Spindle-shaped Ediacara fossils from the Mistaken Point assemblage, Avalon Zone, Newfoundland

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Abstract: The Mistaken Point assemblage of the Ediacara fossils is dominated by rangeomorphs with homologous fractal branching elements. The most distinctive are the fusiform fossils, herein named ***Fractofusus misrai*** n.gen., and n.sp., and ***Fractofusus andersoni*** n.gen., and n.sp. Although endemic to the Newfoundland portion of the Avalonia terrane, they dominated deep sea-floor communities below the photic zone, in the mid-Ediacaran Period (ca. 575–560 Ma). Their biological affinities remain uncertain, but their architecture suggests a phylogenetic position near the base of the Metazoa.

Résumé : L'assemblage de fossiles édiacariens de Mistaken Point est dominé par des rangeomorphes présentant des éléments homologues à embranchement fractal. Les plus distinctifs sont des fossiles fusiformes ici nommés ***Fractofusus misrai*** n.gen. et n.sp. et ***Fractofusus andersoni*** n.gen. et n.sp. Bien qu'ils soient endémiques à la portion terre-neuvienne du terrane d'Avalon, ils dominaient de communautés du fond marin profond sous la zone photique durant la période édiacarienne moyenne (v. 575–560 Ma). Leurs affinités biologiques demeurent incertaines, mais leur architecture laisse croire à une position phylogénétique près de la base des Métazoaires.

[Traduit par la Rédaction]

Introduction

Fossils of the Ediacara biota, best known from the Flinders Ranges in South Australia (Sprigg 1947; 1949), characterize the recently defined Ediacaran Period, the first Precambrian time division to be ratified with a Global Stratotype Section and Point (Knoll et al. 2006). Ediacara-type fossils occur mainly as centimetre- to metre-scale impressions of soft-bodied animals preserved underneath event beds of sandstone or volcanic ash (Narbonne 2005; Gehling et al. 2005). Some Ediacara-type fossils may represent stem groups of modern animal phyla (Gehling 1987, 1988; Conway Morris 1993; Gehling and Rigby 1996; Fedonkin and Waggoner 1997; Lin et al. 2006), whereas others appear to represent failed experiments in the early evolution of multicellular life (Seilacher 1992; Buss and Seilacher 1994; Narbonne 2004). The best-known example of the latter group are the rangeomorphs, an extinct high-order taxon characterized by centimetre-scale fractally branching modules in decimetre- to metre-scale frondose, comb-like, or bush-like structures (Jenkins 1985; Narbonne 2004, 2005). The most distinctive, and by far the most common, rangeomorphs in the Mistaken Point assemblage are fossils colloquially known as "spindle-shaped fossils." These were the first Ediacaran fossils ever discovered or figured from Mistaken Point (Anderson and Misra 1968) and spindles have been figured in virtually every subsequent paper on the Mistaken Point assemblage. Spindle-shaped fossils are endemic to the Avalon Zone of eastern Newfoundland, and large bedding surfaces throughout the Avalon and the northern Bonavista peninsulas (Fig. 1) are crowded with hundreds to thousands of specimens.

The realization that Ediacara fossils occur well below strata bearing undoubted early Cambrian fossils, established their priority in the record of megascopic life on Earth. The discovery of the Charnwood Forest assemblage of the Ediacara biota in Leicester, England by Roger Mason (Ford 1958) confirmed the likely Precambrian position of these enigmatic fossils (Glaessner and Daily 1959) and stimulated a new phase of global research into the origins of animal life on Earth. Glaessner and Daily (1959) recognized that frondose fossils previously described by Gürich (1933) from southwestern Africa (Namibia) were of equivalent age. The discovery, a decade later, of the Mistaken Point assemblage (Anderson and Misra 1968; Misra 1969) in the Conception Group of southeastern Newfoundland greatly expanded the diversity of forms in the Ediacara biota. In the last 40 years, fossils of the Ediacara biota have been discovered on all continents except Antarctica.

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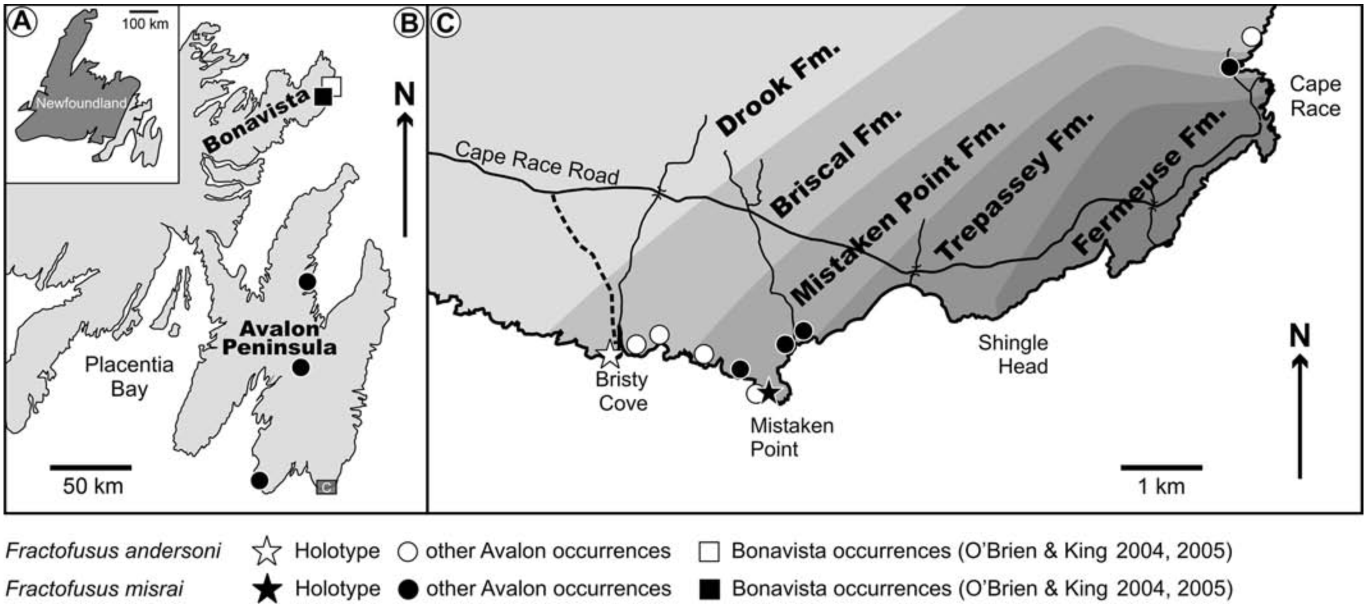
Fig. 1. Type localities and sources of *Fractofusus* n.gen. on the Avalon Peninsula and Bonavista Peninsula, in eastern Newfoundland.



The purpose of this paper is to describe and name the spindle-shaped rangeomorph fossils from eastern Newfoundland.

Mistaken Point assemblage

The Mistaken Point assemblage of the Ediacara biota from southeastern Newfoundland have been described in general terms by Anderson and Misra (1968), Anderson (1978), Hofmann (1971), Anderson and Conway Morris (1982), Landing et al. (1988), Conway Morris (1989), Narbonne et al. (2001) and Narbonne et al. (2005). The formally described taxa from the Conception and St John's groups (Fig. 2) are *Aspidella terranovica* Billings, 1872, *Triforillonia costellae* Gehling, Narbonne, and Anderson, 2001, *Charnia wardi* Narbonne and Gehling, 2003, *Charniodiscus procerus* Laflamme et al., 2004, *Charniodiscus spinosus* Laflamme et al., 2004, and *Thectardis avalonensis* Clapham et al., 2004. Several other taxa formally defined elsewhere have also been recognized in the Mistaken Point assemblage (e.g., *Charnia masoni* Ford, 1958; *Charniodiscus arboreus* Glaessner, 1959*b*, *Ivesheadia lobata* Boynton and Ford, 1995, *Bradgatia* Boynton and Ford, 1995, and the serial body fossils *Palaeopascichnus delicatus* Palij, 1976, *Neonereites renarius* Fedonkin, 1980, and *Yelovichnus gracilis* Fedonkin, 1985), and numerous other taxa from the Ediacaran of Avalon are thus far known only from informal names such as "spindles", "pectinates", and "dusters" (Narbonne et al. 2005). Most of the organisms consisting of fractal frondlets arranged in various growth patterns lack formal descriptions and names largely because their preservation lacks critical detail that might enable reliable diagnosis. However, fusiform rangeomorphs are exceptions in that they are represented by thousands of specimens preserved in sharp relief with detailed morphology.

Stratigraphy

The Ediacaran (late Neoproterozoic) succession on the Avalon Peninsula of southeast Newfoundland has been subdivided into the Conception, St. John's, and Signal Hill groups by Williams and King (1979). The Conception Group resting unconformably on the Harbour Main Group volcanic complex (>608 Ma; Krogh et al. 1988) has been divided into five formations of volcanigenic sediment (Fig. 2) deposited in what is interpreted as a tectonically active deep-water basin, perhaps in an intra- and (or) back-arc setting (Gardner and Hiscott 1988; Dec et al. 1992; Myrow 1995; Wood et al. 2003; Ichaso et al. 2007).). Structural studies of age-equivalent strata in New Brunswick, Nova Scotia, and Great Britain infer the existence of contemporaneous strike-slip motion induced by oblique subduction (Gibbon and Horak 1996; Murphy et al. 1999; Nance et al. 2002).

The Gaskiers Formation of glacial diamictite separates turbidites of the Mall Bay Formation below and the Drook Formation above (Williams and King 1979). This glacial event was short lived judging by the reported age of 580 ± 1 Ma for ash beds immediately above and below (Bowring et al. 2002). The oldest known Ediacara fossils, *Charnia wardi*, *Charnia* sp., *Ivesheadia* sp., and *Thectardis avalonensis*, occur in the upper part of the Drook Formation (Narbonne and Gehling 2003; Clapham et al. 2003) just below an ash bed dated at 575 ± 1 Ma (Bowring et al. 2002). Fossiliferous horizons increase in frequency and diversity up section through the Briscal and Mistaken Point formations. One of the richest fossil-bearing surfaces, referred to as "surface E" in the Mistaken Point Formation (Landing et al. 1988; Clapham et al. 2003), was mantled by a crystal-bearing tuff dated at 565 ± 3 Ma (Dunning, in Benus 1988). On the Avalon Peninsula, fossils of the Mistaken Point assemblage occur only sporadically in the overlying Trepassey and Fermeuse formations of the St. John's Group and the assemblage is replaced by a Fermeuse assemblage dominated by

