Internal structure of Cambrian vendobionts *Arumberia, Hallidaya* and *Noffkarkys* preserved by clay in Montana, USA

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ABSTRACT

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Quilted fossils known as vendobionts have remained enigmatic because preserved as unrevealing impressions in sandstone, for example *Arumberia banksi* Glaessner & Walter, *Noffkarkys storaasli* Retallack & Broz, and *Hallidaya brueri* (Wade) Retallack & Broz from the Ediacaran to Cambrian, Grant Bluff and Arumbera formations of central Australia. These same species are reported here in shaley facies of the Early Cambrian Flathead Sandstone of Fishtrap Lake, Montana. These fossils preserved in three dimensions are infiltrated by clay and confirm that each taxon has distinctive internal chambers reflecting segmentation seen on the surface. Sedimentary structures, petrography and geochemistry of the Montana sediments are evidence that *Arumberia*, *Noffkarkys* and *Hallidaya* lived on supratidal flats of a wave–protected rock–bound estuary unaffected by marine bioturbation, and represent intertidal to supratidal ecosystems widespread from the Ediacaran to Cambrian.

Key–words—Cambrian, Vendobiont, *Arumberia, Noffkarkys, Hallidaya*.

INTRODUCTION

PETROGRAPHIC thin sections now reveal internal structure of a variety of problematic vendobiont fossils which span the Ediacaran–Cambrian boundary: *Arumberia banksi* Glaessner & Walter (1975), *Noffkarkys storaasli* Retallack & Broz (2020), and *Hallidaya brueri* (Wade) Retallack & Broz (2020). These species were previously known from Ediacaran and Early Cambrian sandstone impressions in central Australia (Retallack & Broz, 2020), but Cambrian examples from clayey intertidal facies of the lower Flathead Sandstone near Fishtrap Lake, Montana (Retallack, 2013a), are infiltrated with fine clay in a way that reveals histological organization important to understanding their biological affinities. They are not thoroughly permineralized with calcite, silica, phosphate, or pyrite, like permineralized fossil plants and lichens (Matten, 1973; Gould & Delevoryas, 1977; Taylor *et al.,* 1997; Yuan *et al.,* 2005; Bippus *et al.,* 2017), but do reveal the three–dimensional organization of recalcitrant versus easily decayed tissues that has been helpful in understanding unmineralized fossil plants and lichens (Jennings, 1974, 1985; Retallack, 2009, 2011).

A secondary aim of this study is to re–evaluate the idea of Ediacaran–Cambrian agronomic revolution (Seilacher & Pflüger, 1994; Oji *et al.,* 2018), Ediacaran savanna hypothesis (Budd & Jensen, 2017), garden of Ediacara (McMenamin, 2000), and underground Vendobionta (Grazhdankin & Seilacher, 2002). These terrestrial metaphors have been used to describe changes in seas of the past, but what of Ediacaran–Cambrian changes on land from the large number of recently recognized Ediacaran and Cambrian paleosols (Retallack, 2013b, 2016a, b; Liivamägi *et al.*, 2014)? Rather than assuming that all Ediacaran and Cambrian rocks are marine, there is now the prospect of comparing and contrasting marine and terrestrial evolution. Did the churning of substrate by marine organisms destroy Ediacaran marine matgrounds as a catastrophe or pulsed catastrophe (Schiffbauer *et al.,* 2016; Darroch *et al.,* 2018b; Buatois *et al.,* 2018), or was it a drawn–out transition (Buatois *et al.,* 2014; Shahkarami *et al.,* 2017; Laing *et al.,* 2019), or compromised by sea level changes (Shahkarami *et al.*, 2020)? Or were terrestrial vendobionts ("Mattressland" of Retallack & Broz, 2020) unaffected by the evolution and intensification of marine bioturbation ("Wormworld" of Schiffbauer *et al.,* 2016)?

GEOLOGICAL SETTING AND FOSSILS

The fossils described here from near Fishtrap Lake, in Sanders County, Montana (Fig. 1) are pre–trilobite Early Cambrian in age (522–539 Ma), based on associated trace fossils (Retallack, 2013a). The fossils were all obtained from a 1.7 m thickness of red siltstone, which is a sequence of six thin paleosols within the basal Flathead Sandstone (Fig. 2). These red siltstones have a distinctive assemblage of trace fossils, *Manykodes pedum*, *Bergaueria hemispherica*, *Didymaulichnus lyelli* and *Torrowangea* (Retallack, 2013a). *Manykodes pedum* (Dzik, 2005) is sometimes still referred to as the superseded name *"Treptichnus" pedum* (Buatois, 2018), but the Pennsylvanian ichnogenus *Treptichnus* is inappropriate in several ways, especially its long straight sections of burrow between looping stitches (Maples & Archer, 1987; Rindsberg & Kopaska–Merkel, 2005).

The trace fossils are of Early Cambrian age, stratigraphically below the first appearance of trilobite trace fossils in the Flathead Sandstone (Retallack, 2013a), and well below an early Middle Cambrian assemblage of trilobites of the *Albertella* zone in the Wolsey Shale (Walcott, 1917; Keim & Rector, 1964; Bush, 1989). Sedimentary facies are evidence of a rockbound estuary unconformable on littoral talus of the Mesoproterozoic Libby Formation (Retallack, 2013a), a sedimentary setting comparable with modern Coos Bay, Oregon (Lund, 1973).

The marine trace fossils are all within the beds, which show mineral and chemical trends of weathering, and negative strain and mass transfer of paleosols downward from horizons of abundant vendobionts in growth position (Retallack, 2013a). In contrast the vendobiont fossils *Arumberia*, *Hallidaya* and *Noffkarkys* are on the bed and paleosol tops marked by clay enrichment and more abundant ferruginized
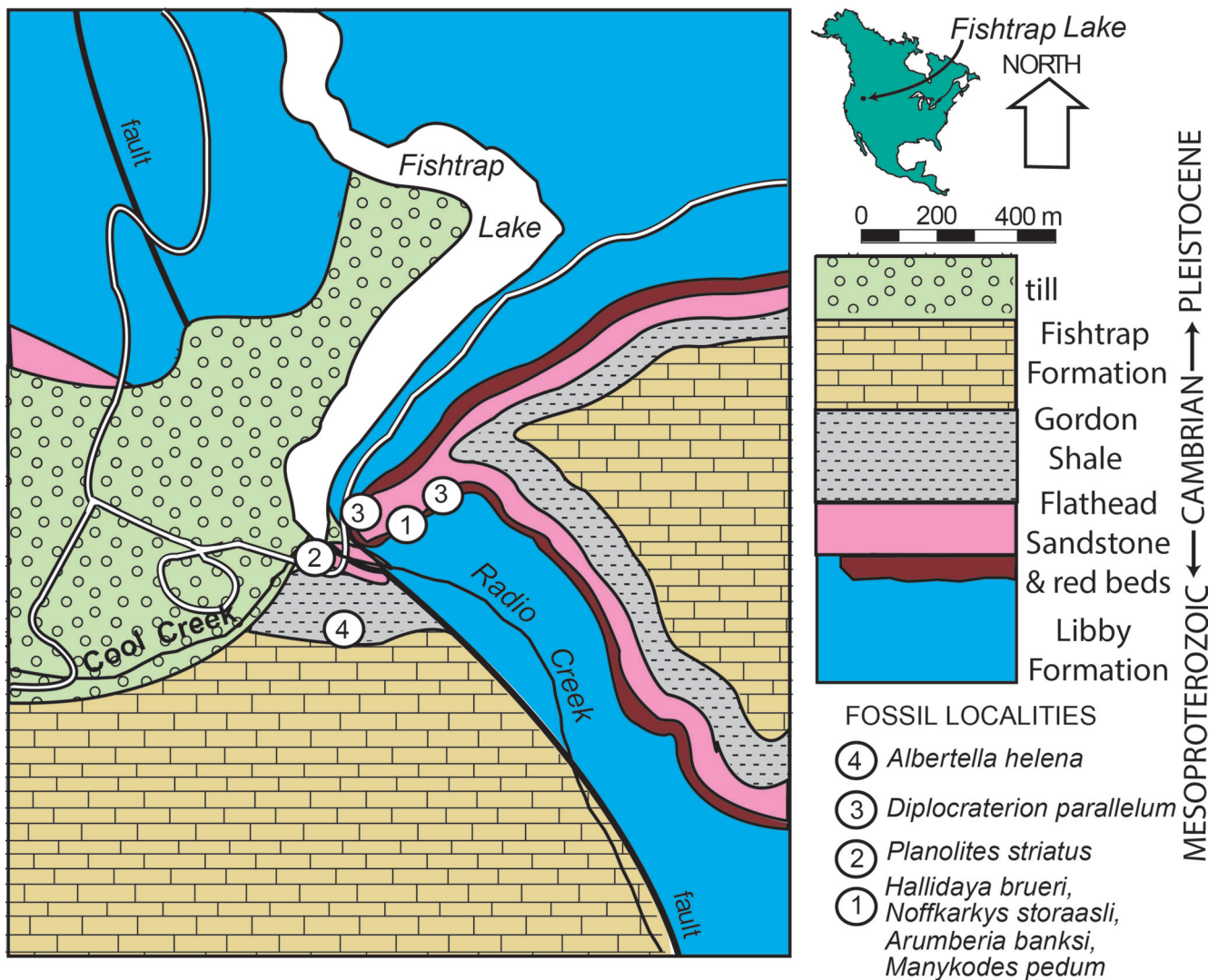

Fig. 1—Geological map of fossil localities near Fishtrap Lake, Montana (Retallack 2013a).

microscopic filaments (Fig. 2). Ferruginized filamentous structures on the tops of the beds vary from 38 volume % in the surface (A) horizons to 12 volume % in subsurface (C) horizons, as determined from point counting thin sections (Retallack, 2013a) and magnetic susceptibility (Retallack *et al.*, 2003). The red paleosols are of two distinct kinds: (1) Radio pedotype with A–Bg–C profile, including Bg horizon with marcasite (Sulfaquent of intertidal flats), and (2) Cool pedotype with A–C horizons only (Fluvent of supratidal flats).

