DEEP-WATER EDIACARAN FOSSILS FROM NORTHWESTERN CANADA: TAPHONOMY, ECOLOGY, AND EVOLUTION

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ABSTRACT—Impressions of soft-bodied Ediacaran megafossils are common in deep-water slope deposits of the June beds at Sekwi Brook in the Mackenzie Mountains of NW Canada. Two taphonomic assemblages can be recognized. Soles of turbidite beds contain numerous impressions of simple (*Aspidella*) and tentaculate (*Hiemalora, Eoporpita*) discs. A specimen of the frond *Primocandelabrum* is attached to an *Aspidella*-like holdfast, but most holdfast discs lack any impressions of the leafy fronds to which they were attached, reflecting Fermeuse-style preservation of the basal level of the community. Epifaunal fronds (*Beothukis, Charnia, Charniodiscus*) and benthic recliners (*Fractofusus*) were most commonly preserved intrastratally on horizontal parting surfaces within turbidite and contourite beds, reflecting a deep-water example of Nama-style preservation of higher levels in the community. A well-preserved specimen of *Namalia* significantly extends the known age and environmental range of erniettomorphs into deep-water aphotic settings. Infaunal bilaterian burrows are absent from the June beds despite favorable beds for their preservation. The June beds assemblage is broadly similar in age and environment to deep-water Avalonian assemblages in Newfoundland and England, and like them contains mainly rangeomorph and arboreomorph fossils and apparently lacks dickinsoniomorphs and other clades typical of younger and shallower Ediacaran assemblages. Fossil data presently available imply that the classically deep- and shallow-water taxa of the Ediacara biota had different evolutionary origins and histories, with sessile rangeomorphs and arboreomorphs appearing in deep-water settings approximately 580 million years ago and spreading into shallow-water settings by 555 Ma but dickinsoniomorphs and other iconic clades restricted to shallow-water settings from their first known appearance at 555 Ma until their disappearance prior to the end of the Ediacaran.

INTRODUCTION

THE EARLIEST-KNOWN occurrences of the Ediacara biota are deep-water assemblages in the Avalon (Misra, 1969; Narbonne and Gehling, 2003; Narbonne, 2004) and Bonavista (Hofmann et al., 2008) peninsulas of Newfoundland and at Charnwood Forest in England (Ford, 1958; Boynton and Ford, 1995; Brasier and Antcliffe, 2009; Wilby et al., 2011) which have been dated at 560–580 Ma (Narbonne et al., 2012). These deep-water biotas are dominated by abundant and diverse rangeomorphs, an extinct clade of Ediacaran life characterized by modular construction of cm-scale elements built by repeated self-similar (fractal) branching (Narbonne, 2004; Narbonne et al., 2009). Rangeomorphs also occur in younger assemblages from both deep- and shallow-water settings (Grazhdankin, 2004; Vickers-Rich et al., 2013; Gehling and Droser, 2013), but none of these later assemblages achieve the abundance and diversity of rangeomorphs seen in the Avalonian assemblages from England and Newfoundland (Shen et al., 2008; Laflamme et al., 2013). Arboreomorph fronds such as *Charniodiscus* (Laflamme et al., 2004; Laflamme and Narbonne, 2008a, 2008b) and simple (*Aspidella*) and tentaculate (*Hiemalora*) discs that reflect attachment discs of Ediacaran fronds (Gehling et al., 2000; Hofmann et al., 2008) occur abundantly in both deep- and shallow-water Ediacaran assemblages worldwide. Several Ediacaran clades including dickinsoniomorphs, kimberellomorphs, and a host of bilateral, tetraradial, pentaradial, and octoradial taxa, are thus far known only from shallower and presumably younger assemblages, principally the White Sea and Flinders Ranges (Xiao and Laflamme, 2009; Erwin et al., 2011;

Laflamme et al., 2013), and contribute to the huge diversity of these shallow-water Ediacaran assemblages.

The first report of deep-water Ediacara-type fossils from Laurentia was an assemblage of discs and the frond *Inkrylovia* along with abundant simple burrows (Hofmann, 1981) from strata now defined as the Blueflower Formation at Sekwi Brook in the Mackenzie Mountains of NW Canada (Figs. 1, 2). Subsequent studies by Narbonne and Aitken (1990) and Narbonne (1994) extended the record of Ediacaran megafossils more than 1 km lower stratigraphically into strata then regarded as the uppermost beds of the Sheepbed Formation (Aitken, 1989) and now referred to the informal "June beds" (Macdonald et al., 2013). Abundant Ediacara-type holdfast discs were described from the bases of the turbidites, but despite intensive search no fronds or other complex Ediacara-type megafossils were found on any turbidite soles in these beds. Narbonne (2005) suggested that this represented a taphonomic exclusion termed "Fermeuse-style preservation", in which infaunal and partly infaunal discs on a muddy sea bottom were readily preserved on the soles of the turbidite event beds that buried them, but the frondose parts of the fossil in the water column were entrained within the turbidity current and typically were not preserved on the turbidite soles. Fronds were incorporated into the overlying turbidite, which lacked internal lithologic interfaces for fossil preservation.

Paleocurrent studies of fossiliferous Ediacaran strata at Mistaken Point and elsewhere throughout the Avalon and Bonavista peninsulas (Benus, 1988; Wood et al., 2003; Ichaso et al., 2007; Mason et al., 2013) show that the organisms lived in a gentle contour-parallel current that may have brought food and
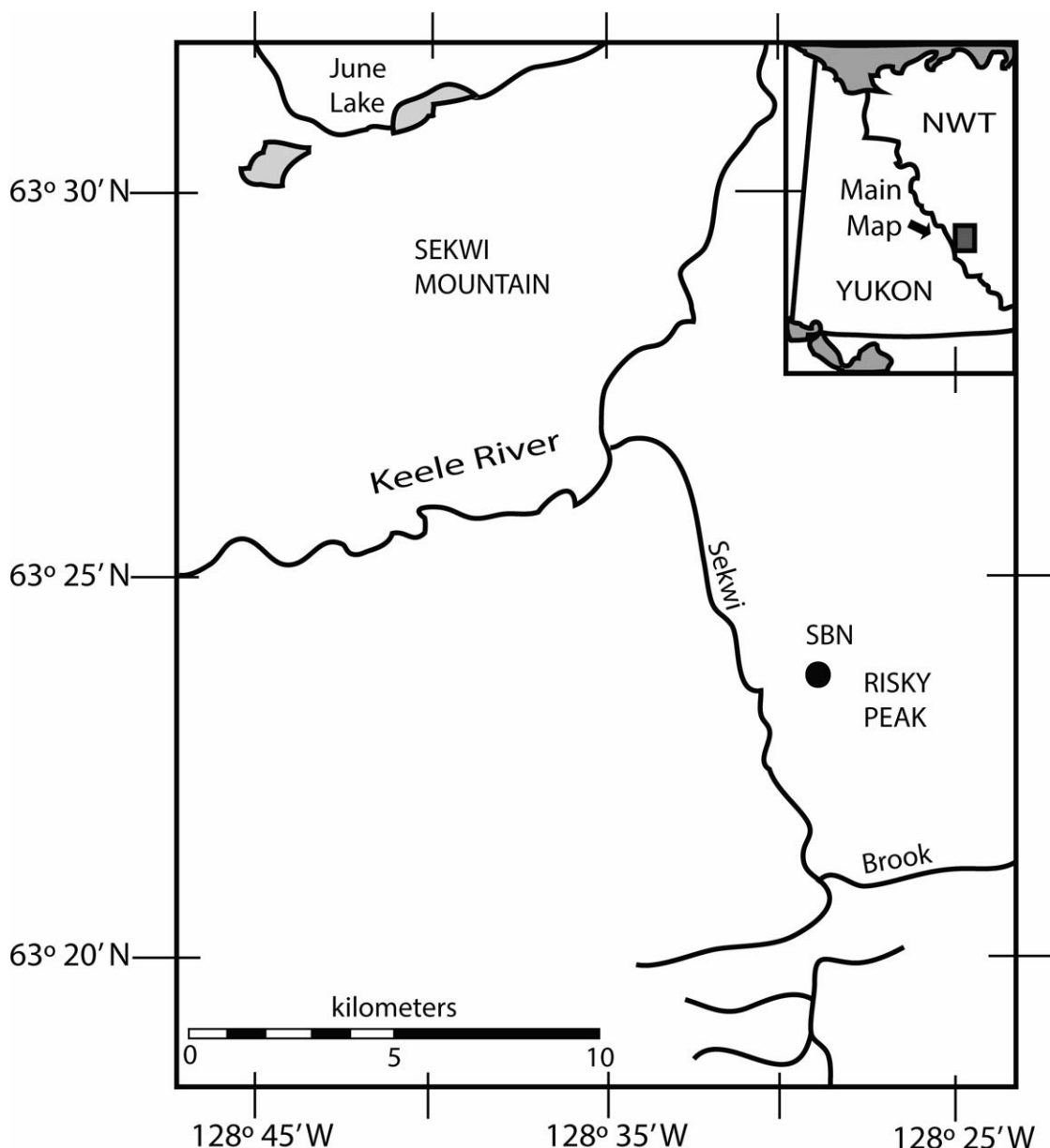
FIGURE *1*—Location of Sekwi Brook North (SBN) in northwestern Canada.

oxygen to these deep-sea communities, and these communities were preserved in situ when they were catastrophically covered by volcanic ash, providing a lithologic interface for their preservation (Conception-style preservation: Seilacher, 1992; Narbonne, 2005). The June beds at Sekwi Brook in NW Canada (Figs. 1, 2) also contains abundant contourites (Dalrymple and Narbonne, 1996), with an especially thick package of contourites immediately below the turbidites that had yielded abundant discoid fossils in previous studies (Fig. 2), but these contourites have gradational bases and lack volcanic ash for normal Ediacaran fossil preservation on the bases of event beds and were not heavily prospected in previous studies.