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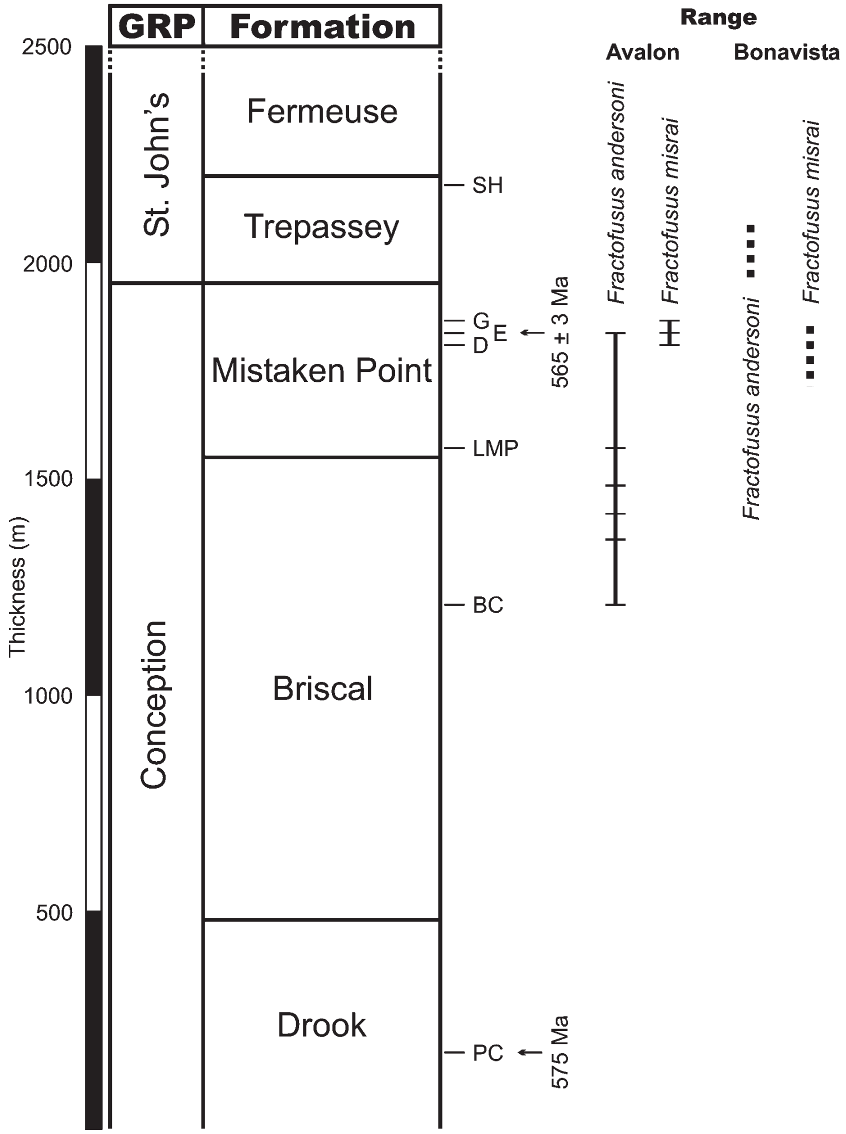
Fig. 2. Stratigraphy of the Ediacaran Avalon succession of eastern Newfoundland. U–Pb ages on zircons from Dunning in Benus (1988), Bowring et al. (2002). Stratigraphic ranges of *Fractofusus* species on the Avalon Peninsula compared with published ranges for the Bonavista Peninsula (Hofmann et al. 2005). Avalon Peninsula fossiliferous horizons: SH, Shingle Head; D, E, G, Mistaken Point beds; LMP, lower Mistaken Point; BC, Brista Cove; PC, Pigeon Cove. GRP, Group.



the simple disc *Aspidella* (Gehling et al. 2000), probably because of the relatively finer grained nature and scarcity of volcanic ash beds in the St. John's Group (Narbonne 2005). However, the St. John's Group is coarser with many more ashes on the nearby Bonavista Peninsula, where typical Mistaken Point fossils including spindles are reported throughout the Conception and St. John's groups (O'Brien and King 2004*a*, 2004*b*, 2005; Hofmann et al. 2005; O'Brien et al. 2006).

Stratigraphic range of *Fractofusus*

On the Avalon Peninsula, *Fractofusus* n.gen. ranges from the midpoint of the Briscal Formation to near the top of the Mistaken Point Formation. Two forms are present at different stratigraphic levels within this succession in the Mistaken Point – Cape Race syncline (Fig. 2). The elongate form, *Fractofusus misrai* n.gen., and n.sp., is not known from the Briscal or lower Mistaken Point formations but occurs in enormous numbers on the surfaces D and E (see Landing et al. 1988, fig. 10) near the top of the Mistaken Point Formation, both at Mistaken Point and elsewhere in the Avalon Peninsula (Fig. 1). In contrast, small specimens of the ovate form, *Fractofusus andersoni* n.gen., and n.sp., occur on numerous surfaces from the middle Briscal Formation to low in the Mistaken Point Formation, with a single specimen also present on surface E near the top of the Mistaken Point Formation.

New discoveries on the Bonavista Peninsula (O'Brien and King 2004*a*, 2004*b*, 2005; Hofmann et al. 2005; O'Brien et al. 2006) provide a critical test of this apparent zonation of *Fractofusus* species from the Avalon Peninsula. The Briscal

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Formation is absent from the Bonavista Peninsula and, as on the Avalon Peninsula, spindles indistinguishable from *F. misrai* occur in the Mistaken Point Formation (O'Brien and King 2004*b*, fig. 3*g* and pl. 4*c*). However, the overlying Trepassey Formation on Bonavista Peninsula contains abundant spindles (O'Brien et al. 2004*b*, pl. 3) that are indistinguishable from *F. andersoni*. Detailed U–Pb dating of the abundant ashes in both the Avalon and Bonavista successions is necessary to work out precise time relationships of the stratigraphic units and to assess any possible diachroneity. Nevertheless, the apparent reversal of biostratigraphy between these two areas implies that the succession of *Fractofusus* species in Avalon does not reflect a simple evolutionary succession. Since there is no evidence of down-slope transport of organisms in the Mistaken Point assemblage, it is possible that the stratigraphic distribution of *Fractofusus* species was a product of ecological partitioning in differing benthic environments. The Trepassey Formation is considered to represented unstable slope sediment that prograded over the slope-toe deposits of the Mistaken Point Formation (Wood et al. 2003). The underlying Briscal Formation accumulated on the basin floor (Myrow 1995). Thus *F. misrai* may have preferred the slope-toe environment represented by the Mistaken Point Formation, and *F. andersoni* the less stable environments higher up the slope and lower down on the basin floor.

Field locations and specimens

Fractofusus is known from strata of the Conception Group on the Avalon Peninsula and has recently been reported from the Conception and St. John's groups on the Bonavista Peninsula (Fig. 1). These strata are generally unsuited to collection of complete fossil specimens because of the cleavage, jointing, and lack of general bed partings. The regional deformation and welded volcaniclastic sediment prevent the rock from easily splitting along bedding, except where a volcanic ash bed has produced a natural parting.

Fractofusus specimens from all localities in Fig. 1 were photographed, and the best preserved were molded using latex rubber. Observations concentrated on the more than 3000 field specimens preserved on significant fossil census surfaces from the Mistaken Point and Briscal formations identified in Clapham et al. (2003). Biometric measurements were made from the latex rubber molds held in the department of Geological Sciences and Geological Engineering at Queen's University, Kingston Ontario. Actual specimens collected in the late 1960s and 1970s from three stratigraphic levels in the Bristy Cove – Mistaken Point area were also studied in detail. Designation of this area as an Ecological Reserve and as a candidate United Nations Educational, Scientific, and Cultural Organization (UNESCO) World Heritage Site provides protection for this site and precludes further collecting of specimens.

The type locality for *Fractofusus misrai* n.gen., and n.sp. is Mistaken Point, from the designated surface E in the upper part of the Mistaken Point Formation 150 m west of Mistaken Point (see Landing et al. 1988, fig. 10; Clapham et al. 2003). The holotype of *F. misrai* (ROM 36502) was collected by D. Collins and M.M. Anderson. This specimen is supplemented by 37 specimens on 33 slabs collected earlier and subsequently acquired by the Royal Ontario Museum. Two moderately preserved specimens of *F. misrai* on a single, weathered, loose slab were collected by M.M. Anderson and are lodged in the Newfoundland Museum (NFM 207A–207B) in St. John's. Judging from the surface texture and colour, the slab was apparently once part of "D surface" at Mistaken Point (Landing et al. 1988, Clapham et al. 2003).

The holotype of *Fractofusus andersoni* n.gen., and n.sp. (ROM 38636) and 21 additional specimens on nine slabs were collected from the upper Briscal Formation about 3 km west of Mistaken Point (locality "BC" of Clapham et al. 2003) by D. Collins and M.M. Anderson and are in the repository of the Royal Ontario Museum. Biometric measurements were obtained for four additional field specimens of *F. misrai* from the Trepassey Formation on the Bonavista Peninsula (H.J. Hofmann, personal communication, 2006).

Taphonomy

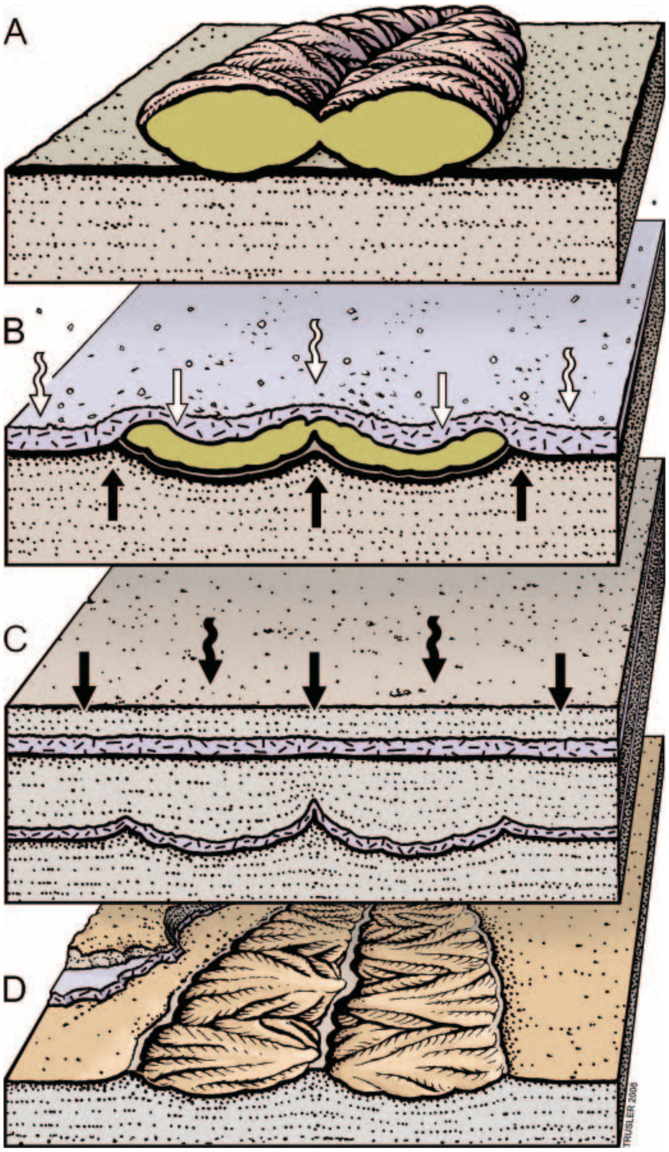
Fossils of the Mistaken Point assemblage are preserved as external molds and casts on the tops of fine-grained volcaniclastic siltstone beds beneath beds of volcanic ash (Narbonne et al. 2001, 2005; Narbonne 2005). The richly fossiliferous surfaces appear to have been preserved by volcanic ash falls. Ash-bearing turbidites floored organisms that had stood erect in life and smothered benthic reclining organisms. The resultant layers of tuff consisted of a few millimetres of coarse crystals below fine ash beds that varied from <1 to 300 mm thick.

F. misrai is preserved in negative epirelief in silicified silty-mudstone, overlain by relatively coarse crystal-bearing volcanic ash. The distinctive, fractally branched modules are preserved as concave impressions (negative relief). The midline, gaps between modules, and outer margins, are positive ridges that may even extend above the bed surface (Fig. 3). Where other Mistaken Point taxa are also preserved on the same surface, *Fractofusus* consistently exhibits the deepest impressions and the highest fidelity of preservation, implying that *Fractofusus* was a benthic recliner whose basal surface was in contact with the sea floor, while most other forms were erect until floored by the ash flow that preserved them and permitted a bed parting. Preservation of the spindles contrasts with the resilient stalks of frond-shaped organisms. Fronds remained resistant until after the overlying ash had hardened, producing an external mold of the stalk and a composite mold of the frond and discoidal holdfast. Being less resilient, spindles collapsed before the ash hardened. The distinctive negative epireliefs observed are external molds of the basal surface of *Fractofusus* (Seilacher 1992).

Some fossil-bearing surfaces are stained red-brown. The observation of actively weathering pyrite on the more recently exposed of these beds suggests that the red stain is limonite after pyrite (see Gehling et al. 2005). The leather-like pattern and pyrite appear to be the textural and mineral products of microbial mats and bacterial reduction of iron beneath the ash cover — a product of the formation of "death-masks" that aided the molding of both the mat and the organisms that lived above the mat (Gehling 1999; Narbonne 2005).

Ash deposits have also influenced the quality of preservation. On surfaces with a crystal tuff at the base of the ash deposit, such as surface E at Mistaken Point, fossils are preserved

Fig. 3. Diagram showing the preservation of a basal mold of *Fractofusus misrai* n.gen. and n.sp. (A) Sectional view of specimen living on a silty, volcaniclastic substrate. (B) Burial and collapse under volcanic ash. (C) Decay and casting by overlying sediment. (D) Erosion of ash bed exposing a ventral mold on the bedding surface (negative epirelief); natural cast rarely preserved as thin ash bed.



with high, positive epirelief. Where there was little or no crystal tuff, such as on surface D at Mistaken Point, the relief of fossil impressions was less. Those fossiliferous surfaces with the lowest relief molds, such as in the Briscal Formation, correspond with very thin ash laminae.