Although the red siltstones are rock now, they were soft soils easily penetrated by filamentous microbial structures.

MATERIALS AND METHODS

This work involved small scale geological mapping of the locality at Fishtrap Lake Montana (Fig. 1), as well as field study of comparable assemblages in the Arumbera and Grant Bluff formations of central Australia (Retallack
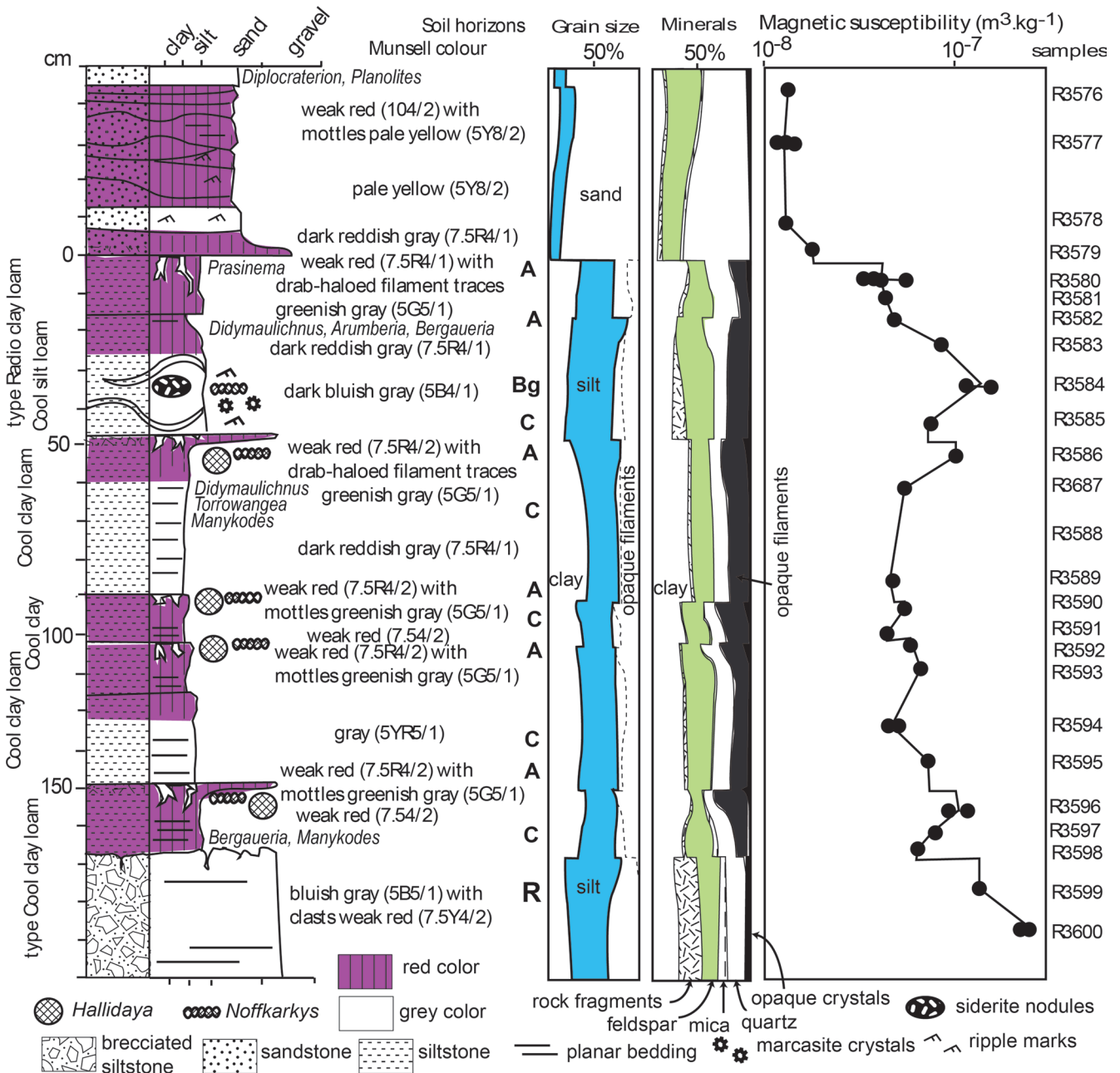

Fig. 2—Measured section of fossil localities in the Early Cambrian Flathead Sandstone near Fishtrap Lake, Montana. Grain size and mineral composition was determined by point counting petrographic thin sections, and magnetic susceptibility measured from hand specimens (Retallack, 2013a).

& Broz, 2020), Synalds, Lightspout, and Bridges formations near Church Stretton, England (Bland, 1984; McIlroy *et al.*, 2005), Jodhpur Sandstone, India (Kumar & Pandey, 2008), Bonney Sandstone in Brachina Gorge, Flinders Ranges, South Australia (Bland, 1984), and Billy Creek Formation in the eastern Flinders Ranges, South Australia (Bland, 1984; Retallack, 2008), as well as museum collections of Geoscience Australia, Canberra A.C.T. New collections of megafossils from all these localities are curated in the Condon Collection of the Museum of Natural and Cultural History of the University of Oregon in Eugene (online catalog at http: // paleo.uoregon.edu/condon/). Several fossils protruding from edges were sacrificed for preparation of petrographic thin sections, and all thin sections were cut vertical to bedding. A previous study reports data from point–counting thin sections, major element geochemistry, and magnetic susceptibility of this sequence (Retallack, 2013a). Laser scans of several specimens were provided by Jesse Pruitt of the Visualization Center of the Idaho Museum of Natural History, Idaho State University, Pocatello.

ARUMBERIA BANKSI GLAESSNER & WALTER 1975

Morphology

Arumberia is a scoop–shaped fossil with radiating furrows from the deepest end (Figs 3C–D, 4E–F, 5C), a strict definition close to the holotypes of the genus recently redescribed (Retallack & Broz, 2020). There has been dispute about whether *Arumberia* is a microbially mantled sedimentary structure, such as a linguoid ripple mark or flute cast, rather than a megafossil (McIlroy & Walter, 1997; McIlroy *et al.*, 2005). Recent study of the type material in Canberra (Geoscience Australia CPC14948) shows that *Arumberia* has inverse topology to a ripple (Retallack & Broz, 2020), but was not a microbially mantled flute cast either, because thin sections of material from Australia (Retallack & Broz, 2020) and in this paper (Fig. 6C–D) show that it has a complex quilted internal structure. This three–dimensional pattern is comparable with thin sections of enigmatic Ediacaran Vendobionta (Seilacher, 1992): Chinese
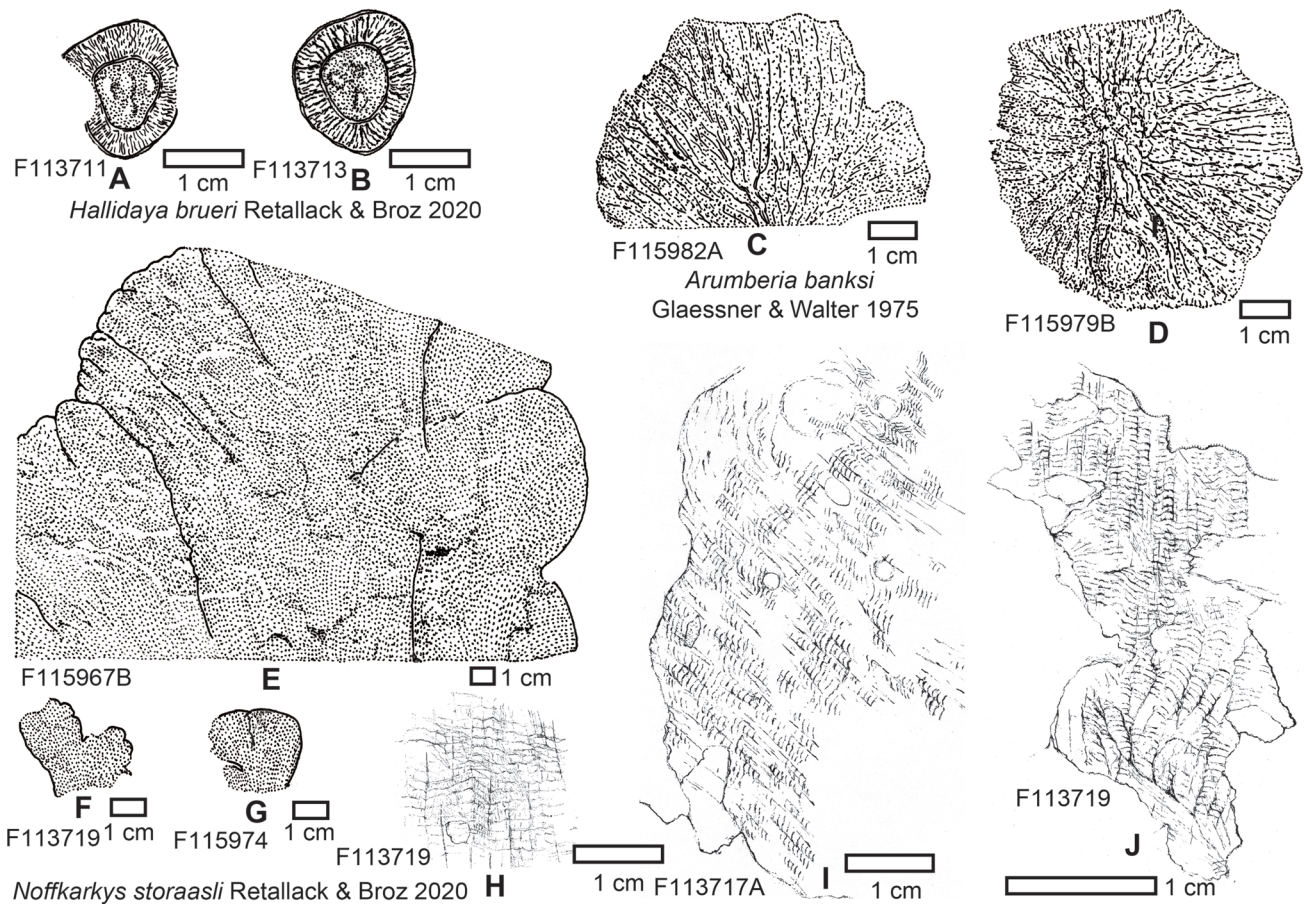