Detailed study of this interval during the summers of 2012 and 2013 resulted in the discovery of fronds and other complex Ediacaran fossils preserved intrastratally within contourite and turbidite sandstone beds. There is no sharp lithologic interface, and the fossil is preserved as an impression along a horizontal parting surface within the bed which was subsequently exposed

during modern weathering, a deep-water equivalent of Nama-type preservation (Narbonne, 2005). These newly discovered fossils significantly enhance the known Ediacaran diversity of NW Canada and provide a new window into the early evolution of large, complex multicellular life outside of Avalonia.

GEOLOGIC SETTING

The late Neoproterozoic Windermere Supergroup is a mainly siliciclastic succession 5–10 km thick that extends throughout western Canada with scattered outcrops as far south as Senora, Mexico (see reviews in Ross et al., 1989; Narbonne and Aitken, 1995; Narbonne, 2007). In the Mackenzie Mountains of NW Canada, the base of the Windermere Supergroup consist of rift-related fanglomerates, redbeds, and evaporites that mark the opening of the proto-Pacific Ocean approximately 780–750 Ma. Later Cryogenian deposits include the Rapitan Formation, correlated with the worldwide Sturtian glaciation and directly dated at 716. 5 Ma in NW Canada (Macdonald et al., 2010) and

the Ice Brook Formation, correlated with the worldwide Marinoan glaciation and probably ending about 635 Ma (Hoffman and Halverson, 2011). Overlying Ediacaran strata in the Mackenzie Mountains represent a mainly passive margin succession that consists of turbiditic sandstones, mudstones, and carbonates deposited on a deep-water continental slope (Aitken, 1989; Dalrymple and Narbonne, 1996, Narbonne and Aitken, 1995; MacNaughton et al., 2000; Macdonald et al., 2013).

The fossils described in this paper are from strata originally referred to the uppermost beds of the Sheepbed Formation by Aitken (1989), a designation that was subsequently used by Narbonne and Aitken (1990, 1995), Narbonne (1994), Dalrymple and Narbonne (1996), and most other workers. However, these strata at Sekwi Brook are coarser than the dark shales that characterize the type Sheepbed Formation (Gabrielse et al., 1973), and at Sekwi Brook are separated from strata similar to the type Sheepbed by a major regional sequence boundary marked by large channel fills (Macdonald et al., 2013; see also Fig. 2). This implies that these fossiliferous strata are considerably younger than the type Sheepbed Formation, which directly overlies Marinoan glacial deposits and does not contain Ediacara-type fossils. This paper follows Macdonald et al. (2013) in referring to these fossiliferous strata using the informal term "June beds".
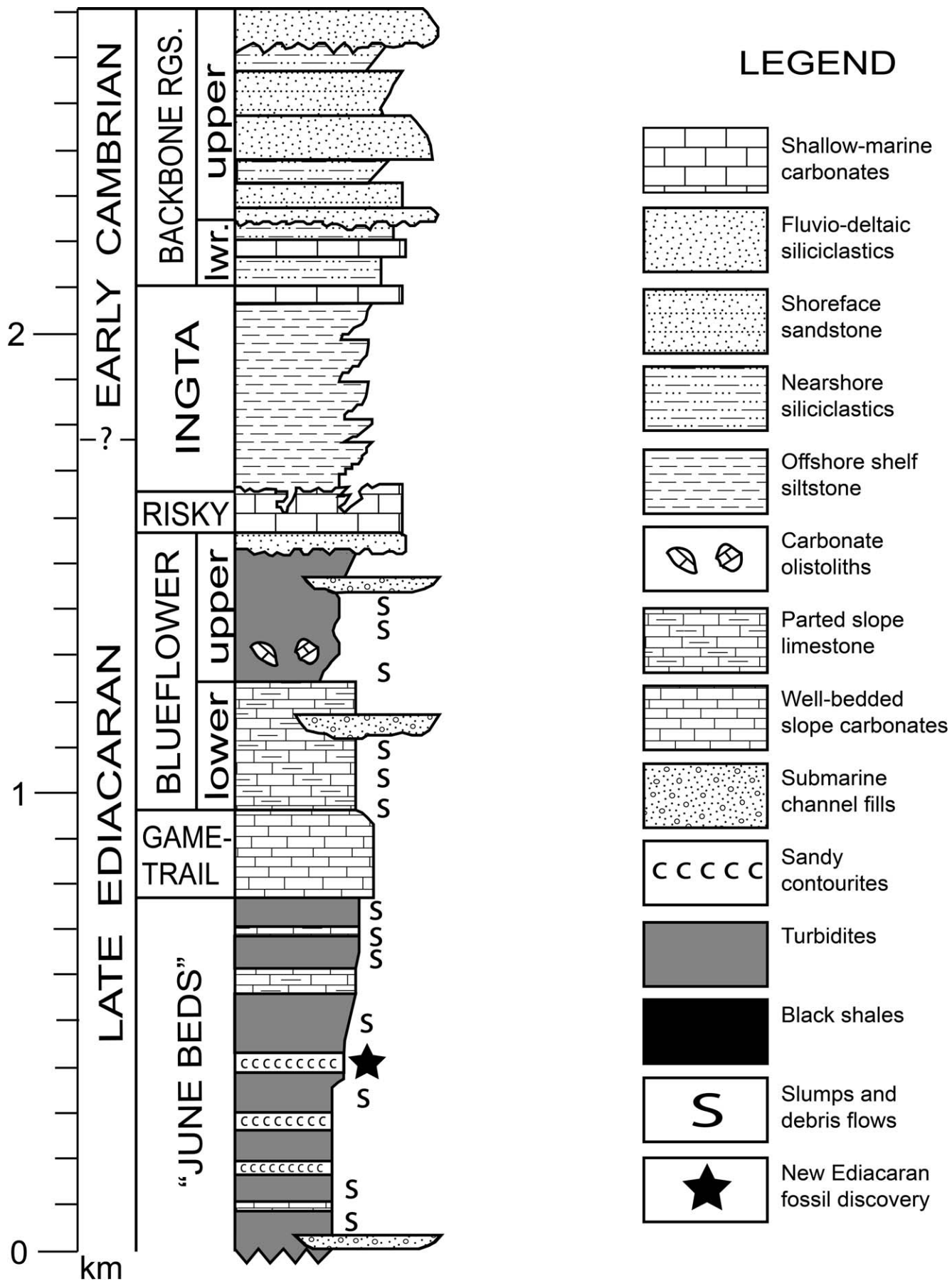
The June beds at Sekwi Brook are Ediacaran in age, and occur stratigraphically mid-way between the Marinoan tillites of the Ice Brook Formation and the base of the Cambrian in the Ingta Formation. There are no radiometric dates in this section, but based on regional and global correlations Macdonald et al. (2013) suggested that an age somewhere in the range of 580–560 Ma is most probable, which would imply a broad equivalence between the fossils of the June beds in NW Canada and the oldest Ediacara-type fossils reported from Avalonian England and Newfoundland.

The Ediacaran sediments at Sekwi Brook accumulated on a southwest-facing continental slope that bordered the ancestral Pacific Ocean (Ross et al., 1989; Narbonne and Aitken, 1995; Dalrymple and Narbonne, 1996; MacNaughton et al., 2000; Narbonne, 2007; Macdonald et al., 2013). Evidence for the presence of a slope is pervasive throughout the June beds, Gametrail, and Blueflower formations (Fig. 2). Slope indicators in the June beds include the dominance of sedimentation by turbidity currents that show a unidirectional transport direction toward the southwest and the common presence of intraformational truncation surfaces (i.e., slump scars), slump folds and poorly sorted debris-flow deposits (Dalrymple and Narbonne, 1996). Large displaced blocks of carbonates and shallow-water sandstone, some of which are demonstrably overturned, are also present locally. Many intervals in the June beds also consist of sandy mudstones that contain an anastomosed set of shear planes; such deposits are interpreted as soft-sediment shear zones related to downslope creep and/or the movement of larger slumps and slides. Wave-generated sedimentary structures are conspicuously absent; the stratigraphically closest evidence of sedimentation above storm-wave base occurs near the top of the Blueflower Formation (MacNaughton et al., 2000; Macdonald et al., 2013), more than one kilometer stratigraphically above the level at which the fossils reported here were found. Calculations imply that deposition is unlikely to have occurred at water depths of less than approximately 750 m, and could have been substantially more than this (Dalrymple and Narbonne, 1996).

Ediacara-type fossils occur abundantly on the soles of thin to very thin-bedded turbidites in the June beds (Narbonne and Aitken, 1990; Narbonne, 1994) and are also now known very sparingly from laminations within these turbidites (this study).

