when complete (Elliott, 2016). Assuming the fossils described here represent previously described taxa, specimens lacking a distinct suture (i.e., consisting of a single vane, Fig. 2C) must have been part of a larger organism with either two (*Ernietta*), three (*Pteridinium*) or as many as six (*Swartpuntia*) vanes in life. As such, all specimens described are incomplete and preserved three dimensionally (as opposed to two-dimensional, bedding plane preservation). Even the high density and relatively well-preserved specimens in the slab presented in Fig. 2 (Smith et al., 2017) are incomplete and variably orientated, consistent with transport and accumulation prior to burial. If observed corrugations within tubular elements of erniettomorphs represent the original bedding of sediment infill, inconsistent orientation between these and bedding of the host matrix is further evidence for pre-burial transport. The features described above are consistent with descriptions of transported erniettomorphs and rangeomorphs found in gutter-casts from the Nama Group, Namibia (Elliott et al., 2011; Vickers-Rich et al., 2013; Ivantsov et al., 2016 but see Maloney et al., 2020; Gibson et al., 2019 for alternative interpretations).

Potential transport also raises questions regarding smooth structures associated with Ediacaran fossils (Figs. 2, 3). Although the general sac-like morphology of these smooth structures broadly overlaps with that of *Ernietta*, the lack of ridges is unlikely due to poor preservation of erniettomorphs (e.g., as described by Hall et al., 2020b) given the fidelity and ability of immediately adjacent forms to impart their ridges onto these otherwise smooth structures. Preservational variation could be tested by comparing the grain size and clay content of these structures relative to adjacent fossils (Hall et al., 2020b), but, at present, their biogenicity remains undetermined. The relative timing between death and transport is also known to play a significant role in the preservational fidelity of soft-bodied organisms (Allison, 1986) but the precise timing of transport is difficult to determine for specimens from the Wood

Canyon Formation.

#### 4.3. Macrofauna, mats and loading

A special case of sampling/preservational bias is relevant to fossils from the lower Wood Canyon: the ability to distinguish biotic signatures of Ediacaran soft-bodied macrofauna from abiotic structures and mat textures. Namely, though we find definitive evidence for erniettomorphs, frondose taxa, mat-bound ripples and load structures, poor preservation and transport prior to burial result in highly overlapping morphologies (Fig. 7). Inferred mat textures may be formed by abiotic processes (Pratt, 2021). Similarly, loading can produce a variety of forms that may resemble the Ediacara Biota. These require differences in density between lithologic units and mobilization of sediment that can involve numerous combinations of biotic and abiotic factors (e.g., Owen, 2003). Some of the most common and easy to recognize are load casts at the base of sandstone beds deposited on top of mud, observed in the heterolithic units of the lower Wood Canyon (e.g., Fig. 5C). Both sedimentological and experimental analyses indicate that density gradients can be produced in many ways and at various scales, from the uneven distribution of sand deposited during a storm event, to minor variations in grain size, packing, angularity and cementation (Owen, 1996, 2003; Strachan, 2002; Tinterri et al., 2016). Such differences in sediment at the time of deposition may or may not be preserved in the geologic record (Owen, 1996, 2003). Organic matter can also produce differences in density and viscosity of sediment, and the unique binding of sand grains by microbial mats in the Precambrian resulted in a variety of features that may resemble Ediacaran macrofauna (e.g., Menon et al., 2016; Nelson and Smith, 2019; Okubo et al., 2023). Specifically, repeated mat textures and ripple casts can undergo several processes resulting in numerous structures that resemble poorly preserved modular taxa (Nelson and Smith, 2019). To add further complication, the tissues of macrofauna themselves could generate subtle density gradients and thus facilitate the formation of load structures.



**Fig. 7.** Cartoon illustration of the various taphonomic pathways that can lead to morphologic overlap between Ediacaran soft-bodied macrofauna, mat-bound ripples and load structures as recognized in the lower Wood Canyon.