Fig. 3—Sketches of Early Cambrian megafossils from Fishtrap Lake, Montana: *Hallidaya brueri* (Wade) Retallack & Broz (A–B), *Arumberia banksi* Glaessner & Walter (C–D), and *Noffkarkys storaasli* Retallack & Broz (E–J).

Yangtziramulus zhangi (Xiao *et al.*, 2005; Shen *et al.*, 2009), Namibian *Pteridinium simplex* (Jenkins, 1992; Grazhdankin & Seilacher, 2002), *Swartpuntia germsi* (Narbonne *et al.*, 1997), and *Ernietta plateauensis* (Jenkins *et al.*, 1981; Ivantsov *et al.*, 2015), and Siberian *Charnia masoni* (Grazhdankin *et al.*, 2008). Also comparable are internal chambers of Silurian *Rutgersella* (Retallack, 2015a) and Devonian *Protonympha* (Retallack, 2018). Despite these constructional similarities, these other fossils have subhorizontal zig–zag sutures, mid–ribs, or vanes not seen in *Arumberia*. Both *Pteridinium* and *Ernietta* have concave–up morphology embedded within sediment, and partly filled with sediment (Grazhdankin & Seilacher, 2002; Ivantsov *et al.*, 2015), like *Arumberia*.

Measurements

Specimens from Fishtrap Lake fall within the 31–124 mm width of type material of *Arumberia banksi* from central Australia (Retallack & Broz, 2020). Specimen P15979A–B (part and counterpart) is the most complete specimen: 82 mm wide (perpendicular to striation) and more than 84 mm long (incomplete). Central striations are 2.5–4 mm apart and each 0.3–0.4 mm wide: dimples (hypichnial mounds) are 1.8–4.6 mm in diameter. Specimen P15982A–B (part and counterpart) is 84 mm wide and incomplete in length. Its striations are spaced at 2.3–5.6 mm and are 0.6–1.6 mm wide.
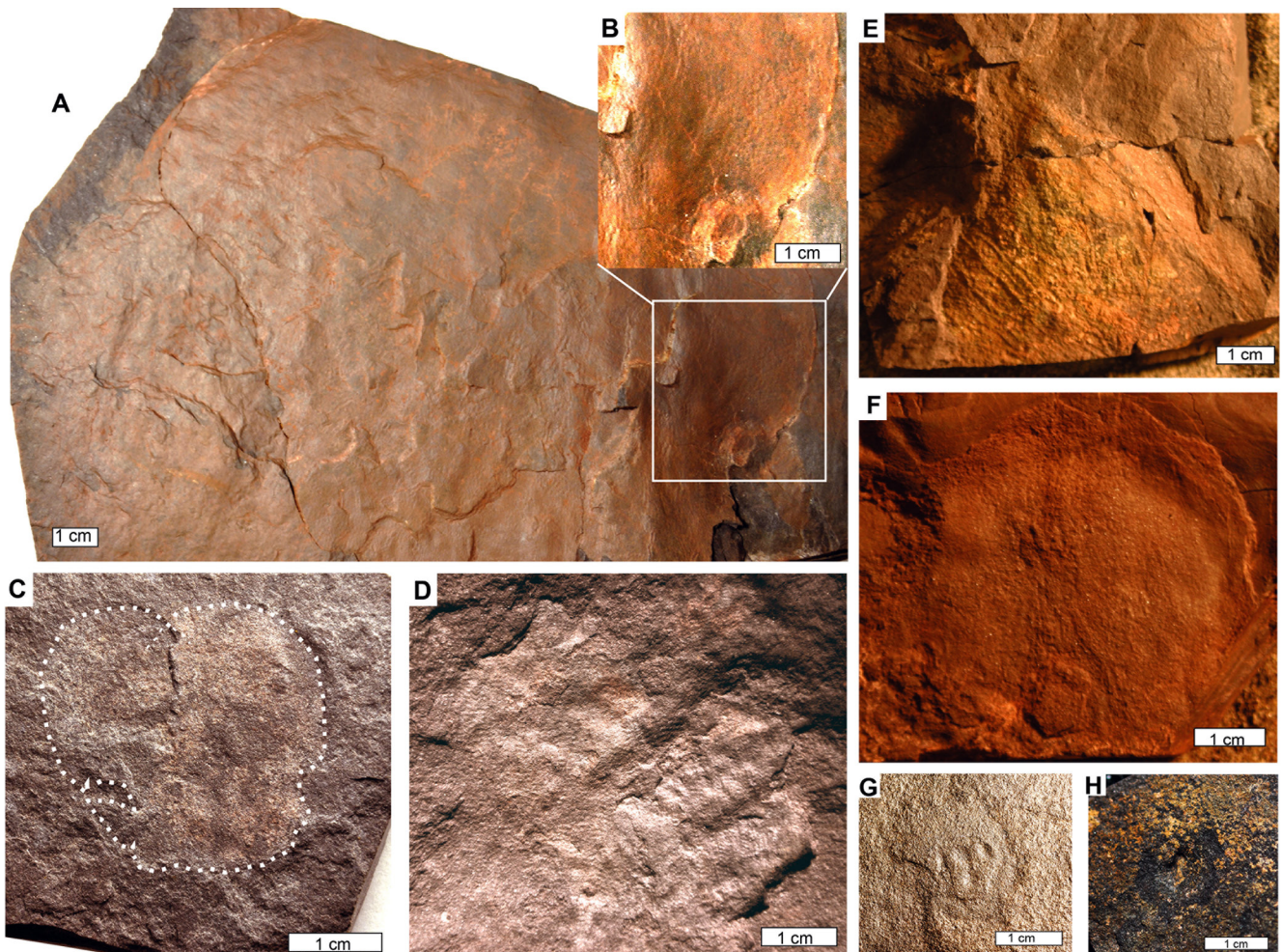

Fig. 4—Fossils from the Early Cambrian Flathead Sandstone at Fishtrap Lake, Montana: *Noffkarkys storaasli* (A–D), *Arumberia banksi* (E–F), and *Hallidaya brueri* (G–H). Specimen numbers (Condon Collection, University of Oregon) and stratigraphic levels (after Retallack 2013a) F115967B at–105 cm (A–B), F115974 at–150 cm (C), F113719 upper side of slab at–150 cm (D), F115982 (E) and F115978 (F) both from–45 cm; F113713 (G) from–100 cm, and F113711 (H) from–150 cm.
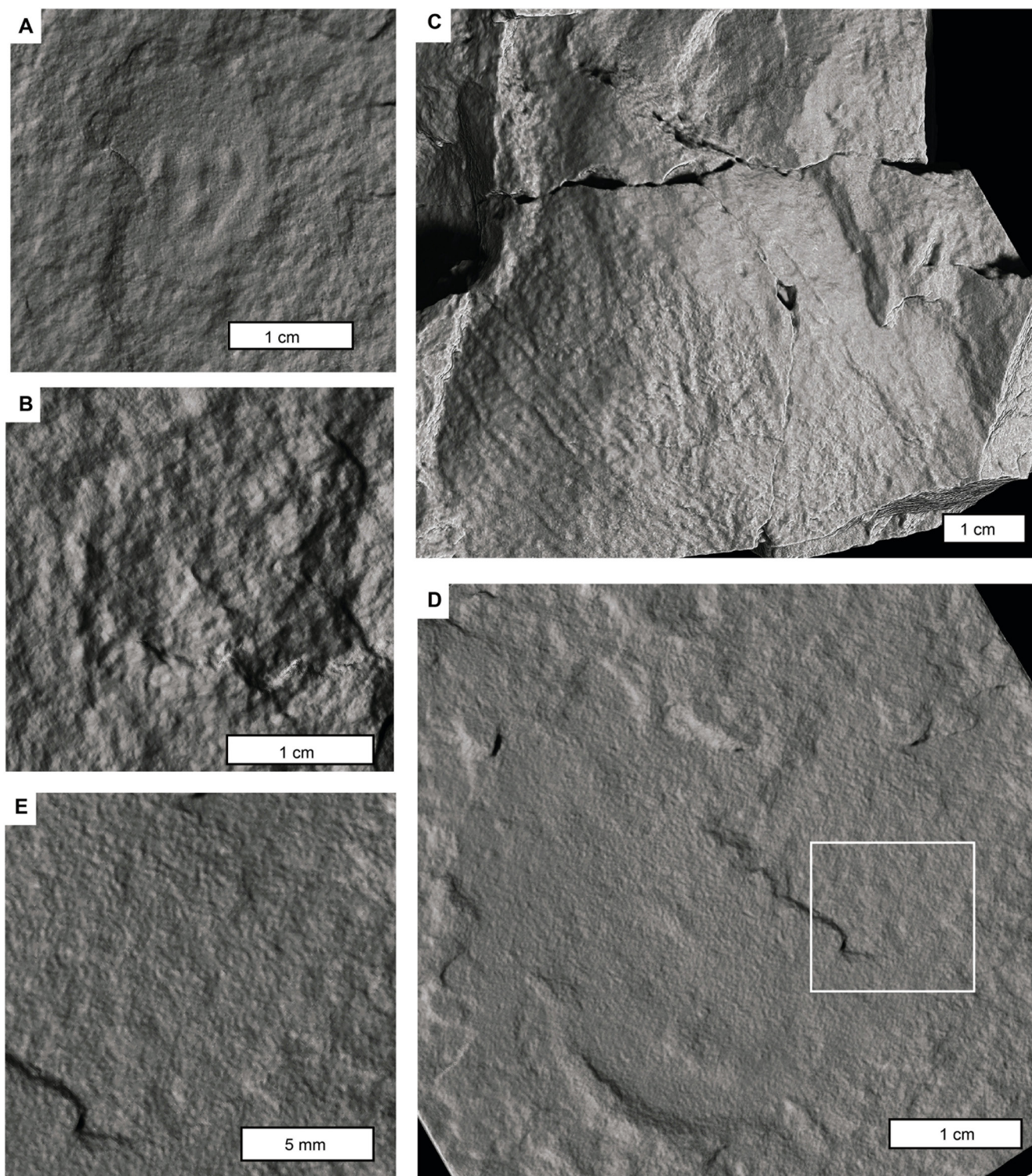
Fig. 5—Laser scans of Early Cambrian megafossils from Fishtrap Lake, Montana: *Hallidaya brueri* (Wade) Retallack & Broz (A–B), *Arumberia banksi* Glaessner & Walter (C), and *Noffkarkys storaasli* Retallack & Broz (D–E), including F113711 (A), F116823A (B), F115982A (C) and F115974 (D–E).