The turbidites are typically <1–3 cm thick, with some rare beds reaching a maximum of 10 cm thick (FA2–FA4 of Dalrymple and Narbonne, 1996). Each bed starts abruptly, but the basal surface is generally not noticeably erosional and mudstone rip-up clasts are rare, which implies that erosion of the substrate was minimal (Fig. 3.1, 3.2). A limited range of grain sizes is present: coarse silt to fine sand predominates, with only rare occurrences of medium sand at the base of the thickest beds. Because of the small grain-size range, upward fining within the beds is only weakly developed. The turbidite beds contain a partial Bouma sequence, and are herein described using this nomenclature (e.g., T_b refers to the "b" division of a turbidite as defined by Bouma, 1962). The thinnest beds (<1–2 cm thick) are typically T_{de} beds, whereas the thicker beds are generally T_{cde} or T_{ce} beds. $T_{b–e}$ beds are present but uncommon. Within the "c" division, ripple climbing is evident, with subcritical (i.e., low-angle) climbing predominating (Fig. 3.2). Loading occurs sporadically and only on the bases of the thicker beds, which implies that the muddy substrate was moderately firm. The beds interpreted as turbidites are formed by discrete waning-flow events that were presumably initiated by failures higher on the slope. The prevalence of the "c" and "d" Bouma divisions, the fine grains size of the sand, and the scarcity of erosional features all indicate that the majority of the turbidity currents were not very energetic and most likely had flow velocities of only a few tens of centimeters per second at most. The fine size of the sand grains permits easy suspension, which leads to low grain concentrations within the disperse sediment cloud that in turn favors relatively slow flow in the turbidity current. The prevalence of subcritically climbing current ripples indicates that deposition from suspension did occur, but traction deposition predominated.

Ediacara-type fossils also occur sparingly on horizontal parting surfaces within sandy contourite beds. Rippled sands formed by contour parallel flows are well described from modern oceans, but the distinction of contourites from thin-bedded turbidites in the rock record has been the subject of some uncertainty (Stow et al., 1998, 2002; Martín-Chivelet et al., 2008; Shanmugam, 2008; Stow and Faugères, 2008). The contourites of the June beds exhibit the key features diagnostic of modern contourites, most significantly current ripples oriented at right angles to the downslope direction as determined by turbidite ripples throughout the succession (Shanmugam, 2008, p. 66). The very fine-grained nature of these contourites and their intimate interbedding with slope turbidites over a stratigraphic distance of nearly 1 km are typical of contourites and not typical of deep-sea axial deposits. The absence of bioturbation in this Neoproterozoic succession further facilitates unequivocal distinction of the contourites. Two end-member varieties of contourite are present in the June beds: sandy and muddy. The sandy contourites consist of beds of coarse silt to very fine sand that are typically 10–20 cm thick (Fig. 3.3, 3.4). The bases and tops of these beds are typically rapidly gradational into the underlying and overlying mudstones. Systematic vertical changes in grain size (i.e., upward fining or coarsening) within the beds are not evident, and instead parallel to gently undulatory lamination is the most abundant structure. Trains of current ripples with a northwesterly paleocurrent direction are interspersed randomly within these beds (Fig. 3.4), which display no predictable vertical succession of structures. Muddy contourites are composed predominantly of fine to very fine silt with randomly interspersed laminae of medium to coarse silt that produces a streaky or pinstripe appearance that differs from homogeneous mudstone that overlies turbidite beds. Some laminae show a subtle thickening
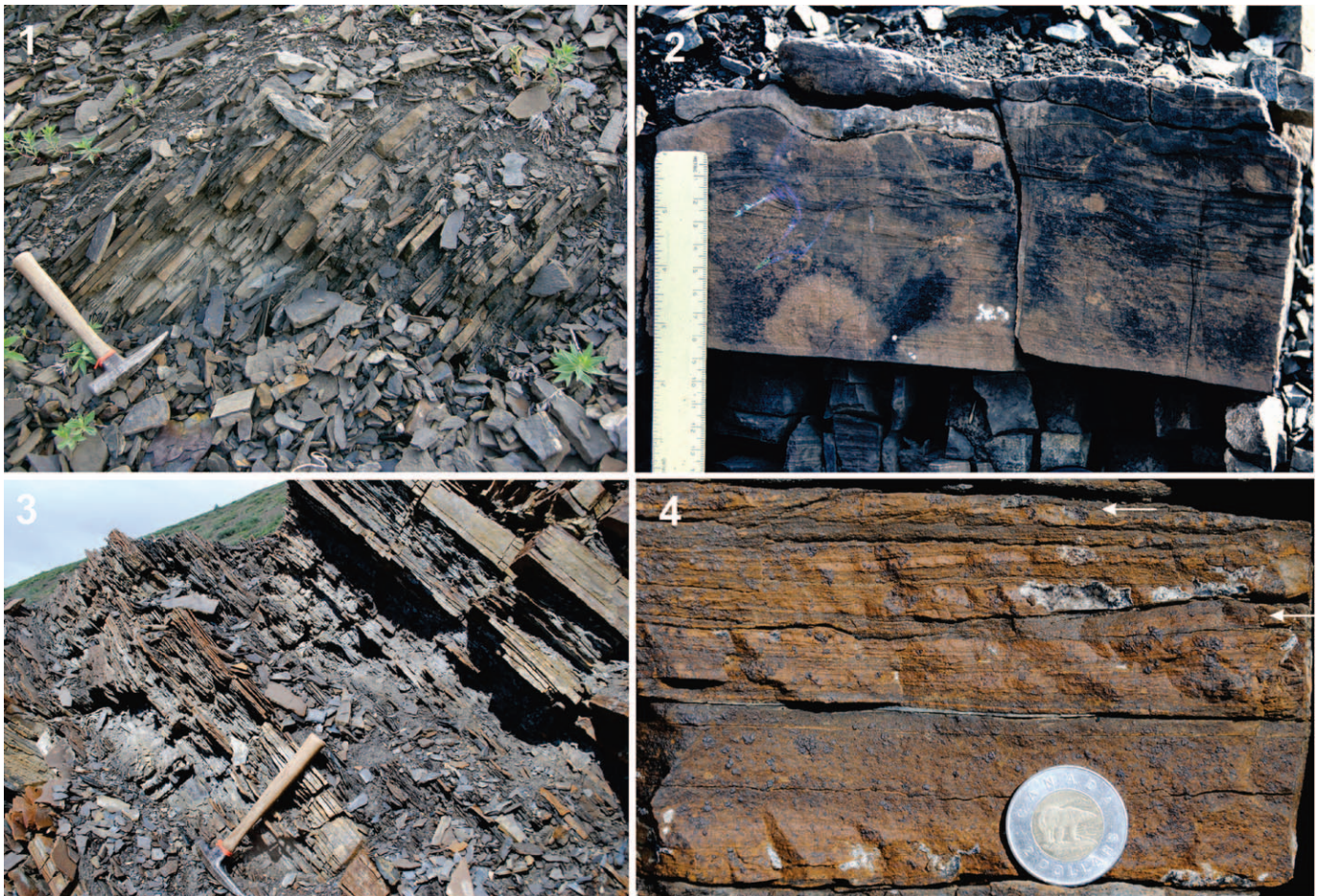
LEGEND

Shallow-marine carbonates

Fluvio-deltaic siliciclastics

Shoreface sandstone

Nearshore siliciclastics

Offshore shelf siltstone

Carbonate olistoliths

Parted slope limestone

Well-bedded slope carbonates

Submarine channel fills

C C C C C   Sandy contourites

Turbidites

Black shales

S   Slumps and debris flows

★   New Ediacaran fossil discovery

EARLY CAMBRIAN

BACKBONE RGS.
upper
lwr.

INGTA

?

RISKY

LATE EDIACARAN

BLUEFLOWER
upper
lower

GAME-TRAIL

"JUNE BEDS"

2

1

0
km

FIGURE 3—Turbidite and contourite facies in the June beds at Sekwi Brook. *1,* general view of thin-bedded turbidites within the main fossiliferous zone; most of the light-colored beds are $T_{(c)de}$ beds with sharp bases; top is to the upper left; *2,* close-up view of a medium T_{b-e} bed that has casts of *Aspidella* on its base, note sharp base and gradational top of the bed, and the subcritical angle of climb of the current-rippled "c" division; flow direction is to the right, downslope to the southwest; this bed rests on muddy contourite deposits that display very thin silt streaks, each of which is only a fraction of a millimeter thick; *3,* general view of contourite deposits, note the alternation between sandy contourites (lighter and more resistant) and muddy contourites (dark, recessive); the sandy contourites display platy breakage because of the prevalence of parallel lamination; *4,* close-up of a sandy contourite bed; the lower part contains parallel lamination, while the upper part displays two current-rippled horizons (white arrows) with flow direction to the left (northwest), separated by parallel lamination that is gently undulatory because it is draped over ripples.

and thinning along their length, with a spacing of 5–15 cm, or consist of discontinuous, flat-based lenses of silt that are interpreted to be incipient current ripples. Sandy contourite beds tend to occur in groups that alternate with muddy contourites, with a spacing of 0.3–0.5 m between intervals dominated by sandy contourites (Fig. 3.3). The transitions from the sandy intervals into the muddier sediment are gradational, giving the outcrop a cyclic appearance. Such cyclicity is very similar in scale to the cyclic textural variations seen in many modern contourite succession (e.g., Llave et al., 2006; Stow and Faugères, 2008; Stow et al., 2008), which is attributed to Milankovich-controlled changes in ocean circulation.

TAPHONOMY

Ediacara-type fossils on turbidite soles (Fig. 4) and intra-stratally within contourite and turbidite sandstones (Figs. 5, 6) in the June beds at Sekwi Brook show significant differences in composition that appear to have been controlled mainly by taphonomic processes involved in the deposition of these different deep-water sandstones.

Fossils are abundant on the bases of thin turbidites and comprise mainly discoid fossils interpreted as frond holdfasts preserved in semi-relief on the bed sole. Discoid fossils are abundant, with several hundred collected thus far. Simple discs referable to the form genus *Aspidella* dominate the assemblage, with a few specimens of tentaculate discs referable to *Hiemalora* and *Eoporpita* (Fig. 4.1, 4.3). A newly discovered striated cone represents the erniettomorph *Namalia* (Fig. 4.2) and a specimen of the frond *Primocandelabrum* (Fig. 4.3, 4.4) are also herein reported. Fossiliferous turbidite soles are typically black and carbonaceous, and commonly exhibit "old elephant skin" textures (e.g., Fig. 4.3) commonly interpreted as a microbial mat on the original sea bottom (Hagadorn and Bottjer, 1997; Gehling and Droser, 2009). Preservation of the fossils in positive relief on the sandstone soles implies that they were at least partly buried in the muddy sea bottom at the time

FIGURE 2—Generalized stratigraphic section of the late Ediacaran–Lower Cambrian succession in NW Canada (after MacNaughton et al., 2000). Quotation marks around "June beds" denote its informal nomenclatural status (Macdonald et al., 2013).