Examples where specimens of *Fractofusus* occur in contact with other specimens and other taxa can be used to assess the order of placement. Where part of a specimen of *Fractofusus* is preserved within the margins of other body fossil imprints, it is apparent that these body fossils overlay the spindles. The surface of *Fractofusus* in contact with the substrate is almost invariably the best preserved of any of the fossils in the Mistaken Point assemblage, because it was molded by the substrate without intervening ash. Volcanic ash intervened between organisms and the substrate where these had been erect in life but were floored by the turbid flow of ash. Consequently, the impressions of floored organisms are always more blurred than the spindles. Where frondose fossils overlay *Fractofusus*, the basal-surface mold of *Fractofusus* is always most prominent. In most cases, where two specimens of *Fractofusus* overlap, the lowermost specimen is preserved in entirety. Specimens of *Fractofusus* may partially overlap that of an adjacent specimen, but with only very rare exceptions, midlines of *Fractofusus* do not cross each other (Fig. 11). This suggests that the profile of *Fractofusus* inhibited overlap by another specimen. In some examples, *Fractofusus* appears to be overlain by the lobate form, *Ivesheadia* (Fig. 5). However, the diffuse impression of *Ivesheadia* includes a textural pattern of the microbial mat that covers entire fossiliferous substrates, such as surface E. It is, therefore, likely that *Ivesheadia* was preserved below the mat (Peterson et al. 2003; Narbonne et al. 2005), and *Fractofusus* lay in contact with the mat-coated sediment, but above *Ivesheadia*.

The composite impressions of Ediacara organisms preserved on these Conception Group beds also suffered from the effects of structural deformation and weathering of surfaces. Regional tectonic deformation is exhibited in rocks on the southern coast of the Avalon Peninsula by pervasive cleavage and tectonic ripples on bed surfaces resulting from an average of 40% shortening perpendicular to cleavage (Seilacher 1999; Wood et al. 2003). Shortening was estimated by the retrodeformation required to restore elliptical discoidal fossils (frond holdfasts or specimens of *Aspidella*) to circles. An independent check was made by ensuring that retrodeformation of discoidal fossils also resulted in rendering of lateral branches perpendicular, or with similar angle in each vane, to the body axis in *Fractofusus*. All measurements of *Fractofusus* were made after retrodeformation using digital photos of field specimens, collected specimens, and latex casts of fossil surfaces (e.g., Fig. 6). Visual evidence of sinuous patterns of cleavage suggests that this surface was not uniformally shortened, perpendicular to cleavage. Thus application of uniform retrodeformation based on discoidal fossils applied to a large area of latex cast involved about 5% error for spindles that were not very close to a disc. Our study confirms the observation made by Anderson and Conway Morris (1982) that there is no relationship between the measures of length or width and number of modules in naturally occurring specimens of *Fractofusus*. However, plots of length versus width of retrodeformed specimens show clear relationships that distinguish the two species. Unless specifically indicated in the caption, all measurements and photographs in this paper are of retrodeformed specimens.

Axial azimuth plots of 578 specimens *Fractofusus misrai* from surface E at Mistaken Point (including vector means of bent specimens) revealed an apparent unimodal orientation on the bedding surface (Fig. 6A). When azimuths were corrected for 40% shortening perpendicular to cleavage, the rose diagram suggests a random distribution within the limits of measurement error and assumptions of uniform shortening perpendicular to cleavage (Fig. 6B). This lack of orientation of *Fractofusus*, in contrast with the pronounced southeast orientation of fronds on the same surface (Seilacher 1999;

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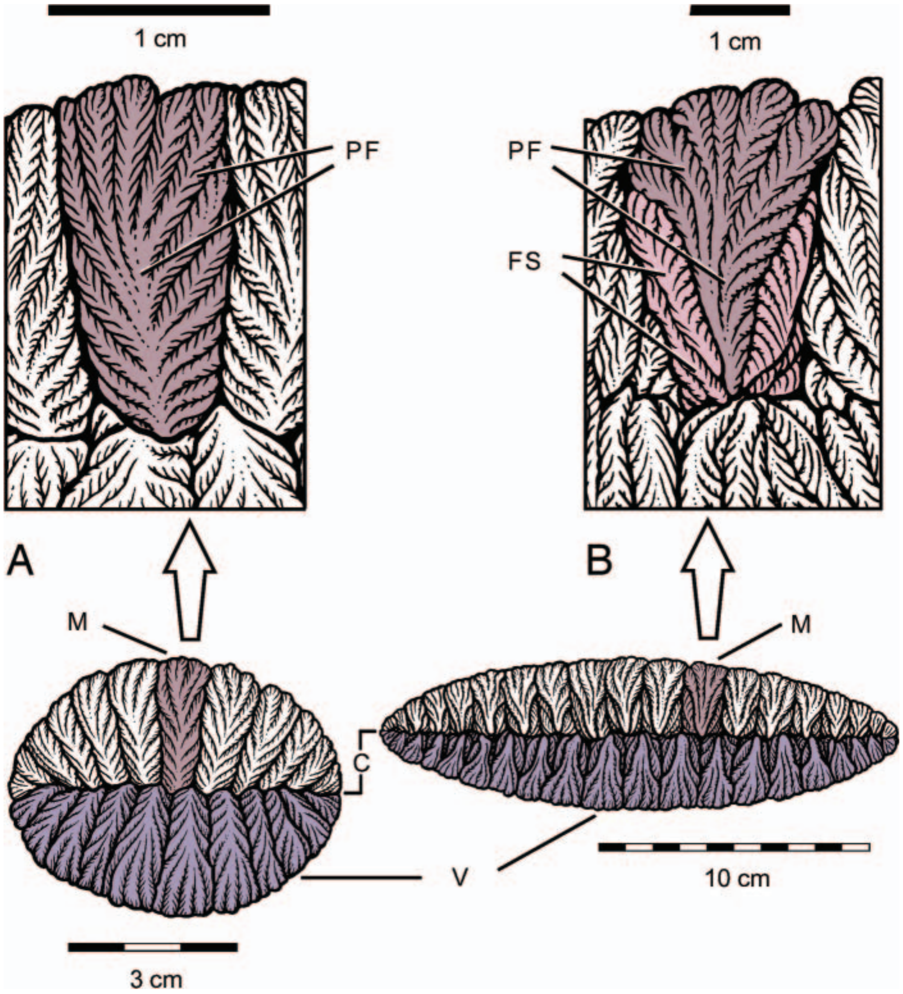
Fig. 4. Labeled sketches of *Fractofusus andersoni* n.gen. and n.sp. (A) and *Fractofusus misrai* n.gen., and n.sp. (B), with enlargements of primary modules and individual frondlets. PF, principal frondlets; SF, subsidiary frondlets; M, module; C, commissure; V, vane.



Wood et al. 2003), demonstrates that *Fractofusus* was not tethered to the substrate.

The fossil surfaces show the sharpest preservation where storms have removed slabs of the overlying strata and the ash beds that produced the partings have most recently been eroded off the substrate. In many of the coastal exposures, fossil impressions are progressively abraded by storm-wave borne pebbles. To prevent enhancement of natural erosion, visitors should be encouraged to remove their abrasive footwear when inspecting fossils, such as those on surfaces D and E at Mistaken Point.

Systematic paleontology

Institutional abbreviations

Specimens are reposited in the collections of the Royal Ontario Museum (ROM) in Toronto, Ontario, and the Newfoundland Museum (NFM) in St. John's, Newfoundland, under the numbers listed. The new taxa are referred to the Rangeomorpha, defined by Pflug (1972) as a class, and considered an order by Jenkins (1985), but potentially of higher taxonomic level (Narbonne 2004, 2005).

Phylum unknown

Class (?) Rangeomorpha Pflug, 1972
Genus **Fractofusus** n.gen.

TYPE SPECIES: *Fractofusus misrai* n.gen., and n.sp.

ETYMOLOGY: Genus name is a compound of the Latin words *fractus* meaning "broken" or "fractured", being the source of "fractal", and *fusus* meaning "spindle".

DIAGNOSIS: A flat-fusiform body consisting of at least two vanes meeting along a straight, to weakly zigzag commissure; each vane consists of serial set of oblong modules extending from the commissure to the outer edge of the vane. Obverse surfaces of each vane apparently identical. Modules decrease in size from the centre to the tips of the vane, and typically show no consistent alternate or opposite arrangement with the modules in the opposite vane. Modules consist of one or more fractal-branching frondlets radiating toward the outer margin but confined and deformed by close-packing with neighboring modules. Frondlets consist of elements that are presumably horn-shaped, widening distally, apparently blind, lacking visible pores of distal openings.

Fractofusus misrai n. gen. and n.sp.
Figs. 4–10.

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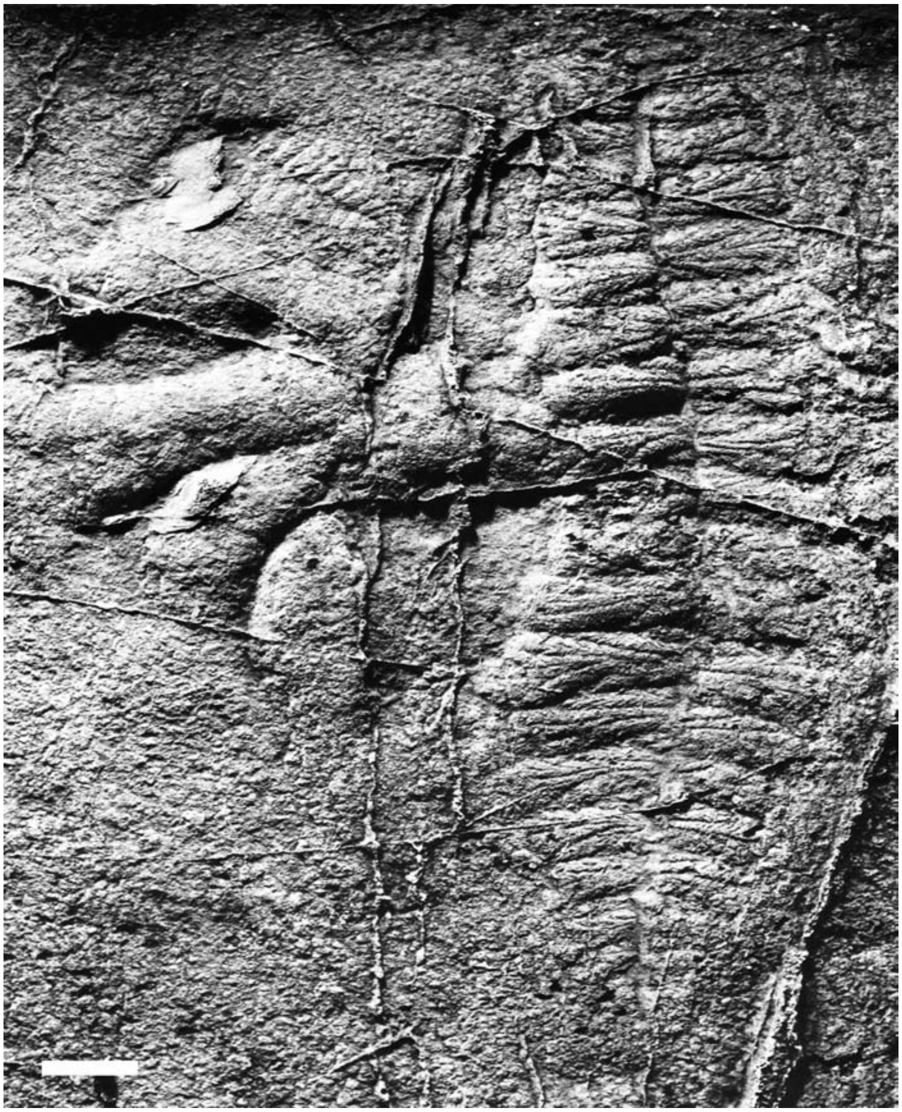
Fig. 5. Latex cast of *Fractofusus misrai* n.gen. and n.sp. overlying a microbial mat coated substrate, with collapsed lobes of *Ivesheadia* below the mat; surface E, Mistaken Point. Scale bar = 1 cm.