Histology

In thin section the clay–poor silty interior of the fossil is very distinct from its clayey matrix with abundant ferruginized filamentous structures (Fig. 6C–D, K). The silty ellipse of the interior is outlined by a very thin organic layer and bisected by a thick, zigzagging, subhorizontal, carbonaceous seam. At intervals of 1–2 mm this central carbonaceous seam has short vertical seams reaching either up or down in the same direction as the flexure at the point of juncture. This distinctive double layer "quilting" (in the sense of Seilacher, 1992) is identical to that of *Dickinsonia* (Retallack, 2016a), *Rutgersella* (Retallack, 2015a), and *Protonympha* (Retallack, 2018), but more complex than the single layer "quilting" pattern of *Yangtziramulus* (Shen *et al.*, 2009), *Pteridinium* (Grazhdankin & Seilacher, 2002) and *Ernietta* (Ivantsov *et al.*, 2015). The vertical struts at inflections also differentiate it from a thin abiotically leached layer. On the other hand, frond fossils, such as *Charnia* and *Swartpuntia*, are internally much more complex with multiple orders of fractal branching (Narbonne *et al.*, 1997; Grazhdankin *et al.*, 2008; Retallack, 2016a).

Biological affinities

Chambered organization and disruption of the substrate below is evidence against interpretation of *Arumberia* as a sedimentary structure, such as a linguoid ripple or flute cast, with or without a mantling microbial mat (McIlroy & Walter, 1997; McIlroy *et al.*, 2005). Modern microbial mat mantles considered comparable with *Arumberia* by Kolesnikov *et al.* (2012), are internally laminated, not chambered and disrupted like *Arumberia* (Retallack & Broz, 2020). By an alternative interpretation (Kumar & Pandey, 2008; Kolesnikov *et al.*, 2012; McMahon *et al.*, 2021), *Arumberia* is a continuous surface microbial texture and not a discrete individual fossil, but that interpretation does not apply to its holotype specimens (Retallack & Broz, 2020) or the material described here. The silt or sand associated with *Arumberia* is similar to equally problematic "psammocorals" (Seilacher, 1992), but these have much higher relief and an outer organic rind enclosing passive sand fill (Savazzi, 2007), not matched by the internal orthogonal organic seams of *Arumberia* at Fishtrap Lake (Figs 6C–D, K) and in Central Australia (Retallack & Broz, 2020, figs 6c, 8b, d, f).

The original interpretation of *Arumberia* is that it was a cup–shaped cnidarian polyp, which fell on its side with some included sediment (Glaessner & Walter, 1975). General objections to cnidarian interpretation of vendobionts (Seilacher, 1992) have led to more recent interpretations as an extinct stem metazoan (Hoyal Cuthill & Han, 2018). The asymmetric scoop shape of *Arumberia* is not like a partially filled polyp of a cnidarian, nor stem metazoan (Retallack & Broz, 2020). Some specimens of *Arumberia banksi* are laterally linked and intergrown without reaction tissue (Glaessner & Walter, 1975), like *Pteridinium simplex* (Grazhdankin & Seilacher, 2002) and *Phyllozoon hanseni* (Retallack, 2007), but unlike integrated tissues of metazoan individuals.

An alternative interpretation is that *Arumberia* was a recumbent, areolate lichen (Retallack, 1994), perhaps a glomerolichen (Retallack, 2015b). Like *Pteridinium simplex* (Grazhdankin & Seilacher, 2002) and *Ernietta plateauensis* (Ivantsov *et al.*, 2015), it lived on and partly buried by sediment and included sediment less clayey than its matrix. In a supratidal paleosol context (Fig. 2) this sediment would have been eolian loess and silt, distinct from fluvial and intertidal clay settling from suspension. Perhaps they had hollows and intersquamule cavities that trapped sediment like window lichens ("Fensterflechten") such as *Lecidea decipiens* and *Eremastrella tobleri* (Vogel, 1955), and *Endocarpon crystallinum* (Timdal, 2017). Silica permineralized *Ernietta* studied in thin section by Pflug (1973, 1994) were constructed of hollow tubular elements, like lichen podetia of woven filaments (Retallack, 1994). Unlike modern podetia of *Cladonia* (Brodo *et al.*, 2001), *Ernietta*, *Pteridinium*, *Yangtziramulus*, *Charnia* and *Arumberia* had a system of tubes amalgamated along their length into sheets.

NOFFKARKYS STORAASLI RETALLACK & BROZ 2020

Morphology

The most striking feature of *Noffkarkys* is its fine regular rhomboid quilts, arranged between radiating grooves (Figs 3E–J, 4A–D, 5D–E). This arrangement is like rhomboid scales of palaeoniscid fish (Wade, 1935; Schaeffer, 1984), but without hard parts, only impressions bulging upwards in shale (Fig. 6A–B, I). These fine quilts are difficult to photograph because of a size that appears like a blur, so alternative images are provided of sketches (Fig. 3H–J) and laser scans (Fig. 5D–E).