FIGURE *4*—Ediacaran fossils preserved on turbidite soles. *1, Hiemalora* (left, ROM 62448) and *Aspidella* (right, ROM 62449); *2, Namalia* Germs, 1968, ROM 62450; *3, Primocandelabrum* Hofmann, O'Brien and King, 2008 preserved on a microbially textured turbidite sole with *Aspidella*-like holdfasts, several of which exhibit stems or fronds (arrows) oriented parallel with ripple-marks in the turbidites, ROM 62457; *4*, close-up of *Primocandelabrum* showing an *Aspidella*-like disc at its base and candelabra-like branches at the distal end of the preserved frond (arrows). The scale bars represent 1 cm or 1 cm increments.

of arrival of the turbiditic sands, and the shape of their basal surface was cast either by collapse of the overlying turbiditic sand into the cavity formed by decay these soft-bodied organisms (Narbonne, 2005) and/or by sand within their bodies (Laflamme et al., 2011). In contrast with their abundance on turbidite soles, discoid frond holdfasts such as *Aspidella* and *Hiemalora* are nearly absent from the bases of the sandy contourites in the Sekwi Brook succession, most likely because these contourite beds exhibit gradational contacts with the underlying mudstones that do not provide a sharp lithologic interface for Ediacaran fossil preservation.

Ediacaran fossils are also sporadically preserved within sandy contourites and turbidites in the June beds, and can be seen when modern fracturing through these beds exposes the intrastratal fossil. There is a strong preservational bias in favor of parts of organisms that were erect in the water column during life, especially the leafy petalodia of fronds such as *Charnia* (Fig. 5.1–5.4), *Charniodiscus* (Fig. 5.5), and *Beothukis* (Fig. 6.1–6.7). This intrastratal preservation represents a deep-water occurrence of Nama-style preservation (Narbonne, 2005) in

which the soft-bodied organisms were preserved as impressions within beds of sandstone. There is no lithological contrast, just the impression of the fossil on both sides of the parting surface (Fig. 5.1, 5.2), which distinguishes this from Fermeuse-style preservation under event beds of turbiditic sandstone or Conception-style preservation under event beds of volcanic ash (Narbonne, 2005). Nama-style preservation in shallow-water sandstones commonly results in thin sandstone wedges separating the sheets of foliate organisms and enhancing their recognition as multifoliate (Jenkins, 1985, 1992; Narbonne et al., 1997, 2009; Grazhdankin and Seilacher, 2002, 2005; Vickers-Rich et al., 2013; Meyer et al., 2014). This is also evident in this deep-sea example of Nama-style preservation, in which a specimen of *Fractofusus* preserved intrastratally within a contourite bed shows multifoliate structure (Fig. 5.6, black arrows) that was inferred but not observed in the flattened specimens of *Fractofusus* in Newfoundland (Gehling and Narbonne, 2007).

Despite their close proximity, there is little overlap between the fossils preserved on the soles of the turbidites (Fermeuse-

FIGURE 5—Ediacaran fossils preserved intrastratally within contourite and turbidite beds. *1–4, Charnia* Ford, 1958: *1,* counterpart negative epirelief of ROM 62452 exposed on an irregular parting in a contourite bed; *2,* positive hyporelief of ROM 62452; *3,* positive hyporelief of a juvenile specimen preserved on a parting in a contourite bed, ROM 62456; *4,* positive hyporelief of a specimen preserved on a parting in a turbidite bed, ROM 62453; *5, Charniodiscus* Ford, 1958 preserved on three different partings within a contourite bed, ROM 62455; *6, Fractofusus* Gehling and Narbonne, 2007, multifoliate specimen consisting of three partly overlapping vanes (black arrows with numbers) composed of rangeomorph elements with self-similar branching (white arrow), ROM 62454. The scale bars represent 1 cm or 1 cm increments.

style preservation of Narbonne, 2005) and those preserved within the sandstone beds (Nama-style preservation of Narbonne, 2005). Fermeuse-style preservation preferentially sampled the basal layer of the community, which consisted mainly of the partly buried holdfasts of Ediacaran fronds. These holdfasts provide relatively little taxonomic information since they cannot presently be related to individual frondose taxa, leading to the apparently low diversity of NW Canada reported in previous global compilations (e.g., Waggoner, 2003; Shen et al., 2008). However, Fermeuse-style preservation provides a superb record of the density and spacing of fronds and other organisms on the sea bottom (Fig. 4) that is essential to paleoecological reconstruction of the living community (Gehling et al., 2000). In contrast, Nama-style preservation sampled higher layers of the community, including the petalodia of three genera of rangeomorph and arboreomorph fronds (Figs. 5, 6). These specimens provide information about the taxonomic composition of the Sekwi Brook assemblage that is critical for
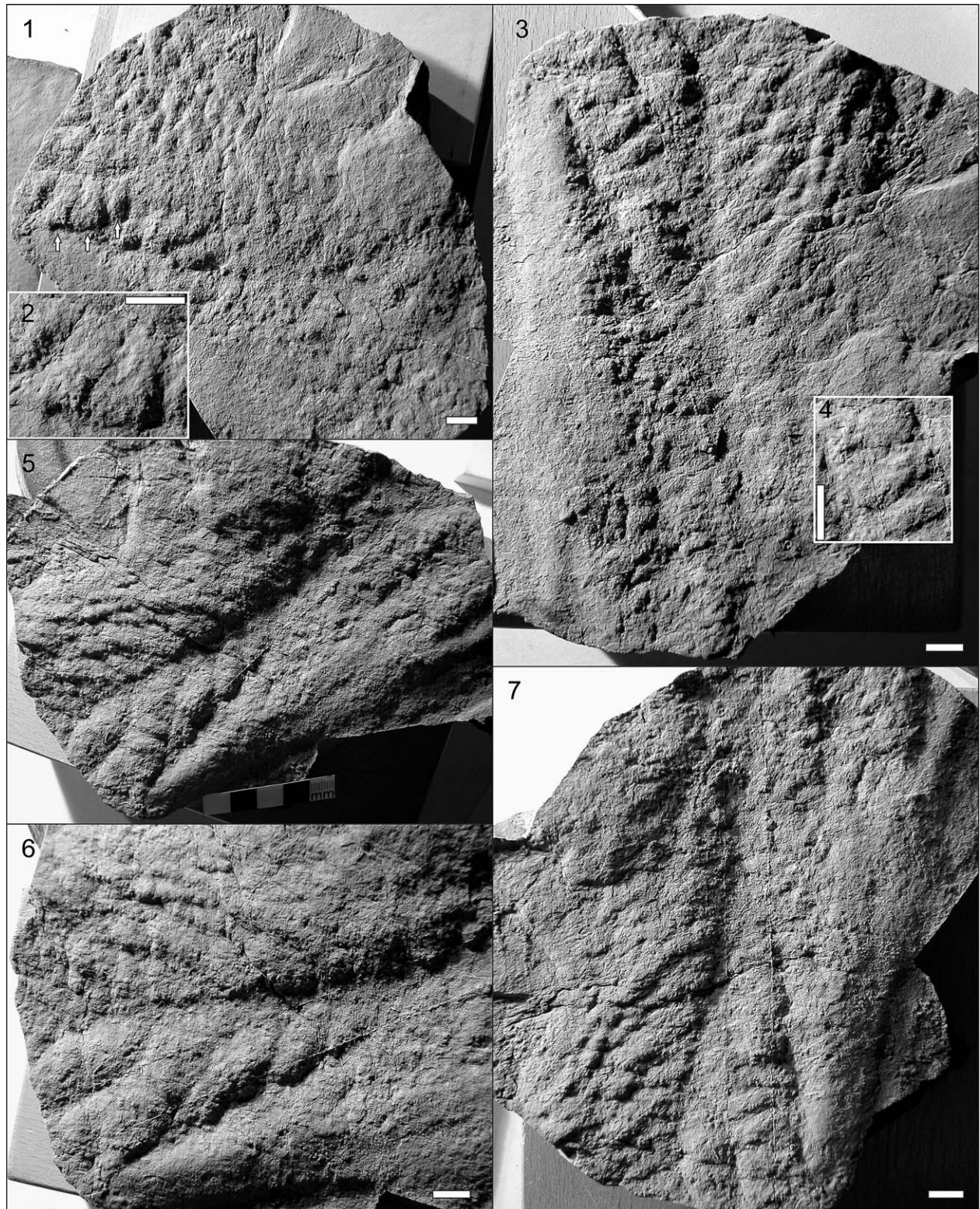
FIGURE 6—*Beothukis* Brasier and Antcliffe, 2009, ROM 62451, views from different orientations to show the full structure; white arrows show individual rangeomorph elements. The scale bars represent 1 cm or 1 cm increments.

paleoecological reconstruction of the original community and for compilations of the taxonomy, ecology, biogeography, and biostratigraphy of the Ediacara biota worldwide.

Fermeuse-style preservation on turbidite soles and Nama-style preservation within the contourite and turbidite beds of the June beds sampled different aspects of the original community, and combining their resultant data sets provides a truer assessment of the taxonomic composition and ecology of the original Ediacaran community than either can possibly provide by itself.