In many cases, the recovery of potential fossils in float precludes comparisons with host sediment, which could be used to investigate the role of soft-sediment deformation. Although examples identified in situ include specimens preserved on bed tops and within matching lithologies – features not commonly associated with loading structures, various experimental and observational data suggest that such structures are possible without biotic influence (e.g., Owen, 1996, 2003; Strachan, 2002; Tinterri et al., 2016). Further, the preponderance of organic mats throughout these sections indicates that several combinations of factors are possible. This likely plays a role in the number of Ediacaran fossils recovered from the lower Wood Canyon, as well as other regions with similar diversity and abundance.

#### 4.4. Biotic signal

In addition to the biases discussed above, observed diversity and abundance could reflect the original community composition of the Ediacara Biota from the lower Wood Canyon. Studies of the latest Ediacaran Nama assemblage indicate reduced global generic richness compared with the preceding White Sea assemblage (Laflamme et al., 2013; Boag et al., 2016; Muscente et al., 2018; Tarhan et al., 2018; Evans et al., 2022; Darroch et al., 2023) and local communities characterized by relatively high dominance and environmental segregation (Darroch et al., 2015, 2018a; Eden et al., 2022). Consistent with this pattern is our observation that, among the five fossil-rich regions identified here, those from Namibia are the youngest and exhibit the lowest total diversity and abundance of the Ediacara Biota (Fig. 6; although note that this excludes mineralized taxa abundant in these latest Ediacaran sections).

The rarity of Ediacara-type taxa in Cambrian strata (although see Jensen et al., 1998; Hoyal-Cuthill, 2022) suggests that most of these forms went extinct prior to the Proterozoic-Phanerozoic boundary (e.g., Seilacher, 1984). A general lack of age-constraints for strata below the Ediacaran-Cambrian boundary, including those from the Wood Canyon Formation, complicates interpretations of the timing and duration of potential extinction events (e.g., Darroch et al., 2018b, Nelson et al., 2023). Compared with other deposits attributed to the Nama assemblage (e.g., those found in Namibia), the lower Wood Canyon is likely significantly younger, with fossil bearing strata immediately below the Ediacaran-Cambrian boundary (Nelson et al., 2023). Thus, the relatively fossil-poor communities observed here may reflect an originally depauperate fauna of the Ediacara Biota, perhaps a result of the same changes that would ultimately lead to their demise. Alternatively, the southern Great Basin may preserve a restricted late Ediacaran setting with overall low diversity and abundance compared to contemporaneous sections globally, although this is difficult to verify. A hypothesized biotic signal also does not exclude taphonomic or sampling factors discussed above. Factors such as pre-burial transport are well-documented at sites exhibiting relatively high diversity and abundance of the Ediacara Biota globally (Elliott et al., 2011; Gehling and Droser, 2013; Vickers-Rich et al., 2013; Ivantsov et al., 2016; Tarhan et al., 2017). Even an optimistic view of the totality of potential biotic structures observed suggests that the lower Wood Canyon is not as diverse as more famous Ediacaran localities.

In our view, the arguments highlighted above suggest that the various biases contributing to the Ediacaran fossil record are unlikely to be solely responsible for the comparably low diversity and abundance observed in the lower Wood Canyon. We note that this is based on known current occurrences of the Ediacara Biota, which are ever increasing, and that various uncertainties are inherent in such analyses. Namely, it is difficult to normalize for the availability of potential fossil bearing rock or the extent of searches for such forms in a given region. One potential solution is a quantitative assessment of the extent and diversity of textured organic surfaces and trace fossils likely preserved via similar taphonomic pathways as those of nonmineralized macrofauna. Comparisons between such features and Ediacara macrofossils are limited, but correlations have been documented, for example at

NENP between the maturity of textured organic surfaces and fossil taxa on discrete bedding surfaces (Droser et al., 2020; Tarhan et al., 2022). Thus, future studies that attempt to normalize fossils occurrence data based on characteristics of textured organic surfaces or trace fossils would be useful in testing the hypothesis of comparatively reduced diversity in the latest Ediacaran.