Most *Noffkarkys* specimens do not show the overall shape because they are larger than the slab. The small holotype from central Australia centered on a slab shows an obovate, laterally lobed, frond. This is most like Ediacaran fronds such as *Beothukis* and *Trepassia* (Narbonne *et al.*, 2009; Brasier *et al.*, 2012), which lack holdfasts or stems, and were also prostrate on the sediment surface (McIlroy *et al.*, 2021). A large collection of *Noffkarkys* from Fishtrap Lake shows considerable variation in size and shape from simple bilobed fronds (Figs 3G, 4C) to complex lobate forms (Figs 3E, 4D). Some lateral margins are overfolded (left in Figs 3E, 4A) as if pushing upwards against resistance to growth in that direction, but other margins are nearly flush with the surface (right side of Figs 3E, 4A). Some specimens show overlap of lobes (Figs 3G, 4C) with one lobe above the other. Regardless of the size
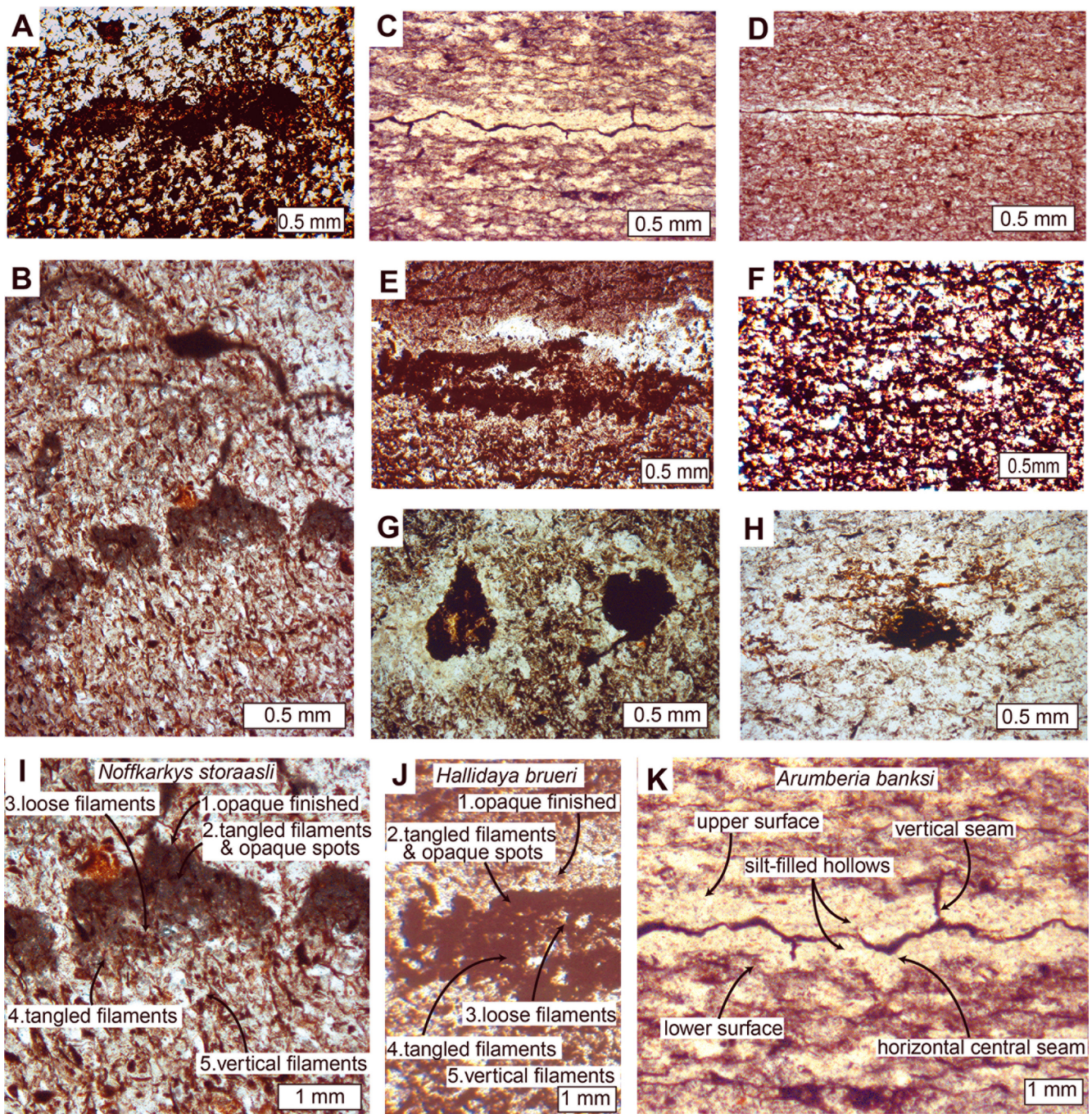
Fig. 6—Petrographic thin sections of quilted (A–D, I, K), discoid (E–F), and filamentous fossils (G–H) and trace fossil (B) from the basal Cambrian Flathead Sandstone at Fishtrap Lake, Montana, with labelled enlargements (I–K from 4, 5, 2 respectively). *Noffkarkys storaasli*, are finely quilted unifacial surfaces (A–B,I), with a finished upper surface grading into filamentous lower part. *Arumberia banksi* Glaessner & Walter is a coarse quilted structure defined by vertical and horizontal organic seams (C–D, K). *Manykodes pedum* (B) burrows have a looping stitch pattern and thin organic walls. *Hallidaya brueri* discoids (E–F, J) have dense upper and lower cortices, sometimes well preserved (E), sometimes decayed (F). Opaque organic filaments have a surrounding gray–green halo (G–H). Specimen numbers (Condon Collection, University of Oregon) and stratigraphic levels (after Retallack 2013a) are R3584 at–40 cm (A), R3598 at–160 cm (B,I), R3581 at–10 cm (C,K), F113720 at–110 cm (D), R3586 at–50 cm (E, J), R3596 at–150 cm (F), R3586 at–50 cm (G–H).

of the lobes or overall thallus, quilts and grooves retain the same size and spacing.

Some *Noffkarkys* specimens imprint planes sub–perpendicular to the bedding, covering fractures and muddy surfaces (argillans) that define the blocky structure of the Cool paleosol (specimens F113703, F115958). On upper bedding surfaces *Noffkarkys* forms lobate molds with striation radiating in all directions from a common centre, but subperpendicular *Noffkarkys* has flabellate shape with grooves radiating upwards. The quilted texture of *Noffkarkys* in one specimen drapes and smooths desiccation cracks, and rounds originally angular polygons of cracks (Retallack, 2013a, fig. 2G). In other cases, *Noffkarky*s overprints a pyrite spherulite of the form commonly known as a "pyrite sun" (Retallack, 2013a, fig. 2D).

Measurements

Fishtrap Lake *Noffkarkys storaasli* falls well within the size range of 13–72 mm wide (Fig. 7C–E) for paratypic material from central Australia (Retallack & Broz, 2020). The largest of 136 specimens collected from Fishtrap Lake (Figs 3E, 4A) is incomplete at 271 mm wide and 223 mm long, with lobes 81–137 mm wide. Projecting backward along the converging seams between lobes to the initial growth center, gives an additional 210 mm, for a total of length of 443 mm. If several such lobes were arranged radially around a growth center as in the Ediacaran frond *Bradgatia* (Flude & Narbonne, 2008; Brasier *et al.*, 2012), then the whole structure could have been 0.9 m in diameter. Spacing of radiating grooves on the central Australian holotype is 1.7 ± 0.2 mm, and quilt widths are 0.5 ± 0.2 mm (Retallack & Broz, 2020), whereas 100 comparable measurements for a Fishtrap Lake specimen (Figs 4C, 5D–E) are 1.5 ± 0.3 mm, and 0.8 ± 0.2 mm (mean and one standard deviation), respectively (Fig. 7C–E).

Histology

Thin sections of *Noffkarkys* reveal that the upward bulging dark quilts are separated by deep grooves (Figs 6A–B, I). Within the quilts are four layers, from the top downwards; (1) dense fabric in a thick (100–200 μm) dark gray layer with opaque spots (20–50 μm diameter); (2) loose fabric in a thick (50–120 μm) semitransparent layer of loosely woven fabric; (3) tangled fabric in a basal thin (50–80 μm) layer of gray densely woven fabric, breached in places; (4) vertical fabric in a layer of vertically oriented, loosely woven, filaments extending downward more than 2 mm. Layer 4 connects in some places in the middle of the quilts with layer 2, and at other places within the quilt defining radial grooves, layer 4 is open to the surface. Openings in the entire structure and diffuse contacts of layers 2–4 compared with the sharpness

of layer 1 give the whole structure strong asymmetry in the vertical plane in which the thin sections were cut.

Filamentous structures seen in thin section are also apparent from scanning electron micrographs in secondary mode, revealing twisted dark tubular features 25–100 μm in diameter which branch downward from quilt margins into the matrix (Fig. 8A–B). At high magnification the clay has the crystal form of illite (Fig. 8C). Under back–scatter electron mode in which brightness of tone indicates atomic number, the grooves and quilt margins of natural fossil surfaces are bright with iron and the quilt faces dull with carbon and clay (Fig. 8D). This thin ferruginous (hematite) film may have aided preservation of the most distinct examples of *Noffkarkys storaasli*.

Biological affinities

Frond fossils like *Noffkarkys*, which also ranges down into the Ediacaran (Retallack & Broz, 2020), were once regarded as cnidarian sea pens (Pennatulacea: Fedonkin *et al.*, 2008), although their apical growth and quilt–like construction is the opposite of sea pens (Antcliffe & Brasier, 2007, 2008). Ford (1958) was first to compare quilted Ediacaran fossil impressions with seaweeds. Modern seaweeds with quilted thalli generally comparable with *Noffkarkys* include *Padina pavonica* (Phaeophyta), *Codium effusum* (Chlorophyta), and *Delessaria serrulata* (Rhodophyta), but these have distinct blades and holdfasts (Bold & Wynne, 2000), not seen in the Montanan or central Australian *Noffkarkys*. Fossil algae are either skeletonized and prone to brittle breakage, or organic and flimsy, preserved as carbonaceous films (Taylor & Taylor, 1993), unlike molds and casts of the flexuous Fishtrap Lake fossils. Histologically the elongate filaments of *Noffkarkys* are more like green algae (Chlorophyta, Codiaceae), than equant cells of red (Rhodophyta) and brown algae (Phaeophyta: Bold & Wynne, 2000), but their stratification into subhorizontal layers is very different. Seaweeds wilt and rot in piles of wrack on beaches and well drained soils (Retallack, 1994), but do not spread with pressure buckling, and coat perpendicular surfaces like *Noffkarkys*.

Seilacher (2007) regarded comparable quilted fossils such as *Dickinsoni*a as xenophyophore foraminifera for the following reasons: (1) quilt size independent of overall size; (2) clastic fill, like stercomere or incorporated substrate; (3) sessile habit on or within sediment; (4) evidence of interpenetration and regeneration; and (5) trails of mobile forms. The Montana fossils have a diffuse lower boundary attaching them to the substrate like xenophyophores, but xenophyophores have brittle calcified skeletons, whereas the Fishtrap Lake vendobionts were pliable, folded, soft–bodied organisms, molding over clasts, cracks, and pyrite suns (Retallack, 2013a). Xenophyophores are marine animals of