Disc-like fossils from the June beds were described by Narbonne and Aitken (1990) and Narbonne (1994) and these descriptions are not repeated here. The newly discovered taxa from NW Canada formally described below are grouped into three of the Ediacaran clades recognized by Xiao and Laflamme (2009), Erwin et al. (2011), and Laflamme et al. (2013). Terminology follows Laflamme and Narbonne (2008a, 2008b) for fronds, Narbonne et al. (2009) and Brasier et al. (2012) for rangeomorphs, and Grazhdankin and Seilacher (2002) for erniettomorphs. Specimens of complex fossils are sparse and most are not as well preserved as in the classic sites such as Newfoundland and the White Sea, and taxonomic assignments are correspondingly conservative. All figured specimens are reposited in the types collection of the Royal Ontario Museum in Toronto (ROM).

Group RANGEOMORPHA Pflug, 1972

This clade encompasses Ediacaran taxa that show modular construction of cm-scale elements exhibiting self-similar fractal branching patterns to produce sheet-, comb-, bush-, or frond-shaped forms. Named genera include *Rangea, Avalofractus, Beothukis, Bradgatia, Charnia, Culmofrons, Fractofusus*, *Frondophyllas*, *Hapsidophyllas*, and *Trepassia*. Rangeomorphs occur throughout most of the upper half of the Ediacaran Period, from about 580–545 Ma, and are especially prominent and diverse in deeper-water, older Ediacaran strata (Xiao and Laflamme, 2009; Narbonne et al., 2012). Some workers have regarded rangeomorphs as primitive radial animals, principally cnidarians (Jenkins, 1985) or ctenophores (Dzik, 2002), but most workers have treated them as an extinct clade of Ediacaran life (Pflug, 1972; Narbonne, 2004, 2011; Brasier and Antcliffe, 2004, 2009; Sperling et al., 2007; Xiao and Laflamme, 2009; Erwin et al., 2011; Brasier et al., 2012; Vickers-Rich et al., 2013; Laflamme et al., 2013).

Genus BEOTHUKIS Brasier and Antcliffe, 2009

Type species.—*Beothukis mistakensis* Brasier and Antcliffe, 2009, by monotypy.

Remarks.—*Beothukis* was originally defined by Brasier and Antcliffe (2009) on the basis of two specimens from the E-surface at Mistaken Point in Newfoundland. Narbonne et al. (2009) used exquisitely preserved specimens from Spaniard's Bay in northern part of the Avalon Peninsula to expand the diagnosis of this taxon. *Beothukis* is similar to *Rangea* and *Avalofractus* in exhibiting second-order branches that typically are symmetrical rangeomorph elements ("displayed and furled" in the terminology of Brasier et al., 2012), but differs in that the primary branches are invariably folded and rotated sideways to show only one side of the rangeomorph structure ("rotated and furled" in the terminology of Brasier et al., 2012). *Beothukis* occurs commonly in the deep-water turbidites of Avalonian Newfoundland, and a single specimen is also known from shallow-water deposits in the Flinders Ranges of Australia (Narbonne et al., 2009), but had not previously been reported from NW Canada or any other localities in Laurentia.

BEOTHUKIS cf. B. MISTAKENSIS Brasier and Antcliffe, 2009
Figure 6.1–6.7

Description.—The single specimen (ROM 62451) is an incomplete petalodium with an axial length of 170 mm (incomplete at both ends) that expands from 67–107 mm wide distally. At least four first-order branches up to 25 mm wide emanate at an acute angle from a well-developed axial furrow and extend to the margins of the petalodium. First-order branches

consist of a pendant array of second-order branches oriented perpendicular to each primary branch axis. Each second-order branch is a symmetrically branching rangeomorph element approximately 10 mm wide.

Remarks.—The NW Canada specimen is similar in size and morphology to the holotype of *Beothukis mistakensis* from Mistaken Point, but its intrastratal preservation in a sandstone bed has resulted in a poorer quality of preservation than the Newfoundland holotype which is preserved under a bed of volcanic ash. Despite this preservational difficulty, individual secondary displayed and furled rangeomorph branches are still visible (arrows in Fig. 6.1).

Genus CHARNIA Ford, 1958

Type species.—*Charnia masoni* Ford, 1958, by original monotypy.

Remarks.—*Charnia* was the first large and complex Ediacaran fossil reported from the northern hemisphere (Ford, 1958). The original specimen was found in Charnwood Forest in central England but the taxon is now known worldwide and has become one of the most iconic of all Ediacaran fossils. Modern studies and syntheses of *Charnia* have been presented by Laflamme et al. (2007) and Antcliffe and Brasier (2008), with further recent updates by Brasier and Antcliffe (2009), Narbonne et al. (2009), and Brasier et al. (2012).

CHARNIA cf. C. MASONI Ford, 1958
Figure 5.1–5.4

Description.—The largest specimen (ROM 62452) is preserved in both part (positive hyporelief; Fig. 5.2) and counterpart (negative epirelief; Fig. 5.1) within a contourite bed of sandstone. The following description refers to orientations visible in positive hyporelief. The specimen is 254 mm long and 48 mm wide, and consists mainly of the right-hand side of the petalodium. At least seven primary first-order branches pass off the midline at an acute angle, with the distal edge of each primary branch overlapping the proximal edge of the adjacent branch to form an imbricate pattern. Well-preserved primary branches are divided into second-order branches 6–8 mm wide oriented at a high angle to the primary branches, and these secondary branches exhibit submillimetric traces of third order branches that are oriented at a high angle to the secondary branches. Another large specimen (Fig. 5.4; ROM 62453) preserved within a turbidite bed is a 60 mm long by 20 mm wide fragment of the left-hand side of a *Charnia* petalodium ("frond" in the terminology of Brasier et al., 2012). Primary branches 5 mm in width are subdivided into second-order branches 2–4 mm wide that are oriented at a high angle to the first-order branches. Tips of some secondary branches are divided into small, mm-scale, third-order branches.

A juvenile specimen 53 mm long and 17 mm wide (Fig. 5.3; ROM 62456) exhibits an ovate petalodium consisting of 10 primary branches 4 mm wide at their bases that pass off both sides of a zigzag central axis in an alternate pattern and taper towards the margin of the frond. Secondary branches are spaced approximately 1 mm apart nearly transverse to the primary branches, with individual secondary branches appearing to pass continuously through several primary branches. A circular depression 6 mm in diameter at the base of the petalodium marks the position of the stem or stalk passing through the bedding plane. The sandy grain-size of the contourite in which this small specimen is preserved precludes analysis of third-order branching or other fine-scale features in this fossil.

Remarks.—The two large NW Canada specimens are incomplete, but the size and arrangement of first-, second-, and third-order branches is remarkably similar to that of the type species, *C. masoni*. The variable preservation of features between different parts of the fossil, ranging from excellent preservation of first-,

second-, and third-order branches in the middle part of the fossil but only undifferentiated first-order branches distally towards the apex can be attributed to the multilevel parting that forms the preservational surface passing irregularly through this intrastratal fossil (Fig. 5.1, 5.2). The juvenile specimen (Fig. 5.3) exhibits key diagnostic features of *Charnia*, including primary branches that pass off both sides of a zigzag central axis in an alternate pattern and secondary branches nearly at right-angles to the primary branches that appear to pass through adjacent primary branches, but with individual primary branches that are deltoid to parallel rather than the mainly sinusoidal branches typical of *Charnia masoni*.

Charnia is a characteristic fossil of the deep-water Avalon assemblage, but also ranges into younger and shallower strata (Laflamme et al., 2013).

Genus FRACTOFUSUS Gehling and Narbonne, 2007

Type species.—*Fractofusus misrai*, by original designation.
Remarks.—Spindle-shaped rangeomorphs were the first Ediacaran fossils discovered at Mistaken Point in Newfoundland (Anderson and Misra, 1968) and the genus *Fractofusus* was subsequently formalized by Gehling and Narbonne (2007). *Fractofusus* is the most abundant and well-known rangeomorph taxon in the Ediacaran of Newfoundland (Misra, 1969; Seilacher, 1992; Clapham et al., 2003; Gehling and Narbonne, 2007; Hofmann et al., 2008), but prior to the present study it had not been reported from outside of Avalonian Newfoundland.

FRACTOFUSUS cf. F. ANDERSONI Gehling and Narbonne, 2007
Figure 5.6

Description.—The single specimen found at Sekwi Brook (Fig. 5.6; ROM 62454) is a fusiform body 75 mm long and 47 mm wide. A smooth, central longitudinal ridge 4 mm wide is flanked on either side by approximately 16 parallel-sided elements that locally preserve a rangeomorph-style pattern of symmetrical, self-similar branching within each element. The central element on each side of the fossil is oriented perpendicular to the longitudinal ridge, but modules are oriented at increasingly lower angles towards the two ends of the fossil to produce a slightly radial aspect to the overwhelming bilateral symmetry of the fossil. The specimen is multifoliate (three-rows), with one vane/row on the right-hand side of the central longitudinal ridge and two partly overlapping vanes/rows on the left-hand side of this ridge.

Remarks.—Gehling and Narbonne (2007) recognized two species of *Fractofusus*, *F. misrae* and *F. andersoni*, that could consistently be distinguished using several independent morphological criteria, a view supported by subsequent discoveries of both species on the Bonavista Peninsula of Newfoundland (Hofmann et al., 2008). The Sekwi Brook specimen most closely resembles *Fractofusus andersoni* in being an ovoid body composed of elements that are simple and arranged in a slightly radial pattern, rather than being strongly elongate and composed of complex elements arranged perpendicular to the midline as in *F. misrae*. The approximately 16 elements on each vane/row of the Sekwi Brook specimen is slightly higher than any previously studied specimens of *F. andersoni*, which typically exhibits 8–14 elements on each vane.