SYNONOMY: “fossil form” Anderson and Misra, 1968, p. 681, fig. 3

“spindle-shaped organism” Misra, 1969, pp. 2136–2137, pl. 1B–1E, 2A, 2C, 3A, 3C, 4C, 5A, 5C, 6C, 7B–7D, 8C–8D

“spindle-shaped colonial organisms” Misra, 1971, figs. 1 (partim), 2A (partim), 2B

“Metazoa from Conception Group” Hofmann, 1971, pl. 25, figs. 1, 2

“spindle-shaped form” Anderson, 1978, figs. 2 (partim), 5

“hydrozoan colony” Glaessner, 1979, fig. 3

“spindle-like impressions” Williams and King, 1979, figs. 11 (partim), 12 (partim), 14A, 14F

“spindle-shaped Hydrozoan” Misra, 1981, fig. 2A (partim)

“spindle-shaped form” Anderson and Conway Morris, 1982, pp. 3–7, pl. 1, figs. 5–9

“hydozoan colony” Glaessner, 1984, fig. 2.25

“unnamed forms Newfoundland” Jenkins, 1985, fig. 8 (partim)

“spindle-shaped form” Landing et al., 1988, figs. 9A, 9F

“spindle-shaped form” Hofmann, 1987, fig. 11 (partim)

Seilacher, 1989, fig. 2 (partim)

“spindle organisms” Conway Morris, 1989, figs. 2.4A (partim), 2.4B (partim)

“spindle-shaped form”; Runnegar and Fedonkin, 1992, fig. 7.5.6

“spindle-shaped forms”; Jenkins, 1992, fig. 4 (partim, labeled “B”)

“spindle-shaped form”; Seilacher, 1992, figs. 1 (partim), 2 (partim), 3 (partim)

“spindle-shaped form”; Nowlan and Neuman 1995, fig. 10.2

“Vendofusus”; Seilacher, 1999, fig. 3 (partim)

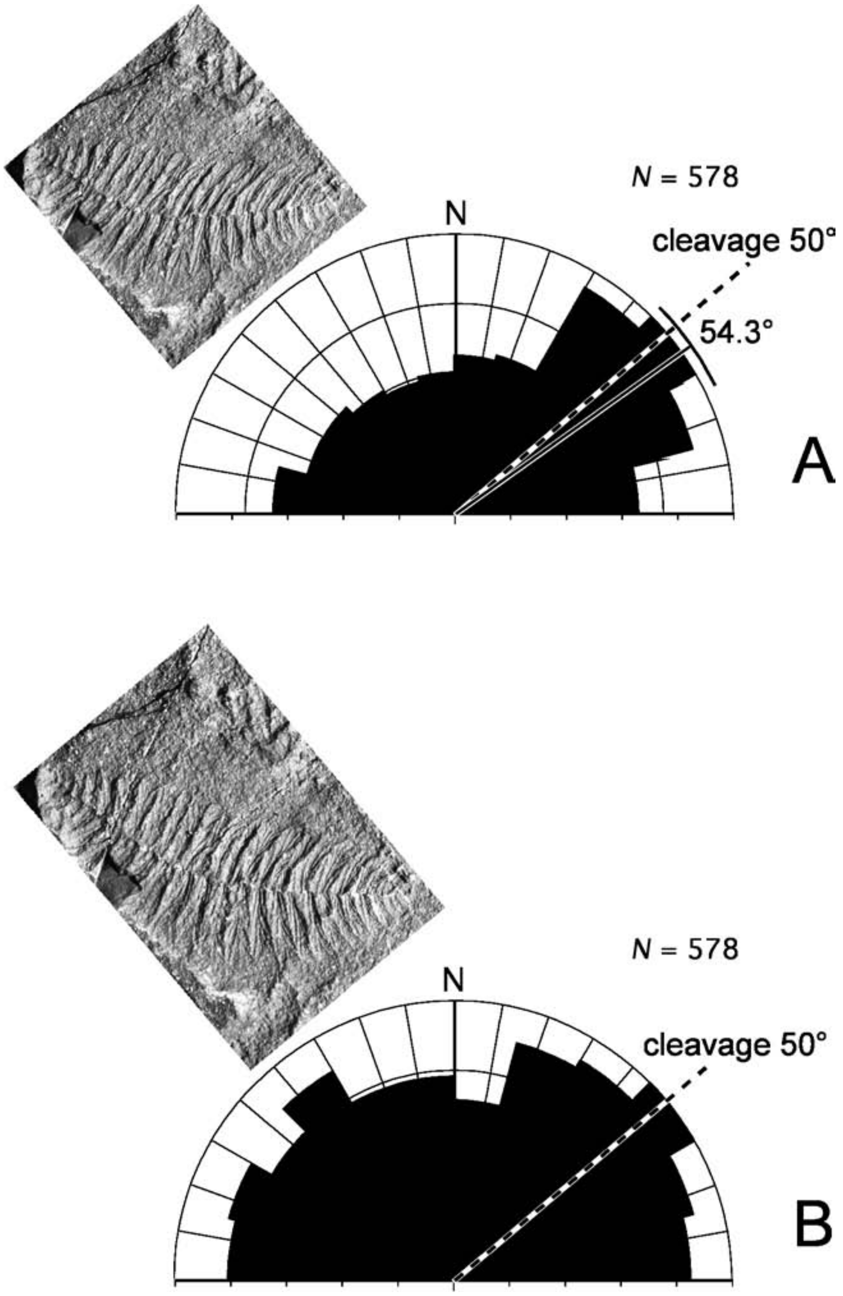
“spindle-shaped form”; Narbonne et al., 2001, p. 31, pl. 1A

“spindle”; Clapham and Narbonne, 2002, fig. 3 (partim, labeled “A”)

“spindle”; Clapham et al., 2003, fig. 8 (partim, labeled “D”)

“spindle-shaped fossils”; Wood et al., 2003, fig. 9 (partim)

Fig. 6. (A) Rose diagram of axial orientations of 578 specimens of *Fractofusus misrai* n.gen. and n.sp. (see photo illustration for example) orientations showing apparent unimodal orientation (vector mean 54.3°) on surface E in the Mistaken Point Formation at Mistaken Point; cleavage direction 40°. (B) Rose diagram of retrodeformed orientations (see photo illustration for example) showing a near random distribution within the limits of measurement error.



"spindle-like form"; O'Brien and King, 2004*a*, pp. 208–209, fig. 3g, pl. 4c

"spindle-shaped rangeomorph"; Narbonne, 2004, fig. 3F

"spindle"; Brasier and Antcliffe, 2004, fig. 1 (partim)

"rangid spindle type 2"; Narbonne et al., 2005, pl. 1C

"spindle-shaped form"; McCall, 2006, pp. 3–7, pl. 1, figs. 66.5–66.9, 68 (partim)

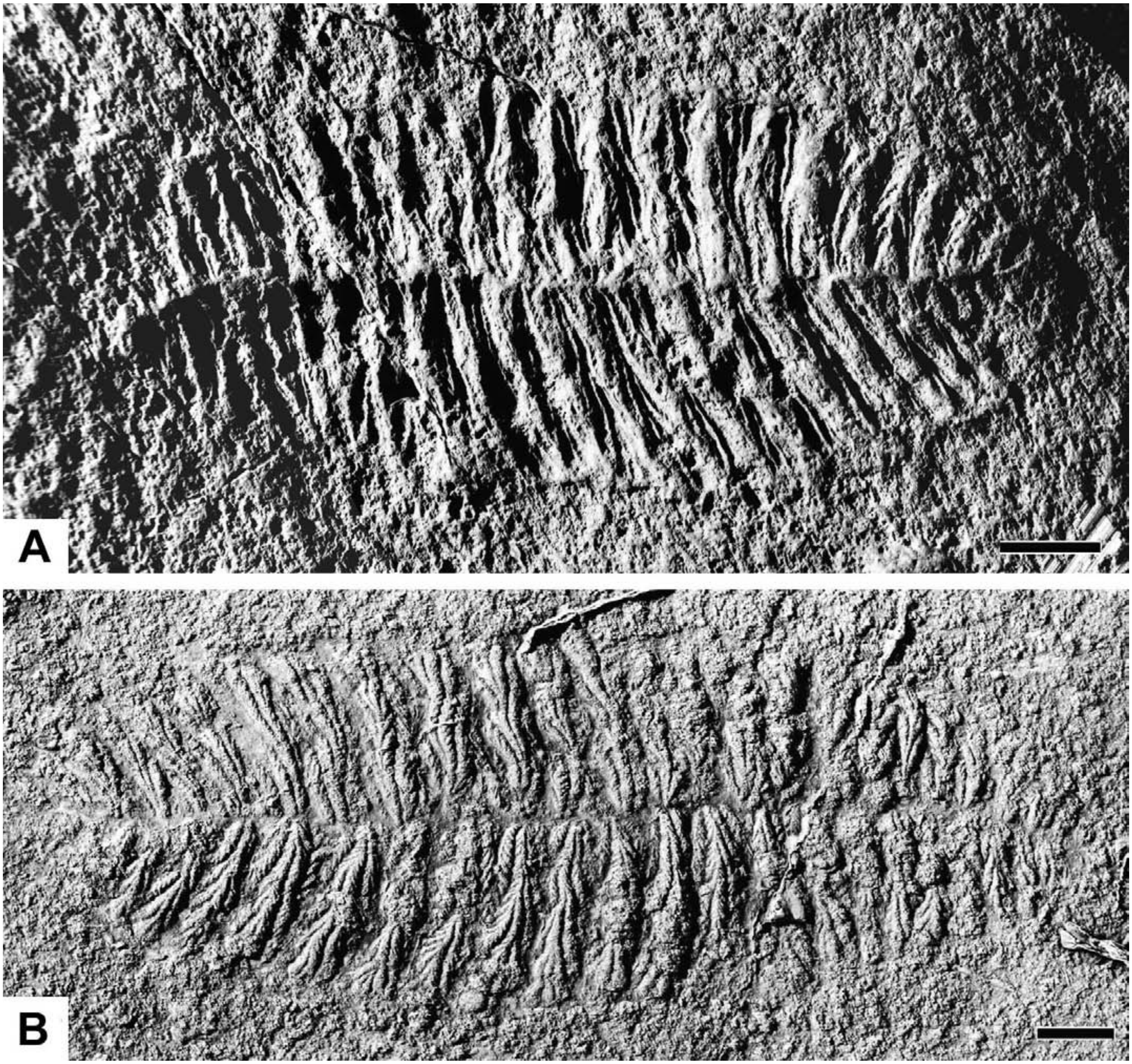
"Charnia (Cnidaria?)"; Lopez-Garcia et al., 2006, fig. 7.12B 'Spindle' rangeomorph"; Bottjer and Clapham, 2006, figs. 3B, 6A

DIAGNOSIS: *Fractofusus* with elongate body; length more than three times width. Vanes constructed from 15 or more modules; adjoining sides of each module nearly parallel-sided, and typically including a central, obovate to triangular principal frondlet, adjoined on both sides by subsidiary frondlets close to the commissure. Distal ends of modules somewhat spatulate.

HOLOTYPE: ROM36502 (Fig. 7)

ETYMOLOGY: For S. B. Misra who, as a graduate student, first drew attention to these fossils at Mistaken Point in 1967.

Fig. 7. (A) Unrestored natural mold of holotype of *Fractofusus misrai* n.gen. and n.sp., ROM 36502; surface E, Mistaken Point Formation, Mistaken Point, Avalon Peninsula, southeastern Newfoundland. (B) Retrodeformed latex cast of holotype. Scale bar = 1 cm.



TYPE SPECIMENS: Holotype ROM 36502 from surface E at Mistaken Point. Paratypes ROM 54357, 57217, 57219, 57220A–57220B, 57221A–57221C, 57222, 57223, 57224A–57224B, 57798–57822 from the type locality and horizon, and NFM 207A–207B from surface D at the same locality. Collection supplemented by more than 100 latexed specimens from the type locality and other localities throughout the Avalon Peninsula (Fig. 1).