Under the assumption that the lower Wood Canyon records the decline of the Ediacara Biota, our work does not directly address the driver(s) of this loss; however, these and similarly-aged deposits globally may hold the clues to this event. Two main hypotheses – environmental change and biotic replacement – have been previously discussed (Laflamme et al., 2013; Smith et al., 2016, 2017; Darroch et al., 2018b, 2023; Cribb et al., 2019; Hodgkin et al., 2021; Evans et al., 2022). The biotic replacement model typically invokes the activities of bioturbators as ecosystem engineers, evidenced by trace fossils of increasing complexity, to have fundamentally altered conditions in a manner no longer suitable for the Ediacara Biota (Darroch et al., 2016, 2022; Cribb et al., 2019). The cooccurrence of trace fossils and the low diversity assemblage of the lower Wood Canyon (e.g., Jensen et al., 2002; Tarhan et al., 2020; O'Neil et al., 2022) may support hypotheses that bioturbators had begun to impact the seafloor in a manner that led to the geologically slow decline of the Ediacara Biota (e.g., Laflamme et al., 2013; Darroch et al., 2015, 2016). However, most trace fossils below the Ediacaran-Cambrian boundary in the southern Great Basin represent simple horizontal burrows (Corsetti and Hagadorn, 2000; Jensen et al., 2002; Nelson et al., 2023) that likely had minimal impacts on the environment (e.g. Tarhan, 2018; Tarhan et al., 2018; Cribb et al., 2023). Sedimentological evidence for organic mats is present throughout the entire Wood Canyon Formation, extending into the Cambrian and overlapping with highly complex trace fossils (Jensen et al., 2002; O'Neil et al., 2022). This further suggests extensive bioturbation did not reach levels required for the exclusion of organic mats until well after the demise of the Ediacara Biota (Tarhan, 2018). Future work detailing macrofauna, mats and trace fossils in the Wood Canyon Formation and correlative units globally should be targeted to further resolve such relationships.

## 5. Conclusions

The lower member of the Wood Canyon Formation exposed in the southern Great Basin contains a relatively low diversity assemblage of soft-bodied Ediacaran fossils, despite decades of exploration. Here we add two new genera to the known record from this unit, including *Pteridinium* and the first rangeomorph petaloid described from the region. Numerous biases, including transport prior to burial and difficulty of identification, may contribute to the general lack of abundant Ediacara Biota from the lower Wood Canyon. Even considering these biases, we propose that this reduced diversity reflects an original depauperate community of such organisms. The age of these rocks indicates that they record some of the youngest examples of this largely enigmatic, soft-bodied group of early animals. One possibility is that this low diversity late Ediacaran community records the decline of such organisms as this biota gave way to more familiar forms, including abundant mineralized taxa, that would subsequently dominate the Phanerozoic fossil record. However, other hypotheses remain plausible and similar evaluation of the characters identified here at other late Ediacaran sites globally may provide refined understanding of these diversity dynamics.

## CRedit authorship contribution statement

**Scott D. Evans:** Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Emily F. Smith:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Prescott Vayda:** Writing – review & editing, Investigation. **Lyle L. Nelson:** Writing – review & editing, Investigation. **Shuhai Xiao:** Writing – review &

editing, Supervision, Resources, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors have no competing interests to declare.

## Data availability

All data used in this study are available either as supplementary online material or publicly accessible repositories. Abundance data are compiled in Supplementary Dataset 1. Supplementary 3D scan files are available as supplementary material (see Appendix A). Physical specimens are deposited at the Smithsonian National Museum of Natural History, the Natural History Museum of Los Angeles County and the Las Vegas Natural History Museum.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloplacha.2024.104547>.

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