All Avalon specimens of *Fractofusus* preserve the basal surface of the fossil under beds of volcanic ash (Conception-style preservation of Narbonne, 2005), and all appear in outcrop as a bilaterally symmetrical pattern of two vanes that meet along a zigzag central commissure (Gehling and Narbonne, 2007; Hofmann et al., 2008). Taphonomic features imply that *Fractofusus* was weakly attached to the sea bottom along its entire length (Seilacher, 1992; Gehling and Narbonne, 2007). Analysis of its community structure and modeling of its fractal

surface imply that it fed by extracting dissolved nutrients from the water column (Clapham et al., 2003; Laflamme et al., 2009).

The simplest possible reconstruction of the Avalonian specimens of *Fractofusus* is as a sheet-like body that lay flat on the sea bottom, but relationships between closely crowded specimens at Mistaken Point and considerations of hydrodynamic properties of various reconstructions of *Fractofusus* led Gehling and Narbonne (2007, fig. 14) to speculate that *Fractofusus* may have been trifoliate, with a third vane/row that extended vertically into the water column but was not preservable in Conception-style preservation in which the specimens were flattened under beds of volcanic ash. Preservation of the NW Canada specimen within a contourite provides additional taphonomic information concerning the 3-D structure of *Fractofusus*. The right hand side of the specimen (Fig. 5.6) shows a single vane (labeled "1") with local preservation of symmetrical rangeomorph elements (white arrow), but two slightly separated and rotated vanes (labeled "2" and "3") are visible on the left hand side of this ridge. The presence of a longitudinal central ridge rather than the central zigzag groove present in the Avalon specimens is also consistent with partial overfolding of a third vane during burial and compaction. None of these features is diagnostic in and of itself, but collectively they support reconstruction of *Fractofusus* with a third vane that extended vertically into the water column (Fig. 7).

Group ARBOREOMORPHA Xiao and Laflamme, 2009

This clade encompasses Ediacaran taxa that possess primary branches that are stitched together into a large leaf-like sheet with tear-drop-shaped secondary branches (Erwin et al., 2011; Laflamme et al., 2013). Taxa include the numerous species of *Charniodiscus* plus similar forms that are closely related or synonymous with this genus. The first arboreomorphs may have appeared as early as 580 Ma (Liu et al., 2012) and definitely by 565 Ma (Laflamme et al., 2004), and arboreomorphs occur commonly from 565–550 Ma in a variety of deep- and shallow-water Ediacaran facies. Earlier workers emphasized the similarities between *Charniodiscus* and modern pennatulacean Cnidaria (e.g., Glaessner and Wade, 1966; Jenkins, 1992; Conway Morris, 1993), however this is presently controversial (Laflamme et al., 2004; Brasier and Antcliffe, 2009). It is more likely that the similar frond morphology reflects a shared ecology rather than ancestry (Laflamme and Narbonne, 2008a, 2008b). We therefore consider the Arboreomorpha as a distinctive Ediacaran clade but without assigning it to any higher taxonomic division at this time.

Genus CHARNIODISCUS Ford, 1958

Type species.—*Charniodiscus concentricus*, by original monotypy.
Remarks.—The morphology of *Charniodiscus* has been reviewed by Jenkins and Gehling (1978) and Laflamme et al. (2004). *Charniodiscus* is common in both shallow-water settings in Australia and the White Sea and deep-water settings in Avalonian Newfoundland and England. *Charniodiscus* occurs in shallow-water equivalents of the Blueflower Formation in the Wernecke Mountains of NW Canada (Narbonne and Hofmann, 1987), but the genus had not previously been reported from the June beds in the Mackenzie Mountains.

CHARNIODISCUS sp.
Figure 5.5

Description.—ROM 62455 (Fig. 5.5) exhibits the basal part of the frond which is preserved at three levels within a contourite bed. The basal stratigraphic level consists of a poorly preserved disc 14 mm in diameter that may be impressed from below the base of the contourite. This passes upward and distally into a stem

FIGURE 7—Reconstruction of the ecosystem represented by the fossils and strata of the June beds at Sekwi Brook. The view is looking north, oblique to both the south-westward dipping continental slope and the north-westward flowing contour-parallel currents that produced the ripples. White patches represent incipient microbial mats of heterotrophic or chemosynthetic bacteria. Lighting in this aphotic environment is an artificial spotlight from the south-east, which allows comparison with images of modern deep-sea contourite fields taken from submersibles. The illustration is by P. Trusler.

25 mm long and 5 mm in diameter that in turn passes distally into the basal part of a petalodium at least 35 mm long (incomplete at the distal end) and 35 mm wide (also incomplete). The basal (preserved) part of the frond row/petaloid consists of six, 3–5 mm-wide first order branches that pass off a central stalk in an alternate (possibly helical) arrangement, with the branches on the right-hand side of the petalodium passing off the near face of the stalk and the branches on the left-hand side passing off the far face of the petalodium at a higher stratigraphic level. This arrangement could represent a taphonomic expression of an alternating branching pattern such as that evident on *C. arboreus* Glaessner *in* Glaessner and Daily, 1959. Millimeter-scale sub-transverse markings are locally evident in the branches.

Remarks.—The leaf-like structure of the NW Canada specimen is consistent with that of *Charniodiscus*, but this intrastratal specimen is too poorly preserved to be resolved to the species level.

Group ERNIETTOMORPHA Laflamme and Xiao, 2009

This clade encompasses Ediacaran taxa characterized by modular construction utilizing cylindrical elements to produce frondose, bag-like, canoe-shaped, or sheet-like constructions that lack any anterior-posterior differentiation (Laflamme et al., 2013). They are especially common in the late Ediacaran of Namibia, where named taxa include *Pteridinium*, *Swartpuntia*, *Ernietta,* and related forms. Abundant erniettomorphs first appear about 555 Ma and range to just below the base of the Cambrian (Narbonne et al., 1997; Xiao and Laflamme, 2009; Narbonne, 2011; Laflamme et al., 2013). Most erniettomorphs occur in shallow-water facies, but *Pteridinium* from the Carolina Slate Belt (Gibson et al., 1984) and the Blueflower Formation at Sekwi Brook (Aitken, 1989; Narbonne and Aitken, 1990) and *Miettia* from the southern Canadian Cordillera (Hofmann and Mountjoy, 2010) are reported from deeper-water facies. Most modern workers regard erniettomorphs as an extinct Ediacaran clade (Pflug, 1972; Gehling and Narbonne, 2007; Xiao and Laflamme, 2009; Narbonne, 2011; Erwin et al., 2011; Laflamme et al., 2013).

Genus NAMALIA Germs, 1968

Type species.—*Namalia villiersiensis*, by monotypy.
Remarks.—The Sekwi Brook fossil is strikingly similar to the holotype of *Namalia*, originally defined from Namibia as a cm-scale conical fossil exhibiting a longitudinally corrugated outer surface. The nomenclatural status of *Namalia* is uncertain: Runnegar (1992) regarded *Namalia* as a preservational variant of *Ernietta plateauensis* Pflug, 1966, whereas Grazhdankin and Seilacher (2002) treated it as a possibly distinct taxon of conical erniettomorphs. The single specimen from NW Canada cannot resolve this broader-scale taxonomic issue, and we refer this specimen to *Namalia* with the recognition that future studies may well confirm Runnegar's (1992) view that the taxon is synonymous with *Ernietta*. *Namalia* was previously known only from southern Namibia, but the closely related taxon *Ernietta* has been reported but not yet figured or described from shallow-water deposits in southern Nevada (Horodyski, 1991). Grazhdankin and Seilacher (2002) regarded *Namalia* as being semi-infaunal during life.

NAMALIA sp.
Figure 4.2

Description.—The single specimen (ROM 62450) is a gently curved, flattened cone 56 mm long (incomplete at its distal end) and 16 mm wide at its widest (distal) end. The outside surface of the cone is marked by strictly parallel-sided corrugations 2 mm wide that increase in number (but not width) from three corrugations at vertex of the cone to 10 at its widest part. Faint,

submillimetric, transverse ridges are locally present on the corrugations. The vertex of the striated cone is gently rounded.

Remarks.—The fossil is strikingly similar to the holotype of *Namalia villiersiensis* Germs, 1968 from the Ediacaran of Namibia in size, shape, and in the presence of longitudinal corrugations on the external surface of the cone. The conical fossil *Thectardis* from the Mistaken Point Formation of Newfoundland is also broadly similar in size and shape to *Namalia*, but *Thectardis* is smooth-walled with no hint of a tubular structure (Clapham et al., 2004). In addition, *Thectardis* is invariably triangular to bullet-shaped in plan view (Clapham et al., 2004), in contrast to the typically gently curved to contorted specimens that characterize *Namalia* from Namibia (Germs, 1968; Grazhdankin and Seilacher, 2002) and Sekwi Brook (Fig. 4.2). It is also unclear why *Thectardis* would be longitudinally striated on its outer surface if it was a sponge as inferred by Sperling et al. (2011).

Germs (1968) regarded *Namalia* as potentially representing a sponge or archaeocyathan but most subsequent workers have instead regarded it as being an erniettomorph, a view with which we concur. The presence of corrugations that are strictly parallel-sided along their entire length despite the distal widening of the NW Canada fossil implies that these corrugations represented rigid tubular constructional units, features diagnostic of the erniettomorphs and unknown from any other known Ediacaran clade. The tubular modular elements that constitute the erniettomorphs can be variably preserved as sharp ridges and broad furrows, broad ridges and sharp furrows, imbricate ridges and furrows, or evenly spaced corrugations (Grazhdankin and Seilacher, 2002) even in different parts of the same fossil specimen (Narbonne et al., 1997). Insertion of new tubular elements along both sides of the flattened cone is strikingly similar to that seen in a specimen of *Namalia* figured by Grazhdankin and Seilacher (2002, text-fig. 9A, 9B) and can be interpreted as representing insertion along the longitudinal suture that characterizes *Ernietta* and *Namalia*. The faint, submillimetric transverse ridges locally visible on the corrugations in the NW Canada specimen of *Namalia* are similar to those observed on the erniettomorphs *Pteridinium* and *Swartpuntia* at Swartpunt in Namibia (Narbonne et al., 1997).