A-B. *Hallidaya brueri*

C-E. *Noffkarkys storaasli*

F. *Avalofractus abaculus*

G-H. *Xanthoparmelia plittsi*

I. *Fractofusus misrai*

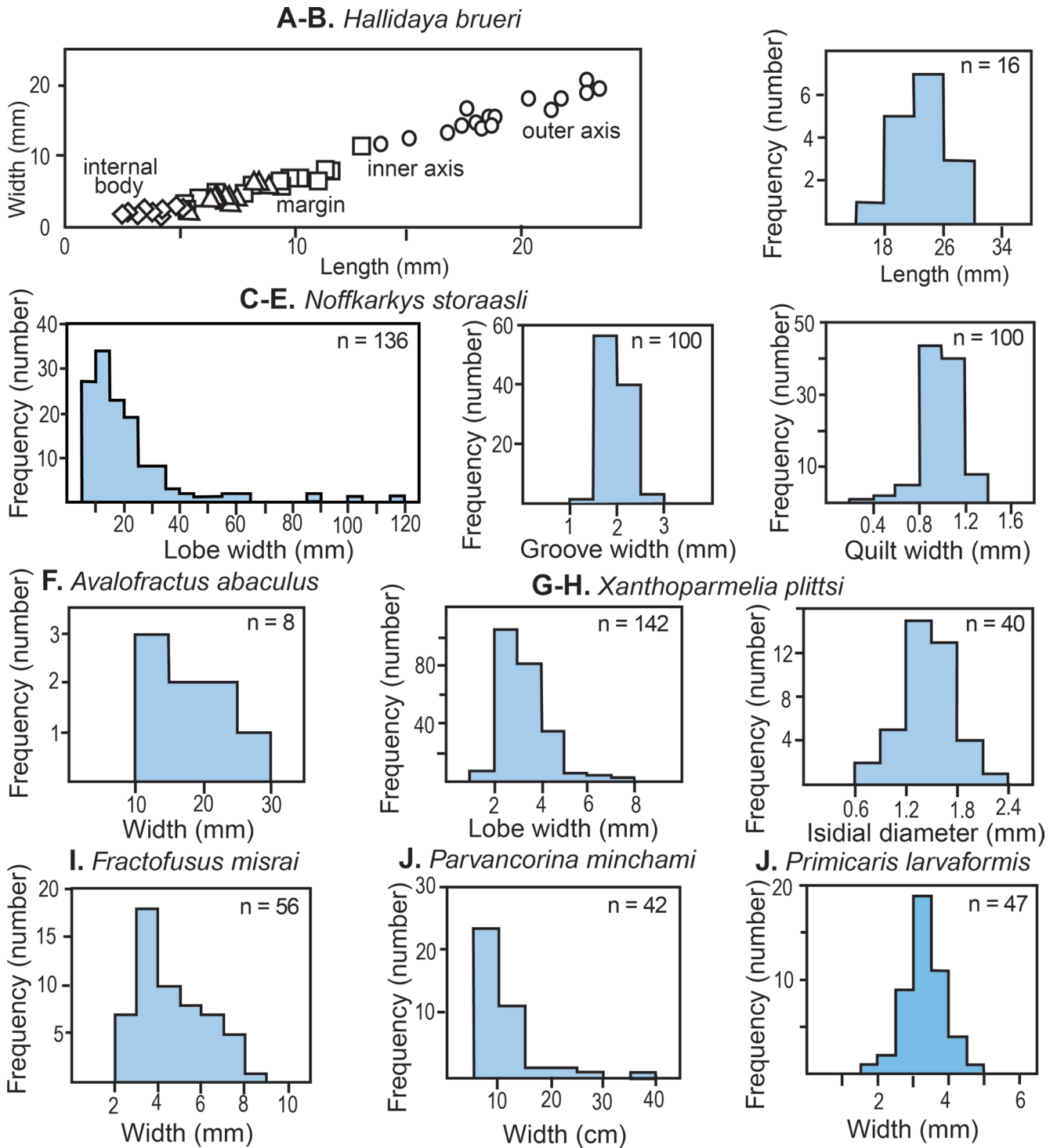**J.** *Parvancorina minchami*

J. *Primicaris larvaformis*

Fig. 7—Size distributions of Early Cambrian megafossils (A–E) from Fishtrap Lake, Montana and comparative modern lichen (G–H), and extinct vendobionts (F, I–J), and trilobitomorph (K). Modern lichen (*Xanthoparmelia plittsi*) is the specimen in collection of Museum of Natural and Cultural History. Sources of size data are Narbonne *et al*. (2009) for F, Gehling & Narbonne (2007) for I, Naimark & Ivantsov (2009) for J, and Zhang *et al*. 2003 for K.

the deep sea, whereas *Noffkarkys* is found in supratidal to non–marine paleosols (Bland, 1984; Kolesnikov *et al.*, 2012).

Noffkarkys storaasli has been described here in terms such as "quilt" and "lobes" that are neutral with respect to biological affinities, but the terminology of lichen thalli more adequately explains both its distinctive morphology (Figs 3E–J, 4A–D, 5D–E) and cross section (Figs 6A–B, I). The five histologically distinct layers from top to bottom can be interpreted as: (1) dense fabric in a thick, dark gray zone with opaque nests comparable with a cortical algal layer;

(2) loose fabric in a loosely woven medulla; (3) tangled fabric in a gray densely woven fabric like a lower cortex; (4) vertical fabric of elongate structures of varying thickness radiating downwards like rhizines. Size distribution data are compatible with organisms with indeterminate growth such as a seaweed, xenophyophore, foraminiferan, or lichen. *Noffkarkys storaasli* vegetative lobes have a log–normal size distribution (Fig. 7C), as demonstrated here for the modern lichen *Xanthoparmelia plittsi* (Fig. 7G), and for vendobionts such as *Aspidella* (Gehling *et al.*, 2000; Peterson *et al.*, 2003;
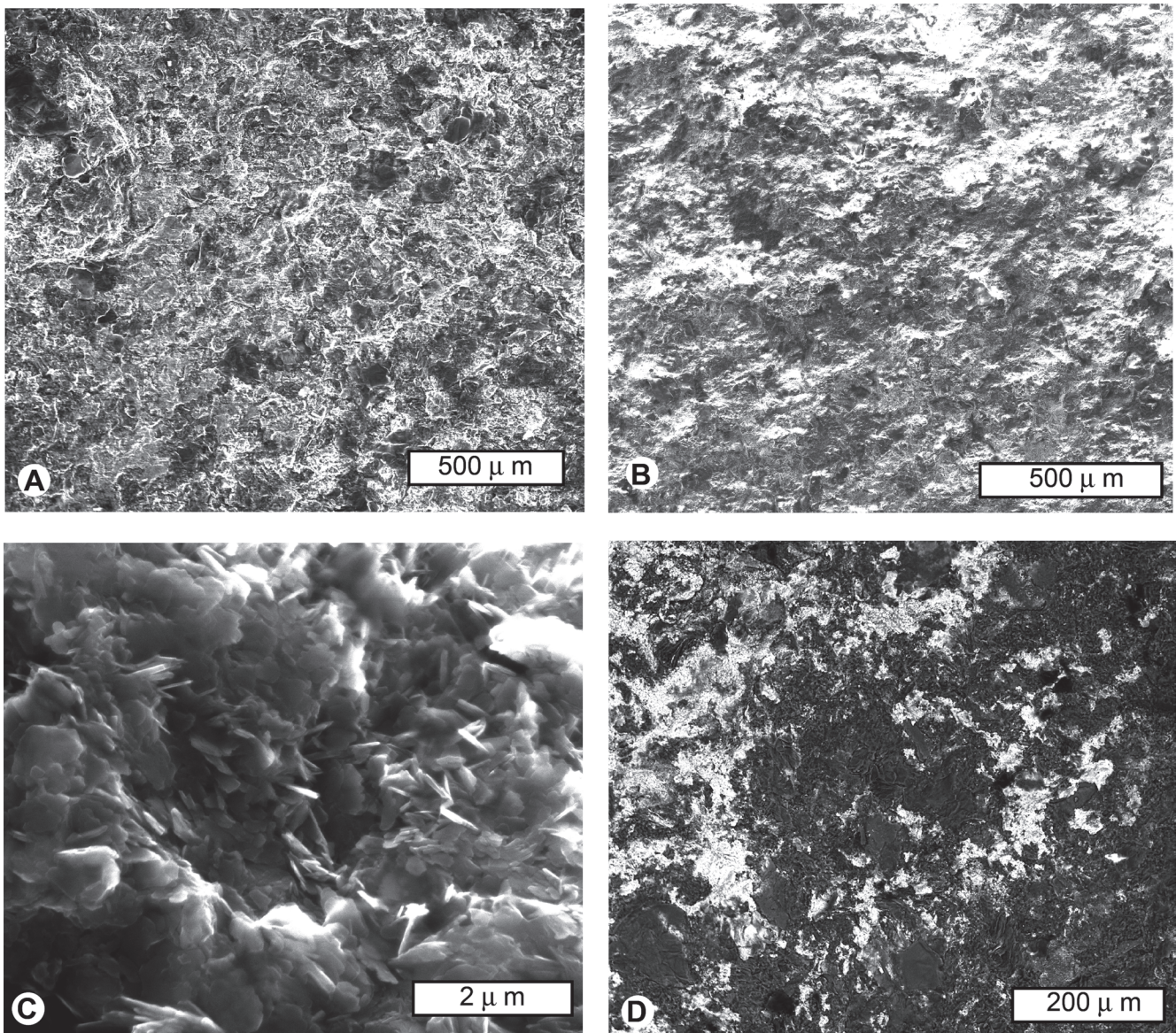

Fig. 8—Scanning electron micrographs of natural surfaces (not cross sections) of the quilted fossil *Noffkarkys storaasli* (specimen F113719 from–150 cm in Retallack 2013a) from Early Cambrian Flathead Sandstone, Fishtrap Lake, Montana. Details of quilt (A–B) shows radial grooves (sloping upper leaf to lower right) punctuated by dark filament insertions. Crystal form of clay (C) is that of illite. Backscatter image (D) shows ferruginous–carbonaceous filaments and grooves (white) in background of clay (gray).