DIMENSIONS: Field specimens typically range from 3 to 22 cm long and 1 to 8 cm wide, after retrodeformation; specimens vary from 15–25 modules per vane (Table 1). The single specimen reported from the Mistaken Point Formation in the Bonavista Peninsula (O'Brien and King 2004*a*, fig. 3*g* and pl. 4*c*) falls within this range (19.9 cm long, 4.7 cm wide, and with 20 modules).

DESCRIPTION: *Fractofusus misrai* n.gen., and n.sp. is described mainly from molds of the lower surface in contact with the substrate. Partially folded-over specimens show that obverse sides of vanes are identical (Figs. 8B, 8C), and that no distinguishing ventral-dorsal characteristics are apparent. The vanes are constructed from a bipolar series of oblong modular units, arranged serially on each vane, and decreasing in size

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Table 1. Morphometric measurements for retrodeformed specimens of *F. misrai*.

Specimen No.	*W*/*L* ratio	Length (*L*) (cm)	Width (*W*) (cm)	No. of modules
ROM MP35602	0.34	14.1	4.7	25
***Fractofusus misrai* holotype**				
Bon_MP-1	0.26	19.9	5.1	20
EQ1-09a	0.35	8.9	3.1	17
EQ1-09b	0.35	6.2	2.2	17
EQ1-09c	0.32	6.3	2.0	16
EQ1-09d	0.24	14.2	3.4	22
EQ1-09e	0.39	5.1	2.0	15
EQ5-11/18a	0.38	8.2	3.1	20
EQ5-11/18b	0.34	18.7	6.4	25
EQ5-11/18c	0.38	5.7	2.2	20
EQ5-11/18d	0.29	12.9	3.7	21
EQ6-12_16a	0.32	9.4	3.0	20
EQ6-12_16b	0.28	21.4	6.0	21
EQ6-12_16c	0.27	17.0	4.7	23
EQ6-12_16d	0.37	7.8	2.9	16
EQ6-12_16e	0.27	11.2	3.0	18
EQ6-12_30c	0.26	16.0	4.2	22
EQ8-01_21rh	0.30	22.4	6.7	21
EY-10/2a	0.32	8.2	2.6	17
EY-10/2b	0.28	8.1	2.3	24
EY-10/2c	0.26	13.8	3.6	21
EY-10/2d	0.28	9.4	2.7	17
EQ4-07/32a	0.37	9.5	3.6	21
EQ4-07/32b	0.31	11.0	3.4	22
EQ4-07/32c	0.29	10.0	2.9	23
EQ4-07/32d	0.29	9.6	2.8	20
EQ14-06/23	0.26	21.0	5.6	18
EY12R-07_14a (x2)	0.28	21.0	6.0	20
EY12R-07_14b	0.36	6.8	2.5	23
EY12R-07_14c	0.38	13.3	5.1	23
EY12R-07_14d	0.35	8.1	2.8	21
EY12R-07_14e	0.36	6.6	2.4	18
EY6-06/35a	0.32	20.7	6.6	19
EY6-06/35b	0.38	9.1	3.5	19
EY6-06/35c	0.38	3.8	1.4	18
EY6-06/35d	0.38	7.3	2.7	23
EQ3R-13_4a	0.34	12.8	4.3	24
EQ3R-13_4b	0.28	8.3	2.4	22
EQ3R-13_4a	0.35	15.5	5.4	19
EQ3R-13_4d	0.39	9.6	3.7	20
EQ3R-13_4e	0.33	3.9	1.3	21
EQ3R-13_4f	0.32	5.6	1.8	17
EY8-11_0a	0.36	21.8	7.8	18
EY8-11_0b	0.30	12.1	3.7	18
EY8-11_0c	0.35	14.2	5.0	20
EY8-11_0d	0.29	9.6	2.8	17
EY8-11_0e	0.33	7.2	2.4	20
EY8-11_0f	0.31	11.5	3.6	17
EY8-11_12	0.33	17.3	5.6	21

Table 1 (*concluded*).

Specimen No.	*W*/*L* ratio	Length (*L*) (cm)	Width (*W*) (cm)	No. of modules
EY8-11_3	0.37	16.4	6.2	18
EY7R-03_23a	0.36	3.0	1.08	20
EY7R-03_23b	0.35	18.3	6.45	20
EY7R-03_23c	0.36	11.5	4.13	17
EY7R-03_23d	0.33	14.5	4.84	21
EQ13	0.38	4.0	1.5	22

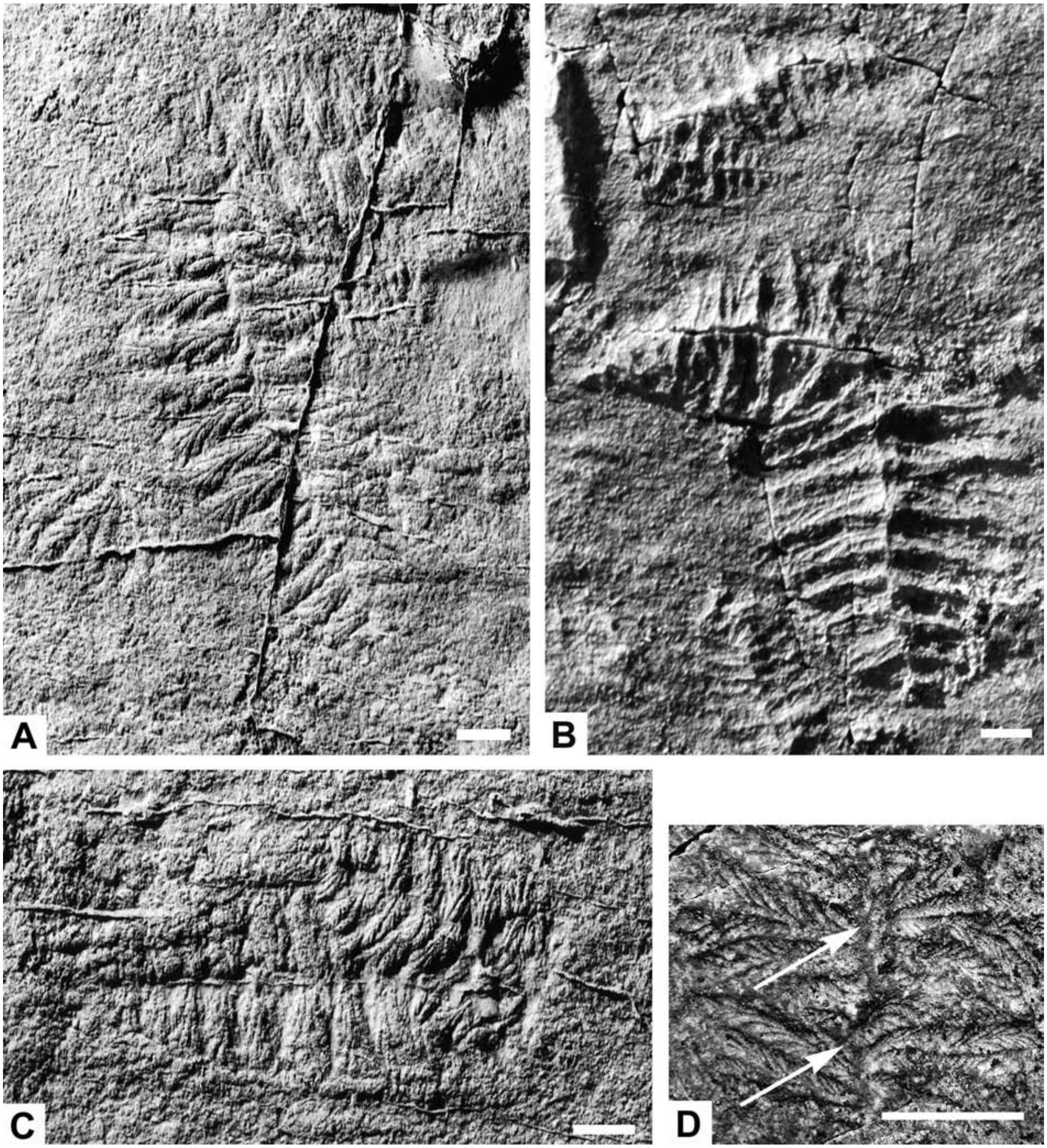
Table 2. Morphometric measurements for retrodeformed specimens of *Fractofusus andersoni*

Specimen No.	*W*/*L* ratio	Length (*L*) (cm)	Width (*W*) (cm)	No. of modules
ROM 38636 R	0.61	4.4	2.7	11
***Fractofusus andersoni* holotype**				
Brist-1a	0.62	2.95	1.84	11
Brist-1b	0.53	2.60	1.40	10
ROM38645a	0.54	3.60	2.00	13
ROM38645b	0.60	2.70	1.70	9
Brista-4	0.54	1.60	0.86	12
ROM74DC34	0.67	2.70	1.80	12
Bon_T-1	0.61	13.00	7.90	13
Bon_T-4	0.75	6.00	4.50	11
Bon_T-2	0.79	5.20	4.10	8+
Bon_T-3	0.73	1.50	1.10	7+

from the mid-point in each vane toward both ends (Figs. 4, 7). Each modular unit consists of a closely packed set of fractally branching frondlets that appear to originate from the commissure. In each frondlet, several orders of branching elements expand and divide toward the outer margin of the vane (Fig. 9). The elements are apparently horn-shaped with blind tips directed inward. Plumose branching within each frondlet produces lateral crowding and rotation of branching elements out of the plane of the vane. On both sides of a vane, each module appears to be convex, consisting of a central, principal frondlet flanked by subsidiary frondlets (Figs. 4B, 8D). Subsidiary frondlets appear asymmetrical.

The gently rounded outer edges of modular units produce a scalloped outer edge to the vanes. Modules juxtaposed across the commissure vary from opposite to alternating positions with no evidence of direct connection across the commissure (Figs. 9, 10). Modules are most convex and in sharpest relief near the centre of each vane and tend to lack definition at the spindle tips as module size decreases. Specimens that are torn when strongly bent in the horizontal plane show a wedge-like gap at module boundaries implying that individual modules were coherent units that are attached strongly to the commissure but not to adjacent modules (Figs. 8A, 8B). Modules opposite the separation gap in bent specimens are laterally compressed, as seen in the lower specimen in Fig. 8B, or overcrossed as seen in Fig. 8A. In contrast, folded specimens, such as that in Fig. 8C and the upper one in Fig. 8B, feature an acute angle in the