The presence of *Namalia* in deep-water deposits of the June beds represents a significant age and environmental extension of its known range in Namibia.

Group uncertain
Genus PRIMOCANDELABRUM Hofmann, O'Brien, and King, 2008

Type species.—*Primocandelabrum hiemaloranum* Hofmann, O'Brien, and King, 2008, by monotypy.
Remarks.—*Primocandelabrum* consists of a subtriangular petalodium attached to a discoid holdfast by a stem. The holdfast is well preserved and can closely resemble either *Hiemalora* or *Aspidella*. The petalodium is typically poorly preserved, even in the holotype from Bonavista Peninsula in Newfoundland, and this has hindered determination of the affinities of *Primocandelabrum*.

PRIMOCANDELABRUM sp.
Figure 4.3, 4.4

Description.—This frondose specimen (ROM 62457) consists of a holdfast disc, short stem, and the proximal part of a poorly preserved triangular petalodium that passes distally into the overlying turbidite sandstone. The disc is preserved in negative hyporelief, the stem is preserved in positive hyporelief, and the petalodium is preserved in a mix of negative and positive hyporelief. The holdfast disc is 40 mm in diameter with a hemispherical central boss 4 mm in diameter, an annulate inner

ring 20 mm in diameter, and an outer flange that is smooth except for a few radial markings. A hemicylindrical stem 9 mm wide and 15 mm long apparently passes from the edge of the inner flange to join a poorly preserved, triangular petalodium at least 70 mm long and 65 mm wide that passes distally into the overlying turbidite bed. The upper part of the petalodium consists of a candelabrum-like array of six bundles of hemicylindrical branches that diverge and thicken towards the distal termination of the preserved frond. The lower third of the petalodium and five of the six candelabra-like arrays at the distal end of the fossil are covered by a thin smooth layer of uncertain origin, but a subparallel pattern of fine tubules can be seen where this has broken through to reveal the structure beneath.

Remarks.—The specimen from the June beds resembles *Primocandelabrum* sp. (Hofmann et al., 2008, fig. 12.5) from the Bonavista Peninsula of Newfoundland, and like it exhibits a candelabrum-like array of hemicylindrical branches (Fig. 4.4, arrows) attached to an *Aspidella*-like disc by a short stem. This specimen from the June beds occurs on the microbially textured sole of a T$_{bcde}$ turbidite covered with numerous specimens of *Aspidella*. The disc that forms the holdfast of *Primocandelabrum* is morphologically similar to the *Aspidella* specimens on this surface, and if found separately from this frond the disc would probably be referred to as a flat-convex morph of *Aspidella* (Gehling et al., 2000, text-fig. 6H, 6G), specifically to taxa formerly referred to *Cyclomedusa radiata* Sprigg, 1947 or *C. plana* Glaessner and Wade, 1966. Its preservation as a negative hyporelief may imply either partial uprooting of the holdfast during current flow (Tarhan et al., 2010) or preservation of the upper rather than lower surface of the holdfast.

The subtriangular shape and longitudinal ridges on the petalodium superficially resemble *Namalia* (Fig. 4.2) but the ridges on *Primocandelabrum* petalodium are considerably more irregular, and locally appear to converge, diverge, bend, and probably branch, and thus differ significantly from the exceptionally regular wall construction of an erniettomorph such as *Namalia*. The microbial surface on which this specimen occurs is thick and highly textured, which may have enhanced its preservation. The presence of a stem and frond attached to one of the *Aspidella*-like discs on this surface confirms views that *Aspidella* represents the holdfast of a frond (Gehling et al., 2000; Tarhan et al., 2010) rather than a microbial colony or jellyfish. Complete fronds with their basal attachment disc preserved on the same surface are common under volcanic ash falls at Mistaken Point but are rarer under sandstone event beds (Narbonne, 2005; Tarhan et al., 2010). The surface that contains *Primocandelabrum* also shows two additional stem impressions emanating from *Aspidella*-like discs (see arrows in Fig. 4.3) and the specimen of *Primocandelabrum* on this surface shows a decreasing quality of preservation distally from a well-preserved disc to a moderately preserved stem to a poorly preserved petalodium that passes upward into the overlying turbidite (Fig. 4.4).

Primocandelabrum is a core taxon of the deep-water Avalon assemblage, and has previously been reported from the Bonavista and Avalon peninsulas of Newfoundland (Hofmann et al., 2008) and from Charnwood Forest in England (Wilby et al., 2011).

IMPLICATIONS FOR THE EVOLUTION OF EDIACARAN LIFE IN THE DEEP SEA

Reconstructing the ecosystem represented by the fossils and strata of the June beds requires integration of the sedimentary structures (Fig. 3), Ediacaran fossils preserved on turbidite soles (Fig. 4), and Ediacaran fossils preserved intrastratally within beds of contourite or turbidite sandstone (Figs. 5, 6). Two end-member views are possible—the flat muddy surface after a turbidite or during intervals with only weak development of a contour current, or the more dynamic rippled sandy contourites

that are reconstructed in Figure 7. The ripple marks and oriented fronds reflect the presence of a north-west flowing contour current that was commonly in the hydraulic regime for ripple formation (Dalrymple and Narbonne, 1996). The taxonomy, size, and spacing of the Ediacaran organisms on this deep-sea floor reflect the fossils found on the surfaces and within the sandstone beds. Further details are available in the figure caption.

The fossils of the June beds are broadly similar in age to those of Avalonian Newfoundland and England (Macdonald et al., 2013), and these assemblages collectively record the early evolution of large, complex eukaryotes after three billion years of mostly microbial evolution. With the exception of *Namalia*, a new discovery that represents a significant extension to the previously known range of the erniettomorphs, all of the newly discovered taxa from the June beds (*Beothukis*, *Charnia*, *Charniodiscus*, *Fractofusus*, and *Primocandelabrum*) are shared with Mistaken Point. This implies that the June beds at Sekwi Brook should be considered a core occurrence of the Avalon Assemblage, previously described from the Avalon and Bonavista peninsulas of Avalonian Newfoundland and Charn-wood Forest of Avalonian England.

Statistical analyses of Ediacaran fossil occurrences worldwide have revealed three distinctive assemblages, typically termed the Avalon, White Sea, and Nama assemblages (Waggoner, 2003; Shen et al., 2008). These assemblages were originally regarded as reflecting biogeograhy (Waggoner, 1999), but the presence of *Fractofusus* (formerly known only from Avalonia) and *Namalia* (formerly known only from Namibia) in these deep-water strata adjacent to Laurentia confirms that many elements of the Ediacara biota were globally distributed (Waggoner, 2003; Narbonne, 2005; Shen et al., 2008; Laflamme et al., 2013). There has been considerable discussion of the factors that may have caused these distinct assemblages, with a majority of the controversy focusing on the relative importance of age versus environmental controls (Waggoner, 2003; Grazhdankin, 2004; Narbonne, 2005; Shen et al., 2008; Grazhdankin et al., 2008; Gehling and Droser, 2013). The fossil assemblage herein described from the June beds suggests that these two factors may, in fact, be intimately inter-related. Ediacaran fossil assemblages in Newfoundland, Charnwood Forest, and Sekwi Brook are either directly or indirectly dated at approximately 580–560 Ma (Narbonne et al. 2012; Macdonald et al., 2013) and represent strata deposited in oceanic slope and basin plain environments that were considerably below both storm wave-base and the base of the euphotic zone (Misra, 1971; Benus, 1988; Aitken, 1989; Dalrymple and Narbonne, 1996; Carney, 1999; Wood et al., 2001; Ichaso et al., 2007; Mason et al., 2013). This combination of being both the oldest and the deepest-water assemblage of the Ediacara biota known anywhere resulted in the unique biology of the core Avalon assemblage.