Hofmann *et al.*, 2008) and *Dickinsonia* (Retallack, 2007). Comparable log–normal size distributions are presented here for other problematic fossils (Fig. 7F, I–J; data from Gehling & Narbonne, 2007; Hofmann *et al.*, 2008, Narbonne *et al.*, 2009; Naimark & Ivantsov, 2009), and can be contrasted with normal size distributions of undisputed metazoans, such as the Cambrian *Primicaris larvaformis* (Fig. 7J, data from Zhang *et al.*, 2002; Lin *et al.*, 2006).

HALLIDAYA BRUERI (WADE) RETALLACK & BROZ 2020

Morphology

Hallidaya brueri (Wade, 1969) has been emended to include its constant associate "*Skinnera brooksi*", as the lower and upper surfaces, respectively (Retallack & Broz, 2020). These are discoid fossils with a marginal area of radiating, branching striations and central area with three or more elliptical to lobate bodies, unlike other problematic discoid fossils reviewed by MacGabhann (2007) and Razumovskiy *et al.* (2015). The fossils are biconvex discoids, preserved as hypichnial ridges on the lower side with wide striated margin and few central bodies, and as epichnial grooves on upper side within narrow striated margin and many central bodies. The distinct central and marginal portions distinguish *Hallidaya* from non–fossil circular structures such as liesegang banding (Merino, 1984), nodules (Retallack, 1997), or accretionary lapilli (Reimer, 1983). Fishtrap Lake *Hallidaya* vary in distinctness and relief (Figs 3A–B, 4G–H, 5A–B), and some may have been partly decayed.

Measurements

Type material of *Hallidaya brueri* from central Australia is 5–50 mm in diameter (Retallack & Broz, 2020), like the best preserved one from Fishtrap Lake (Figs 3A, 4G, 5A), which is 22.8 mm in diameter, with a margin 3.3–7.1 mm wide, and central ovoids 2.6–3.4 mm wide and 3.7–5.8 mm long. All 15 specimens from Fishtrap Lake are 19.0 ± 2.8 mm in diameter (mean and standard deviation), with margin 7.2 ± 1.3 mm wide, central ovoid length 8.9 ± 2.2 mm, and central ovoid widths 6.2 ± 1.8 mm.

Histology

In thin section, *Hallidaya brueri* is biconvex (Fig. 6E–F), thus explaining its negative relief on the upper side and positive relief on the lower side. The overall biconvex disc has dark carbonaceous–ferruginous clay on both sides of a central area of loose filamentous fabric, except for an irregular region of the bottom center where elongate features arch downward into the sediment below. An elevated central lumpy region of unusually thick, clayey–carbonaceous material corresponds

with the inner subtriangular ring of the compressions. Other discoid outlines of comparable size were seen in thin section (Fig. 6F) with much thinner opaque outlines, a wider area of loosely woven fabric in the center, and a wider lower opening. These impressions may have been less distinct because of decay of dark organic matter back to the most decay–resistant outer envelope.

Biological affinities

Hallidaya, like *Arumberia* and *Noffkarkys*, is known in Cambrian as well as Ediacaran rocks, in which discoid fossils have traditionally been regarded as jellyfish, polyps, or sea pen holdfasts (Sprigg, 1947; Fedonkin *et al.*, 2008). These discoid fossils are more strongly impressed in the center than the margins, where cnidarian muscle masses should be located (Seilacher, 1992), and they make surprisingly thick impressions for such deeply buried fossils (Retallack, 2007). Other discoid fossils such as *Arkarua* and *Tribrachidium* have been interpreted as echinoderms comparable with Edrioasteroids (Fedonkin *et al.*, 2008). Cnidarian or echinoderm affinities for *Hallidaya* are ruled out by their fibrous histology (Fig. 6E–F, J). Associated filaments are not fungal decay of metazoans, because filaments are stouter (50–200 μm), longer and more branched than those of saprophytic fungi such as yeasts, moulds and rot fungi. Saprophytic hyphae are only 2–5 μm wide when preserved in amber (Poinar, 1992) and in permineralized fossil wood (Stubblefield & Taylor, 1988). Furthermore, these poorly preserved elongate elements radiate away from the lower center of the fossils rather than converging into them and coating their surfaces like saprophytes. Finally, the elongate elements are denser within, rather than outside, the fossils and decay does not seem to have opened large empty spaces for clay or silt infiltration. Metazoa, even decayed ones, are an unlikely explanation for *Hallidaya* or other comparable discoids (MacGabhann, 2007).

Discoid fossils have also been interpreted as microbial colonies (Steiner & Reitner, 2001; Grazhdankin & Gerdes, 2007). Bacterial colonies can be concentrically banded and have complex radial and infolded patterns (Ben–Jacob *et al.*, 1994; Shapiro, 1998), but not structures differentiated into central and marginal zones like *Hallidaya*. Microbial colonies collapse completely during burial compaction to form hypichnial ridges (Retallack, 2016a), unlike histologically differentiated and thick *Hallidaya* (Fig. 6E).

Finally, discoids have been compared with lichenized fungi and fungal fruiting bodies (Retallack, 1994; Peterson *et al.*, 2003), because of peculiarities of their sessile growth, decay without marginal collapse, and compaction–resistance. *Hallidaya brueri* has been described here in terms such as "margin" and "ellipsoidal bodies" that are neutral with respect to biological affinities, but the terminology of fungi and lichens gives an array of options for its distinctive morphology (Figs
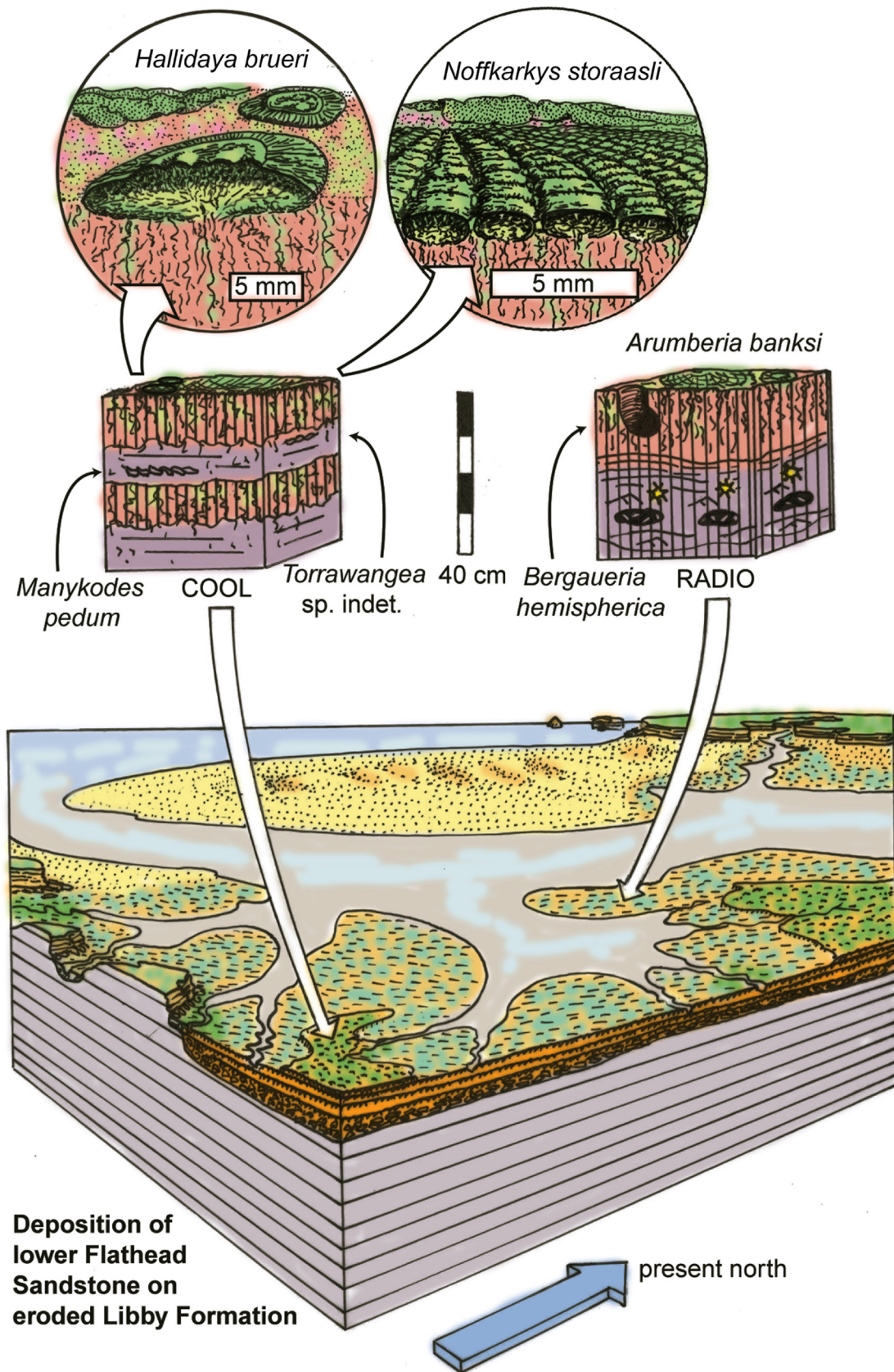
Fig. 9—Reconstructed paleoenvironment of Early Cambrian megafossils from the lower Flathead Sandstone near Fishtrap Lake, Montana.