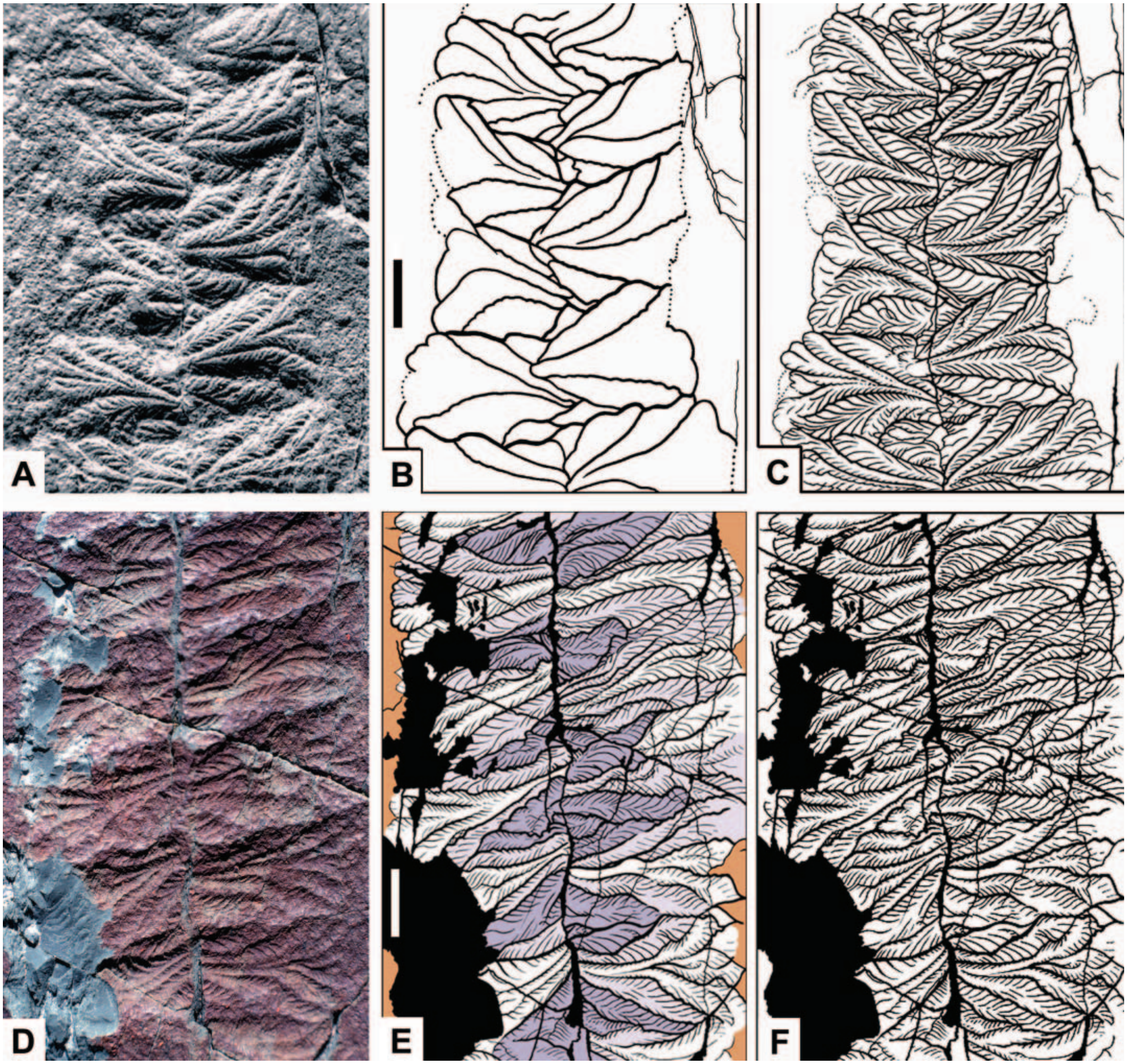
Fig. 8. Structural characteristics of *Fractofusus misrai* n.gen. and n.sp. (retrodeformed) from surface E at Mistaken Point. (A) Separation of modules at 90° bend (latex cast with *Bradgatia* sp. on left side of *F. misrai*). (B) Folded specimen (top); parting of modules at 90° bend in large specimen of *F. misrai*; straight specimen (bottom); natural mold in epirelief (field photograph). (C) Latex cast of asymmetrically folded specimen of *F. misrai*, showing morphology of both sides of a vane preserved as an external mold in the substrate. Note: axial ridge is not a biological structure, but the fill of a crack. (D) Origin of fractal branching at commissure with insertion points of subsidiary frondlets (arrowed) between primary branching sites of principal frondlets; natural mold (field photograph). Scale bars = 1 cm.



commissure and composite molding of some overlapping modules.

DISCUSSION: The origin or bud of each fractal branching array of frondlets is not usually preserved in external molds of either side of a vane. The origin of fractal branching is, therefore, interpreted as being within the commissural surface marking the junction of each pair of vanes along the axis of the spindle (Fig. 4). The commissure is really a projection of a commissural plane onto the natural mold. Growth was apparently nucleated at various levels within the commissural plane to produce both opposite and alternate arrangements of modules along the mold of the axis of a specimen (Figs. 9, 10). A few well-preserved specimens show that growth of the module is achieved by addition of subsidiary frondlets flanking the principal frondlet attach-

Fig. 9. Two unrestored field specimens of *Fractofusus misrai* n.gen., and n.sp. A–C and D–E, from surface E at Mistaken Point. (A) Latex cast of field specimen 1. (B) Outlines of modules and frondlets within each module in A. Scale bar =1 cm. (C) Detailed sketch of A. (D) Field photograph of specimen 2 with conchoidal fracture damage. (E) Shading of subsidiary frondlets in D. Scale bar = 1 cm. (F) Detailed sketch of D.

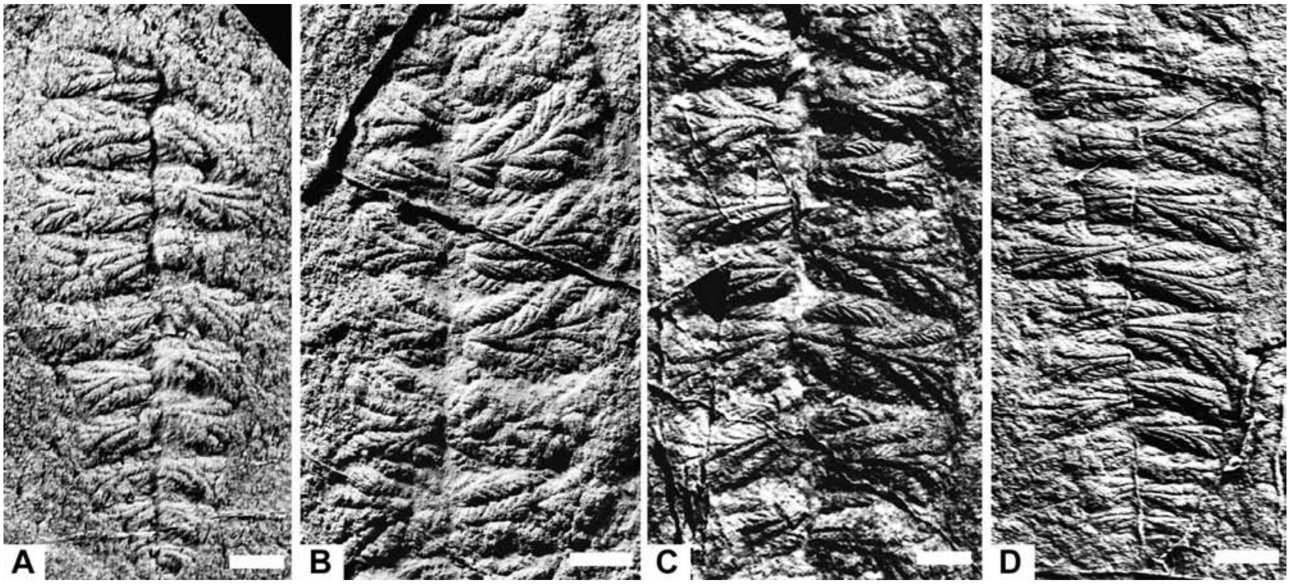


ment site on the commissure (Fig. 8D). In other specimens, compaction of modules against the commissure appears to obscure details of budding.

The lack of well-defined order to the placement of modules implies that their arrangement is a function of growth by subsidiary budding on either side of a principal frondlet. As subsidiary frondlets expanded by fractal division from budding sites during growth, there was a consequent competition for space within the module. The subsidiary frondlets filled the triangular spaces between neighboring principal frondlets in *F. misrai* (Fig. 9). The external molds of these frondlets reveal that the plane of fractal branching of frondlets rotated such that only one side of the frondlet was exposed in subsidiary modules (Figs. 9A–9C). In the most expanded specimens, principal frondlets generally show symmetrical branching. However, in the holotype, some of the principal frondlets are rotated with respect to the plane of the vane (Fig. 7), suggesting that the external frondlet morphology was quite plastic.

The general relationship between size and number of modules in each vane is difficult to determine because of the number of specimens that had to be excluded because the

Fig. 10. Modular configurations in relatively expanded specimens of *Fractofusus misrai* n.gen. and n.sp. Retrodeformed images of latex casts from surface E, Mistaken Point, southeastern Avalon Peninsula. (A) EY12R. (B) EQ8R. (C) EQ2R. (D) EY6R. Scale bars = 1 cm.



small modules on either end of a specimen were too faint to produce consistent counts in both vanes. However, a plot of number of modules vs. length is essentially flat (Fig. 13A), implying that the number of modules was established very early in the growth of a specimen after which size increase involved fractal isometric expansion of modules.

The external mold of folded-over portions of specimens show the same convex, branching elements and modular units (Fig. 8C). Since both sides show near identical impressions, it is apparent that each module is a biconvex, obovate cluster of elements branching fractally from an origin that was within or on either side close to the commissural plane. After retrodeformation, there is considerable variation in the shape of frondlets within modules (Fig. 10). This may represent lateral compaction along the axis of the spindle or just different degrees of inflation of frondlets in modules from one specimen to another. The holotype is one of the most flaccid specimens in that modules appear to be composed of narrow or contracted frondlets where third-order branching elements are not as visible as in other specimens of comparable size and preservation. Module length (measured perpendicular to the spindle commissure or long axis) divided by width (measure parallel to the spindle axis) is greater than in most specimens.

It is apparent that modular units are constructed from cojoined principal and subsidiary frondlets (fractally branching bodies), since specimens bent at right angles in the plane of the vanes show separation at the junctions of modular units (Figs. 8A, 8B), rather than splitting across or within the module. The lack of splaying of the separated modules at the split demonstrates the unity of each module and suggests a single modular-space enclosed by fractal quilting rather than clustering of independently inflated frondlets.

Fractofusus andersoni n.gen. and n.sp.
(Fig. 12)

SYNONOMY: “oval-shaped spindle”; Narbonne et al., 2001, p. 31
“rangid spindle type 1”; Narbonne et al., 2005, pl. 1B
“oblate spindle-like form”; O’Brien and King, 2005, pl. 3

DIAGNOSIS: *Fractofusus* with 13 or fewer modules in each vane; ovate, with length typically less than two times width. Outline of each module expanding slightly from the commissure toward the distal margin of vane. Each module exhibiting a single, principal pinnate frondlet with no evidence of subsidiary frondlets. Modules inclined at <90° to commissure on either side of central module; distal ends straight.

ETYMOLOGY: For Michael Anderson who discovered this species and documented most of the localities of *Fractofusus* on the Avalon Peninsula.

MATERIAL: Holotype ROM 38636 from the Briscal Formation at Bristy Cove. Paratypes ROM 38636, 38638, 38640A–38640B, 38645A–38645E, 38646, 38647, 38648A–38648D, 38649A–38649C, and 38650A–38650B from the type locality and surface, and ROM 57822 from the surface E at Mistaken Point.

DIMENSIONS: Holotype 2.7 cm × 4.4 cm. Specimens vary from 1.5 to 13 cm long and 0.8 to 8 cm wide, after retrodeformation, and with 8–13 modules per vane (Table 2).

DESCRIPTION: *Fractofusus andersoni* n.gen. and n.sp. is known from large numbers of specimens 1–2 cm long, from surfaces that have been either naturally polished or were coated in limonite, and a few higher relief specimens. This oval shaped *Fractofusus* is constructed from modules that show a principal frondlet with primary branching that alternates on either side of a central element (Figs. 4, 12). Elements in the primary branches expand progressively toward the distal end of the frondlet (Fig. 12). As a result, there is a general widening of each module distally from the commissure to the outer edge of the vane. No over-folded specimens of *F. andersoni* are known, presumably because its small size and ovate shape prevented folding; however, it is assumed

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Fig. 11. Sketch of overlapping specimens of *Fractofusus misrai* n.gen. and n.sp. Fan-shaped rangeomorph, *Bradgatia* sp., left centre. Sketch from latex-mold EY7 from surface E, Mistaken Point. Scale bar = 5 cm.

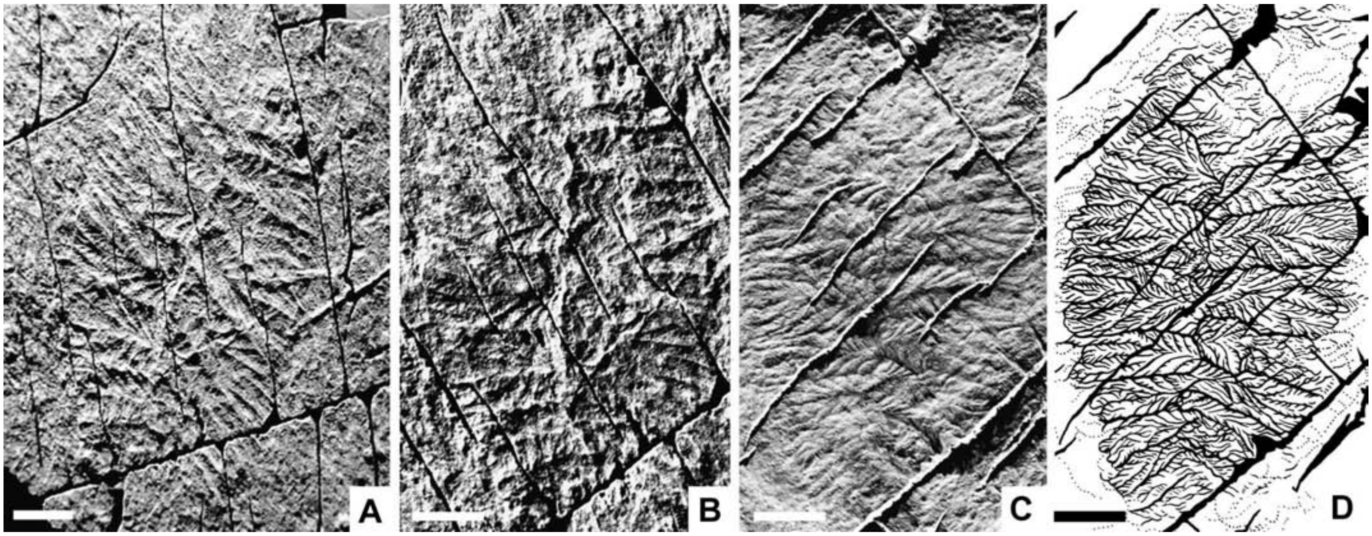
that this species, like *F. misrai,* has identical ventral and dorsal morphology.