The newly described fossils from the June beds in NW Canada also provide constraints on the ecological evolution of biological complexity. The Ediacara biota was formerly treated as a single taxonomic entity, with different authors suggesting affinities of the Ediacara biota with primitive animals, or vendobionts, or protists, or lichens (see reviews in Narbonne, 2005; Xiao and Laflamme, 2009; Erwin et al., 2011), but modern syntheses are increasingly regarding it as representing a mixture of separate clades united mainly in their Ediacaran age and their soft-bodied construction (Narbonne, 2011; Laflamme et al., 2013). An analysis of the composition, temporal constraints, and environmental distribution of the Ediacaran biota worldwide implies that these distinct clades of early
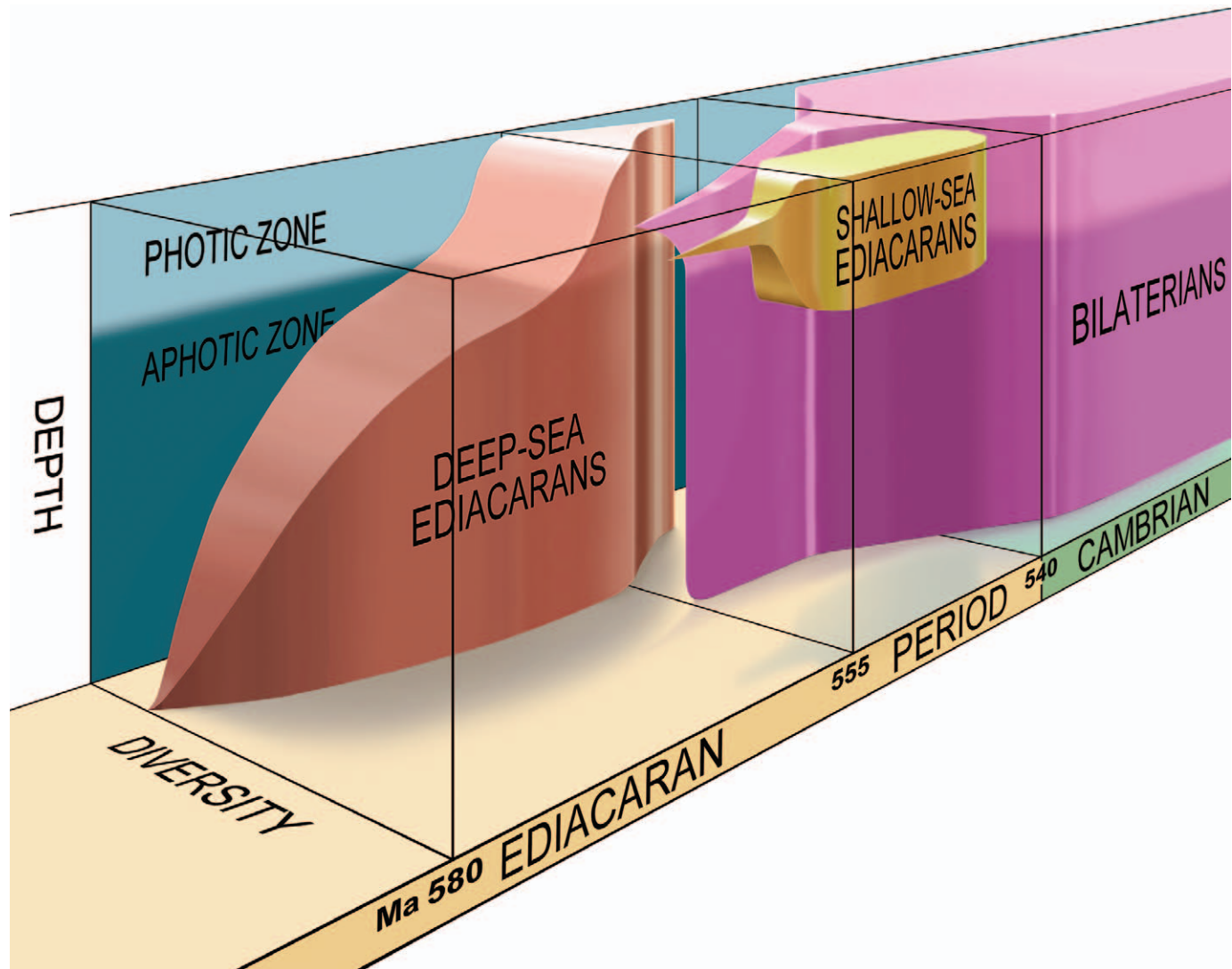
Figure 8—Ecological context of the Ediacaran evolution of complex multicellularity. Deep-water Ediacarans (rangeomorphs and arboreomorphs) appeared abundantly in deep-water environments approximately 580 Ma and had spread into shallow-water environments prior to their late Ediacaran disappearance. Shallow-sea Ediacarans (dickinsoniomorphs, kimberellomorphs, and clades showing bilateral and tetraradial symmetry) lived in shallow-water environments from their first known appearance 555 Ma until their late Ediacaran disappearance. Bilaterian burrows occur abundantly in both deep- and shallow-water settings from approximately 555 Ma until the present day.

complex multicellular life arose in different environments at different times during the Ediacaran Period (Fig. 8). The ecological and temporal distributions shown in this figure reflect modern methods in process sedimentology and are consistent with all known Ediacaran radiometric dates and chemostratigraphic correlations worldwide. However, some Ediacaran successions have not yet been constrained geochronologically, and the distributional patterns herein presented will be subject to continual testing and refinement as new radiometric dates and new fossil discoveries are reported.

With this caveat in mind, the congruence of an old age and a deep-water environment in all known occurrences of the core Avalon assemblage implies that at least two key clades of early large and complex eukaryotes, rangeomorphs and arboreomorphs, may have arisen in deep-water Ediacaran environments (Fig. 8). These two clades are also known from younger assemblages in both deep-water (e.g., Khatyspyt Formation of Siberia; Grazhdankin et al., 2008) and shallower-water environments (Grazhdankin, 2004; Vickers-Rich et al., 2013;

Gehling and Droser, 2013). These later assemblages are grouped with the Avalon assemblage by some authors (e.g., Grazhdankin et al., 2008), but rangeomorph abundance and diversity is significantly decreased and other taxa not known from the core Avalon assemblage occur in association with these later assemblages. This distribution is consistent with the model that rangeomorphs and arboreomorphs originated in deep-water environments soon after the widespread oxidation of the deep sea and migrated into shallow-water habitats later in the Ediacaran. The relative scarcity of rangeomorphs from strata that postdate 555 Ma, even from moderately deep-water occurrences such as the Khatyspyt Formation of Siberia (Grazhdankin et al., 2008), Blueflower Formation at Sekwi Brook in NW Canada (Narbonne and Aitken, 1990), and Miette Group of SW Canada (Hofmann and Mountjoy, 2010), implies a gradual reduction in the importance of rangeomorphs throughout the latter part of the Ediacaran until their extinction near the end of this period (Laflamme et al., 2013).

In contrast with the diverse rangeomorph communities reported from deep-water environments in Newfoundland, England, and NW Canada, the oldest-known occurrence of Ediacaran clades characteristic of shallow-water environments (e.g., dickinsoniomorphs, kimberellomorphs, and clades showing bilateral and tetraradial symmetry) is about 555 Ma (Fig. 8; Xiao and Laflamme, 2009; Narbonne et al., 2012; Laflamme et al., 2013). It seems unlikely that their earlier apparent absence represents a global taphonomic exclusion since unfossiliferous shallow-water (or at least cratonic) strata of this age are interpreted to occur in Australia, China, Oman, and probably elsewhere (Macdonald et al., 2013, fig. 13), and thus the apparent absence of typical shallow-water Ediacaran assemblages and clades of this age is most consistent with their evolution in shallow-water environments at about 555 Ma (Fig. 8). These iconic shallow-water Ediacaran taxa are strikingly absent from the early and deep-water Avalon assemblage of the Ediacara biota in England, Newfoundland, and NW Canada, and from Cambrian deposits including fossil Lagerstätten (Narbonne, 2005; Laflamme et al., 2013), and appear to have been strictly restricted to shallow-water environments from the time of their first appearance approximately 555 Ma until their disappearance near the end of the Ediacaran.

A third pattern is shown by infaunal burrows attributed to bilaterian animals (Fig. 8), which are abundant in both deep- and shallow-water Ediacaran assemblages younger than about 555 Ma and occur abundantly in these facies throughout the Phanerozoic (Seilacher et al., 2005). Bilaterian burrows have been reported from shallow-water strata in Uruguay that may be as old as 585 Ma (Pecoits et al., 2012, 2013) but the Ediacaran age of these fossils is controversial (Gaucher et al., 2013). Bilaterian burrows are absent or exceedingly rare from the older and deeper-water Avalon assemblage and from age-equivalent shallow-water facies of this age anywhere (Jensen, 2003; Droser et al., 2005; Liu et al., 2010), despite the presence of facies that are ideal for their preservation (Fig. 4). This pattern is exemplified by the deep-water succession at Sekwi Brook, in which the June beds contain only sessile Ediacara-type body fossils whereas the younger Blueflower Formation contains both Ediacara-type body fossils and diverse trace fossils (Narbonne and Aitken, 1990; Carbone and Narbonne, 2014).

Taphonomic factors also profoundly affected the composition of the Avalon assemblage in local stratigraphic sections. Flinders-style preservation (Narbonne, 2005) under the thick cyanobacterial mats that preserved diverse assemblages in shallow-water deposits of Australia and the White Sea (Gehling, 1999; Gehling et al., 2005; Darroch et al., 2012) is absent since these mats could not exist in the aphotic deep-sea environments of the Avalon Assemblage. Instead, the combination of turbidite event sedimentation and the presence of a thin mat of non-photosynthetic microbes led to Fermeuse-style preservation, which selectively preserved the semi-infaunal holdfasts of fronds (Gehling et al., 2000; Narbonne, 2005; Laflamme et al., 2011) to produce low diversity assemblages dominated by discoid form genera such as *Aspidella* and *Hiemalora* (Narbonne et al., 1990; Farmer et al., 1992; Gehing et al., 2000; Narbonne, 2005). It is instructive to note that deep-water turbidite formations dominated by discs, such as the Trepassey and Fermeuse formations of Newfoundland and the June beds of NW Canada, locally preserve complex and diverse fossils under the few beds of volcanic ash (Mason et al., 2013) or intrastratally within sandstone beds (this study) that punctuate these turbidite successions, implying that the apparent low diversity of these Ediacaran turbidites reflects taphonomic rather than ecological factors. Conception-style preservation under volcanic ash beds (Seilacher, 1992; Narbonne, 2005) and Nama-style preservation intrastratally within turbidites and contourites (Narbonne, 2005; Narbonne et al., 2009; this study) preferentially preserved surficial and erect organisms living on the sea floor, leading to spectacular assemblages of Ediacaran life such as those at Mistaken Point and Charnwood Forest, and providing critical windows into the paleobiology of Ediacaran deep-sea environments.

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