3A–B, 4G–H), and cross section (Fig. 6E). The "ellipsoidal bodies" for example, could be peridioles like those of bird nest fungus (*Nidula candida*), puffballs within a fringe like *Geaster saccatum*, pycnidia like those of the lichen *Verrucaria mucosa*, coralloid isidia comparable with *Xanthoparmelia plittsi*, or apothecia of *Caloplaca diphyodes* and *Placopsis gelida* (Brodo *et al.*, 2001). Of these options a fungal fruiting body is compatible with its normal size distribution (Fig. 7B) comparable with reproductive structures (isidia of Fig. 7H) as opposed to log–normal distribution of vegetative lobes of lichens (Fig. 7G). Thin sections of *Hallidaya* do not show parallel and vertical filaments like a hymenium above a woven filamentous area like a hypothecium of a lichen apothecium (Brodo *et al.*, 2001). Nor do the internal bodies of *Hallidaya* have well defined margins like those of lichen apothecia (Brodo *et al.*, 2001). *Hallidaya brueri* is most like a foliose lichen with a prothallus (distinct margin of unlichenized tissue), and its central depressions are comparable with diffuse reproductive organs such as soredia or isidia.

IMPLICATIONS FOR CAMBRIAN EVOLUTION AND ECOLOGY

The fossil assemblage described here now allows visualization of an earliest Cambrian coastal landscape that was far from barren of life (Fig. 9). In the terminology of Retallack (1992) basal Cambrian vegetation of Fishtrap Lake was a polsterland, a vegetation formation of clumps of non–vascular plants or lichens. It can also be described as a rugose biological soil crust (Belnap, 2003), or as a perimorphic microbiotic soil crust (Eldridge & Greene, 1994). It was neither a smooth and subterranean microbial earth (Retallack, 1992), smooth biological soil crust (Belnap, 2003), nor cryptomorphic microbiotic soil crust (Eldridge & Greene, 1994). Nor was it dotted with large plants as in a brakeland (Retallack, 1992), pinnacled or rolling biological soil crust (Belnap, 2003), or hypermorphic microbiotic soil crust (Eldridge & Greene, 1994). Polsterlands are not only intermediate in ecological successional colonization of bare surfaces (Eldridge & Greene, 1994), but also likely evolutionary intermediates in the colonization of land on geological time scales (Retallack, 1992).

The assemblage of *Arumberia*, *Noffkarkys* and *Hallidaya* described here was a widespread terrestrial community during both Ediacaran and Cambrian. In addition to Fishtrap Lake, red–beds with *Arumberia* are known from 13 regions: (1) Ediacaran, Maihar Sandstone, near Maihar and Khoh, India (Kumar & Pandey, 2008); (2) Ediacaran Jodhpur Sandstone near Khatu, India (Kumar & Ahmad, 2012; Srivastava, 2014); (3) Ediacaran, Bonney Sandstone, Brachina Gorge, Flinders Ranges, South Australia (Bland, 1984); (4) Ediacaran, Grant Bluff Formation near Mt Skinner, Northern Territory, Australia (Wade, 1969; Retallack & Broz, 2020); (5) Ediacaran, Grant Bluff Formation at Central Mount Stuart, Northern Territory, Australia (Retallack & Broz, 2020); (6), Ediacaran Arumbera Sandstone at Ross River, Valley Dam and Hargrave Lookout, Northern Territory, Australia (Glaessner & Walter, 1975; Mapstone & McIlroy, 2006; Retallack & Broz, 2020); (7) Ediacaran Ust Sylvitsa, Chernyi Kamen and Zigan formations of the Ural Mountains, Russia (Becker, 1980, 1985; Kolesnikov *et al.*, 2012); (8) Ediacaran Moshakov Formation near Artyugino, east Siberia (Liu *et al.*, 2013); (9) Ediacaran Gibbett Hill Formation of Newfoundland, Canada (Bland, 1984); (10) late Ediacaran or Early Cambrian, Synalds, Lightspout, and Bridges formations near Church Stretton, England (Bland, 1984; McIlroy *et al.*, 2005); (11) Early Cambrian, Billy Creek Formation, Flinders Ranges, South Australia (Bland, 1984; Retallack, 2008); (12) late Ediacaran or early Ordovician, Rozel Conglomerate on the British Channel island of Jersey (Bland, 1984; Went, 2005); and (13) late Ediacaran or early Ordovician Pluorivo Formation near Erquy and Bréhec, France (Bland, 1984). An additional 3 localities for *Arumberia* in Namibia, China and Sweden are uncertain as to identity of the fossils or the facies in which they were found (Bland, 1984).

At Fishtrap Lake the vendobionts *Arumberia*, *Noffkarkys* and *Hallidaya* are abundant on selected horizons, and there is no evidence that they interacted with marine trace fossils *Manykodes pedum*, *Bergaueria hemispherica*, *Didymaulichnus lyelli*, and *Torrowangea* within the intervening beds (Fig. 2). Chemical and magnetic susceptibility indications of oxidation in the vendobiont surfaces did not extend to the beds with trace fossils (Retallack, 2013a). This is interpreted here as estuarine supratidal flats of near–marine sediments colonized by vendobionts (Fig. 9).

Evidence of interaction in vendobiont communities is rare globally (Mitchell *et al.*, 2019). One example of a trail ploughing through a *Dickinsonia* has been interpreted as scavenging of a buried body (Gehling & Droser, 2018), but the fossil has good relief unlike known decayed and deflated *Dickinsonia* (Retallack, 2007). The clear mounded levees on either side of the "burrow" are evidence that this is a surface trail, and evidence of herbivory or fungivory rather than scavenging. No such interaction between vendobionts and animals was seen in large collections of Cambrian fossils from Fishtrap Lake, or Ediacaran localities in central Australia (Retallack & Broz, 2020). The rarity of vendobiont interactions has been quantified by Mitchell & Butterfield (2018) and Mitchell *et al.* (2019). These largely sessile communities were more like plant and lichen communities than benthic marine communities. Similarly, Darroch *et al.* (2018a) demonstrate high rank order differentiation in Ediacaran communities. This is also similar to communities of lichens (Kuusinen, 1994; Dietrich & Scheidegger, 1997; Thor *et al.*, 2010) and plants (Ulrich *et al.*, 2016). Beta diversity in Ediacaran communities is higher than in any known benthic marine community, either modern or fossil (Finnegan *et al.*, 2019), and more like terrestrial communities (Kessler *et al.*,

2009; Fernandez–Going *et al.*, 2013). There are multiple other lines of evidence that some vendobiont communities were non–marine: soil–like mineral and grain size modal variation within beds below them (Retallack, 2012), soil–like tau analysis depletions (Retallack, 2013a), $\delta^{18}O–\delta^{13}C$ correlation within carbonate nodules (Retallack, 2016c; Broz *et al.*, 2021), low boron assay (Retallack, 2020), high Ge–Si ratios of early diagenetic silica cement (Retallack, 2017), and eolian interbeds inferred from granulometry (Retallack, 2019; McMahon *et al.*, 2020).

The Ediacaran–Cambrian transition has been envisaged as an "agronomic revolution" of marine burrowing organisms destroying and replacing marine Ediacaran matgrounds (Seilacher & Pflüger, 1994; Oji *et al.*, 2018). One way to interpret the Cambrian co–occurrence of interbeds alternating with marine trace fossils and vendobionts at Fishtrap Lake, would be as an intermediate stage in a protracted transition from Ediacaran matgrounds to fully bioturbated marine siltstones (Buatois *et al.*, 2014; Shahkarami *et al.,* 2017; Laing *et al.,* 2019). This view is difficult to maintain in view of the geochemical and magnetic susceptibility evidence (Retallack, 2013a) that the vendobionts were not on microbial submarine matgrounds, but well drained polsterlands. Nor does evidence from Fishtrap Lake support the idea that marine fossils destroyed Ediacaran marine matgrounds as a terminal Ediacaran catastrophe, or dual late Ediacaran catastrophes (Schiffbauer *et al.*, 2016; Darroch *et al.*, 2018a; Buatois *et al.*, 2018). The *Arumberia–Noffkarkys–Hallidaya* community of Fishtrap Lake, and many other localities listed above are evidence that this community did not go extinct at the end of the Ediacaran, and may have persisted into the Ordovician (Bland, 1984; Went, 2005; Budd & Jensen, 2017). Other vendobionts *Rutgersella* and *Protonympha* persisted in intertidal to terrestrial habitats in the Silurian (Retallack, 2015a) and Devonian (Retallack, 2018). Thus terrestrial "Mattresslands" of vendobionts (Retallack & Broz, 2020) were unaffected by the evolution and intensification of burrowing organisms of marine "Wormworld" (Schiffbauer *et al.*, 2016). Unfossiliferous Cambrian microbial matgrounds (Shahkarami *et al.*, 2017; Laing *et al.*, 2019) are additional evidence that these kinds of environments persisted (Grazhdankin & Gerdes, 2007; Kolesnikov *et al.*, 2012), and were not completely eradicated by evolving marine bioturbation during the earliest Cambrian.

An alternative to the idea of marine diversification through burrowing is the Ediacaran "savanna hypothesis" (Budd & Jensen, 2017; Mitchell *et al.*, 2020), which despite the terrestrial name, refers to the way in which large unskeletonized marine fossils created heterogeneous habitats replacing more uniform earlier marine matgrounds. Budd and Jensen (2017) considered vendobionts key heterogeneities for this change, but if vendobionts were terrestrial creatures as is apparent in this study and others (Retallack 2013b, 2016b, 2020), the marine savanna hypothesis would be more

likely due to Ediacaran sea weeds, which did indeed grow in size and complexity (Bykova *et al.*, 2020; Del Cortona *et al.*, 2020). Reconstruction of the widespread Ediacaran and Cambrian *Arumberia–Noffkarkys–Hallidaya* assemblage as ground–hugging communities (Fig. 9), suggests that titles such as "Garden of Ediacara" (McMenamin, 2000), and "Underground Vendobionta" (Grazhdankin & Seilacher, 2002), were descriptions rather than metaphors.

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