Comparisons

After retrodeformation, *F. misrai* and *F. andersoni* differ significantly in shape (Figs. 13B, 13C). The ovoid fusiform shape of *F. andersoni* is a product of widening of each module toward the periphery, and modules in each vane are inclined toward the spindle apices on either side of the central module (Fig. 4A). Conversely, most modules in *F. misrai* are perpendicular to the commissure and do not widen significantly toward the periphery because of insertion of subsidiary frondlets on either side of the principal frondlet (Fig. 4B). Modules show relatively regular second-order branching on each side in *F. andersoni* (Fig. 4A). In *F. misrai*, first-order frondlet branching is plumose, whereas in *F. andersoni* branching is pinnate. Second-order frondlet branches are more elongated in *F. misrai* than in *F. andersoni*. Consequently modules widen away from the commissure in *F. misrai*, resulting in triangular gaps between the modules near the commissure that are filled by subsidiary frondlets. Such subsidiary frondlets appear to be absent in *F. andersoni,* resulting in module sides that taper toward the commissure.

In both species of *Fractofusus*, the number of modules in either vane shows no clear relationship to length (Fig. 13A), and even the smallest specimens of *F. misrai* exhibit more

Fig. 12. (A) *Fractofusus andersoni* n.gen. and n.sp., ROM 38636, original specimen from Briscal Formation, east of Bristy Cove, Mistaken Point Ecological Reserve, Avalon Peninsula, southeastern Newfoundland. (B) Retrodeformed image of natural mold (epirelief) with cleavage and joints. (C) Retrodeformed image of latex cast. (D) Sketch of holotype based on latex mold C. Scale bars = 1 cm.



modules than large specimens of *F. andersoni*. The absence of specimens with sub-adult numbers of modules cannot be taphonomic since features <1 mm are faithfully preserved on the surfaces. More likely, early growth of *Fractofusus* occurred during an unfossilizable embryonic stage of development. This suggests that the number of modules is species specific and was determined early in the ontogeny, with subsequent growth mainly by inflation.

Reconstruction

Reconstruction of the original architecture of *Fractofusus* must take into account the fact that external molds preserve just the surface of the organism in contact with the substrate at the time of burial. Several lines of evidence suggest that the basal surface in contact with the substrate had some considerable relief. The modules produced concavities separated by ridges. These intermodular ridges are connected to a commissural ridge, which in turn is higher than the surrounding bed (Figs. 3C, 3D). Folded specimens of *F. misrai* demonstrate that both sides of vanes were identical, being composed of biconvex modules constructed from fractally branching frondlets (Figs. 8B, 8C). The commissure or long axis in most folded specimens is kinked at an acute angle. However, a few specimens appear to have been folded about the short axis of the spindle, in the same direction as the long axis, resulting in an impression of just one half of a spindle. There are no known specimens where one vane is folded about the long axis, parallel to the commissure, over the other vane, leaving just the mold of a single complete vane. Furthermore, almost all specimens preserved in contact have only the tip of one spindle overlapping part of one vane of another (Fig. 11). A study of specimens in contact on surface E at Mistaken Point (the horizon with the best preserved molds) has shown just two pairs, where one specimen has its axis crossing the axis of the other. It is, therefore, possible that *Fractofusus* had one or more vanes out of the plane of the substrate. Detailed studies of three-dimensionally preserved specimens of *Pteridinium* within sandstone beds in Namibia (Grazhdankin and Seilacher 2002) and Australia (Jenkins 1992) have shown that *Pteridinium* had three vanes. However, specimens preserved in two-dimensions on bedding surfaces in Namibia typically provide no hint of the third vane (Narbonne et al. 1997). The Mistaken Point style of burial is comparable to other bed-surface associations of the Ediacara biota in preserving three-dimensional soft bodies as two-dimensional imprints. Thus a consideration of possible configurations of vanes in *Fractofusus* is important:

(1) A three-vane organism (Fig. 14B) would dictate certain preservational characteristics. Folding would have resulted in an acute angle between the folded portions of the spindle as a result of rotating the uppermost vane so that it came in contact with the substrate, twisting one of the basal vanes into a vertical position. A third vane would have limited crossover of specimens. In cross-section the three vanes would produce stronger relief at the commissure than the two-vane model, and result in the less well-preserved tips of spindles in basal molds, since they would not have been in contact with the substrate in life.

(2) A four-vane model (Fig. 14C) would produce similar basal mold relief, but could only fold directly over the commissure. This condition is less common than acutely folded specimens. It might be expected to produce overprinting and double edges in some molds, neither of which is seen in the Mistaken Point specimens.

Unconstrained experiments with a series of two-, three-, and four-vane paper models on a flat surface in a strong wind, showed that three-vane specimens tended to spin horizontally around a vertical axis at their midpoint but invariably came to rest with their long axis perpendicular to the direction of flow. Four-vane models showed a tendency to rotate around the horizontal body axis and produced no consistent orientation of specimens. Two-vaned models either remained in place, in the boundary layer, or lifted off and

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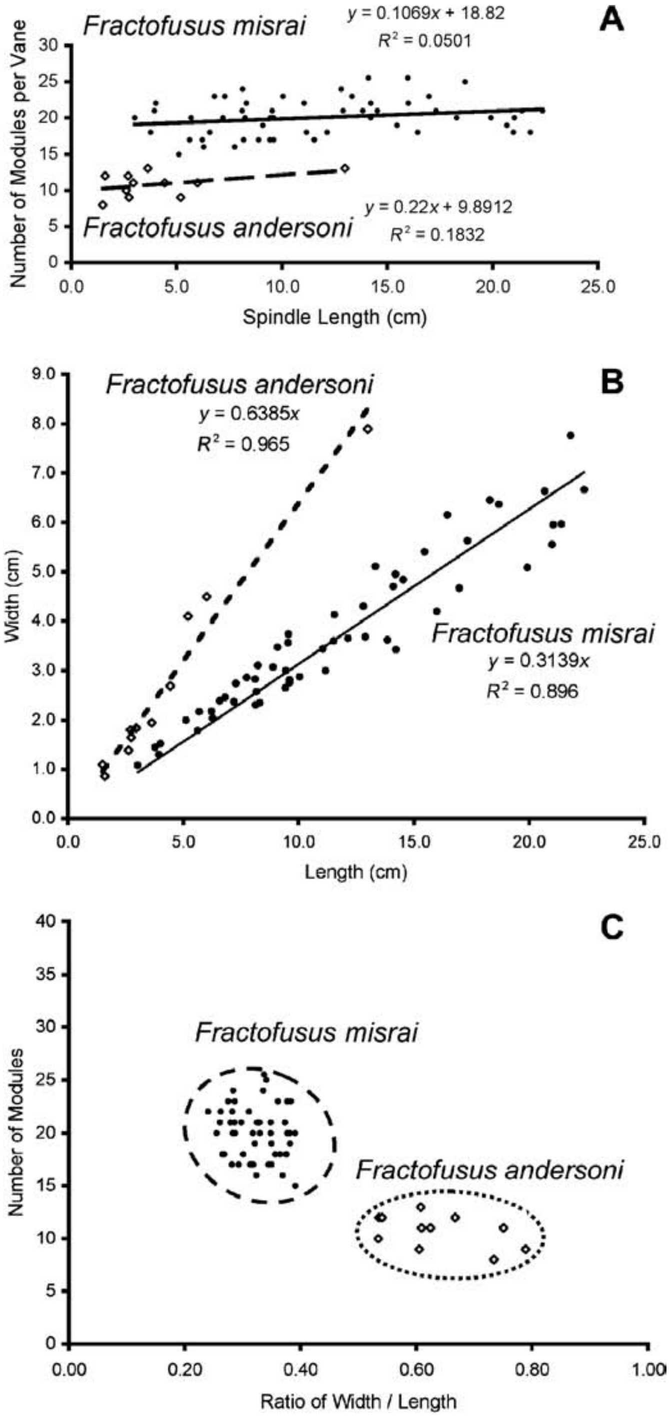
Fig. 13. Biometric data for retrodeformed specimens of *Fractofusus misrai* n.gen. and n.sp. (N = 45) (solid circles) and *Fractofusus andersoni* n.gen. and n.sp. (N = 11) (open diamonds). (A) Number of modules per vane vs. length for both species. (B) Spindle width vs. length for each species. (C) Scatter plots of modules per vane vs. width/length ratio for both species.



were transported off the test surface. The fact that restored orientations of *Fractofusus* on surface E at Mistaken Point showed no preferred orientations (Fig. 6) may falsify the three-vane model. Alternatively the turbulence of ash-transporting currents near the sea floor may not have been able to effect a preferred orientation with any form of untethered benthic organism.

Although these three- and four-vane models have specific aspects that are attractive, neither can be convincingly demonstrated, and Ockham's Razor demands that the simpler reconstruction of a two-vane spindle be considered unless and until further information provides a contradiction. A relatively flat, two-vane spindle consisting of inflated, quilted modules is consistent with the observed characteristics of *Fractofusus*. However, this two-vane model (Fig. 14A) does not immediately suggest a viable mode of life. It is not clear why the morphology of both sides would have been identical if one side was in contact with the substrate in life. Unlike other Ediacara organisms with fractal construction, there is no evidence of attachment to the substrate of an erect lifestyle.

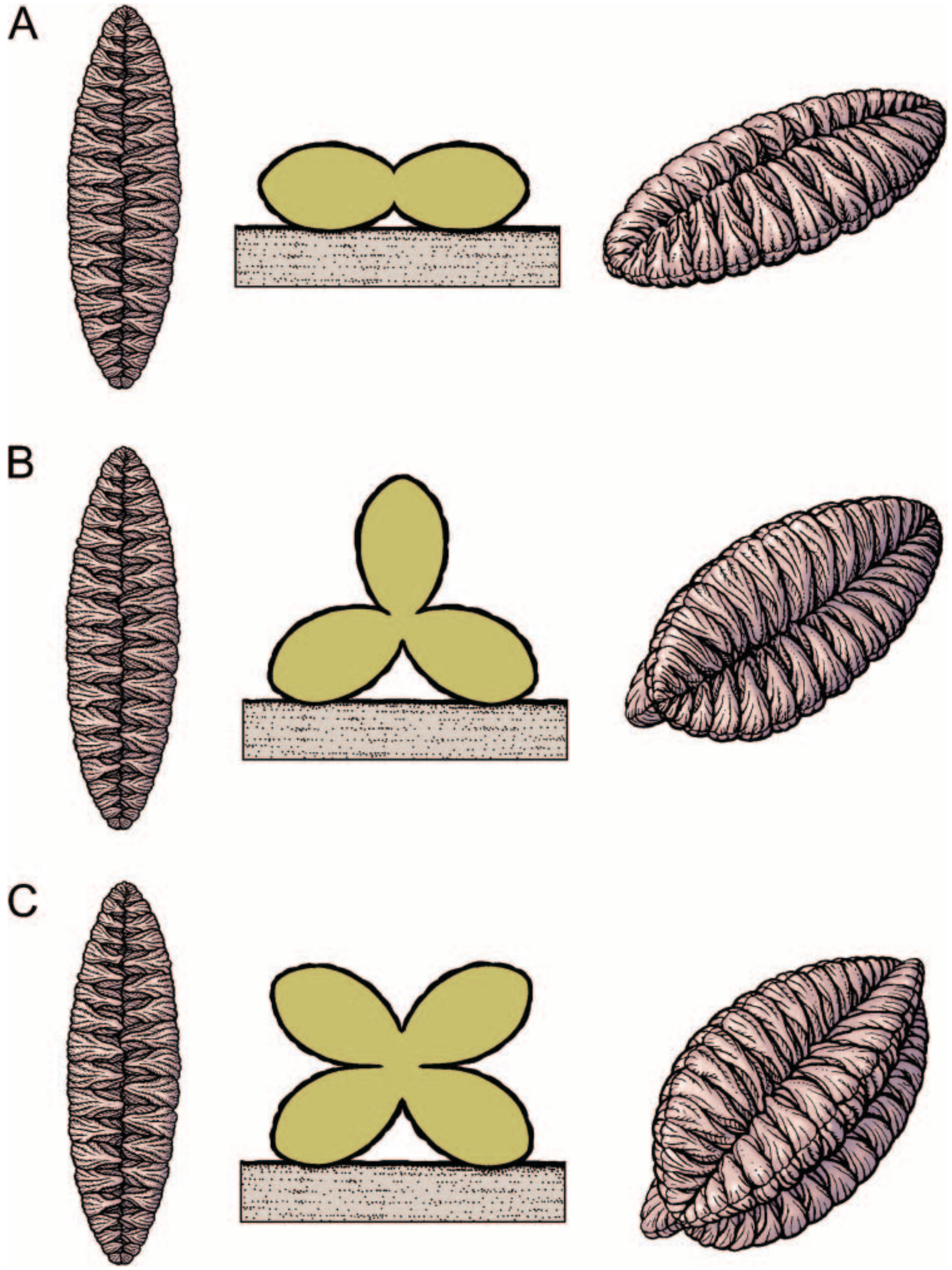
The possibility that *Fractofusus* may represent the fragmented units of a larger organism has been considered. The spindle-shaped form of *F. misrai* bears a superficial resemblance to the primary branches on a rare, un-named network form in the Mistaken Point Formation on the Avalon Peninsula (Narbonne et al. 2001, pl. 1G). The possibility that the specimens of *Fractofusus* were shed branches from these network forms was rejected after close examination of the best-preserved specimens. The secondary branches differ in significant ways from *Fractofusus* modules; they increase in size from the base to the distal tips of primary branches, branch at an acute angle toward the distal end, and are not in contact. Furthermore, there is no preserved structure on *Fractofusus* that could be interpreted as an attachment point.

The random orientations of *Fractofusus* on bedding surfaces (Fig. 6) might be considered as evidence of an assemblage of pelagic organisms floored by ash-fall events. However, the crisp molding of their basal surface rather than intervention of crystal-bearing ash beneath the body is the best taphonomic evidence that they were benthic recliners in life. The overlapping of some specimens of *Fractofusus* provides evidence of some transport owing to turbulence associated with the contour currents (Wood et al. 2003), while folding (for example, Fig. 11) seems to have been a product of turbulence accompanying turbid currents associated with the ash fall or ash-laden density flows that preserved them (Seilacher 1992).

Paleobiology

Rangeomorphs, described by Narbonne (2004) from the Conception Group in the Spaniards Bay region of Newfoundland, comprise fractal branches, some as frondlets with a central stalk (Narbonne 2004, figs. 2A, 3A) and others as plumose frondlets (Narbonne 2004, figs. 2C–2D, 3B–3C). Fractally branching frondlets are the smallest observed structures in *Rangea*, *Charnia*, *Bradgatia*, and several unnamed branching forms in the Avalon succession of eastern Newfoundland colloquially known as the "network", "tree", and "brush" (see Clapham and Narbonne 2002; Narbonne et al. 2005). However, for most of the rangeomorphs that were elevated above the sea floor, the detail of the fractal branching is poorly preserved because they were floored by ash-fall events ensuring that their composite molds were formed within the ash layer rather than against the substrate mud. It is important to emphasize that the fine impressions of frondlets

Fig. 14. Potential models for reconstruction of *Fractofusus* n.gen., each with basal mold, cross-section, and oblique view. (A) Two-vane model. (B) Three-vane model. (C) Four-vane model.



in *Fractofusus* from Mistaken Point and Bonavista Peninsula are sharply preserved because these organisms were already in contact with substrate before being mantled by volcanic ash. The newly described rangeomorphs fronds from Spaniards Bay on the Avalon Peninsula that are exceptionally preserved within the substrate sediment show these frondlets to be composed of blind elements and not bearing tubular openings at a resolution of <0.03 mm (Narbonne 2004).

The spindle-shaped *Fractofusus* is perhaps the most constrained of the rangeomorph constructions, and thus provide an important end member for understanding this group. The bipolar arrangement of modules along vanes meeting in a zigzag to straight commissure in both species of *Fractofusus* is arguably one of the simplest constructional forms within the rangeomorphs. The random arrangement of spindles on bedding surfaces, where tethered fronds are preserved in current-oriented arrays, and the lack of a holdfast demonstrate that *Fractofusus* had no attachment organ.

Fractal growth of elements in all rangeomorphs shows considerable crowding that is not simply a taphonomic artifact. In frondose rangeomorphs, such as *Charnia* and *Rangea*, most of the surface area is not in contact with their external environment because fractal branches are close packed. Reconstructions of *Rangea* by Jenkins (1985), Dzik (2002), and Grazhdankin and Seilacher (2005) indicate fractal quilting within a very confined unipolar, fusiform morphospace. If fractal growth was a mechanism for maximizing surface area, the involution of frondlets and frond leaves observed in rangeomorphs, such as *Rangea* and *Charnia*, would not be expected for both benthic recliners and erect branching organisms. After accounting for the effects of taphonomic distortion, this convoluted fractal morphology in rangeomorphs may be better explained as a fundamental mode of construction rather than just an ecological adaptation for maximizing surface area. The close packing involved in rangeomorph fractal growth may have represented a fabricational strategy that gave greater strength to an unmineralized body wall than could be achieved with a smooth enclosed body form of the same gross geometry. Seilacher (1989, 1992) proposed the concept of Vendobionta, a lost clade of giant syncytial organisms constructed from repeated "pneu" or inflated units, that collectively gave a fluid-filled body rigidity while allowing various gross body geometries to be used.

Many common members of the Ediacara biota cannot be readily included in the Vendobionta, or be regarded as stem group Cnidaria and Porifera. Organisms, such as *Kimberella* and *Dickinsonia*, were capable of locomotion and feeding that required muscular contraction (Fedonkin and Waggoner 1997; Gehling et al. 2005). Assemblages of small, high-relief Ediacara organisms, such as *Spriggina*, *Parvancorina*, and *Tribrachidium*, arguably represent stem group bilaterians (Gehling 1991; Gehling et al. 2005). However, serially and fractally constructed vendobionts, such as *Pteridinium* and *Rangea*, included in the Petalonamae (Pflug 1972), and related taxa, such as *Phyllozoon* and *Swartpuntia*, still appear to fit well with Seilacher's concept of the Vendobionta. Jenkins (1992) redefined the Petalonamae to include only the simplest vendobionts, constructed from simple tubular or bean-shaped "pneu", such as *Pteridinium*, *Phyllozoon*, and *Ernietta*. The Rangeomorpha (Pflug 1972, Jenkins 1985, 1992; Grazhdankin and Seilacher 2005) are vendobionts with fractally convoluted "pneu". They represent not only a finer scale of quilting but one that involved far more surface area of body wall than required in the simple repetition of tubular units in petalonamids.

Rangeomorph fossils dominated the earliest stages of Ediacaran mega-organismic evolution, comprising more than 75% of the diversity in the Mistaken Point assemblage and filling most ecologic roles in the community (Clapham et al. 2003; Narbonne 2005; Bottjer and Clapham 2006). Rangeomorphs are demonstrably amongst the oldest member of the Ediacara biota, judging by their prominence in the Avalon association of eastern Newfoundland, where the earliest members occur from just below an ash bed dated (U–Pb dates from zircons) at 575 ± 1 Ma (Bowring et al. 2002). Petalonamids, such as *Phyllozoon*, *Pteridinium*, *Ernietta*, and *Swartpuntia* are apparently restricted to the younger Ediacaran White Sea and Nama associations around the globe, which have been dated at 555–543 Ma (Grotzinger et al. 1995; Martin et al. 2000; Condon et al. 2005). If, as proposed by Seilacher (1989, 1992), rangeomorphs and petalonamids are sister groups within the Vendobionta, then it is curious that the simpler mode of construction is confined to the younger Ediacaran associations. Perhaps the energy requirements for the construction of quilted body walls led to the selection of the simpler, serial construction using tubular modules.

The petalonamid *Phyllozoon hanseni* Jenkins and Gehling, 1978, so common in the Ediacara biota of South Australia, resembles *Fractofusus* in that it appears to be composed of two vanes consisting of serial tubular modules arranged in alternating positions on either side of a commissure. Both forms occur in assemblages where large numbers of individuals are found in close association and where there is no evidence that individuals were tethered to the substrate. However, the simple tubular modules of *Phyllozoon* contrast with the fractally convoluted modules of *Fractofusus*. Both forms lack direct evidence for a third vane that is clearly present in *Pteridinium* (see Grazhdankin and Seilacher 2002 and references therein). However, the shared construction involving serial arrangement of modules along vanes joined to form a body axis suggests that they were organisms of a similar biological grade. The Russian three-vaned form, *Ventogyrus chistyakovi* Ivantsov and Grazhdankin, 1995 shows some similarity in construction, but includes more complex biological structures, such as a canal system.

Grazhdankin and Seilacher (2005, 2002) consider that *Rangea* and *Pteridinium* were obligate, infaunal organisms, rather than simply being products of burial in sand turbidites. This interpretation of *Pteridinium* (Grazhdankin and Seilacher 2002) does not explain the flattened specimens preserved on bed soles. It is likely that transported specimens of *Pteridinium* were rarely preserved unless infilled during transport and weighed down by sand. Certainly, there is no evidence that *Fractofusus* was infaunal. Unlike many key taxa in the Ediacara biota, rangeomorphs and petalonamids share not only constructional similarities but also similar taphonomic responses to burial. Rather than being preserved as bed-sole external molds, they either collapse or are partly filled by the sediment that buries them. There is no evidence of contraction halos, internal contraction wrinkles, or any other evidence of muscular tissue or internal organs. They lack true bilateral symmetry or evidence of motility. There is no clear indication of pores, stomates or any other openings in the fractal modules.

The question of rangeomorph affinities has proven more controversial. Jenkins (1985) included *Fractofusus* along with other fractally branching taxa within Pflug's (1972) Rangeomorpha, and this has been accepted by most subsequent workers. Jenkins' (1992) interpretation of the Rangeomorphs as octocorals was based on his interpretation of the unseen tips of fractal elements as feeding polyps. However, this is contradicted by the evidence afforded by folded specimens for convexity of both sides of *Fractofusus* modules and also the small-scale elements in specimens of *Rangea* described by Narbonne (2004). Dzik (2002) regarded these taxa as fossil ctenophorans, but this suggestion has not garnered support by subsequent workers, most of whom regard rangeomorphs as extinct body plans that were not ancestral to any modern living organisms (Narbonne 2004, 2005; Brasier and Antcliffe 2004; Grazhdankin and Seilacher 2005). Rangeomorphs occupied what appears to have been a range of tiering niches, and this has been used as evidence that they extracted food from seawater in a manner similar to modern animals (Clapham and Narbonne 2002). However, their mode of feeding is not clear from the preserved morphology of rangeomorphs such as *Fractofusus*. The fossilized remains show no direct evidence of fine or coarse body openings that might be utilized in filtering. A comparison with protistans and fungi is questionable, because the fractal regularity of the *Fractofusus* body plan is greater than that observed in either living protistans or fungal fruiting bodies. Their occupation of benthic environments below the photic zone rules out a photosymbiosis for rangeomorphs. Based on available evidence, it seems most likely that *Fractofusus* and other rangeomorphs represent a stem group near the base of the animal phylogenetic tree (Narbonne 2004, 2005).

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