

## Article

# Pleistocene Bryozoans from the Clyde Clay Formation of Scotland, and the Holocene Retreat of Cold-Water Species

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**Abstract:** Although bryozoans are a diverse phylum of aquatic invertebrates with a rich fossil record, very little has been written about bryozoan faunas from the latest Pleistocene at a time of rapid global change when temperatures increased dramatically and the sea-level rose. Two species of cyclostome and eight species of cheilostome bryozoans are here described from the late Devensian Clyde Clay Formation of Greenock, Scotland, based on historical material in the collections of the NHM, UK. All are illustrated for the first time from this deposit using scanning electron microscopy. Three of the species (*Tubulipora* cf. *marisalbi*, *Rhamplostomella radiatula* and *Schizomavella porifera*) are unknown from the seas around Scotland at the present-day but occur in colder waters to the north. This is consistent with the poleward retreat of cold-water species as seawater temperatures increased at the end of the Pleistocene.

**Keywords:** Bryozoa; Pleistocene; Scotland; biogeography; global warming



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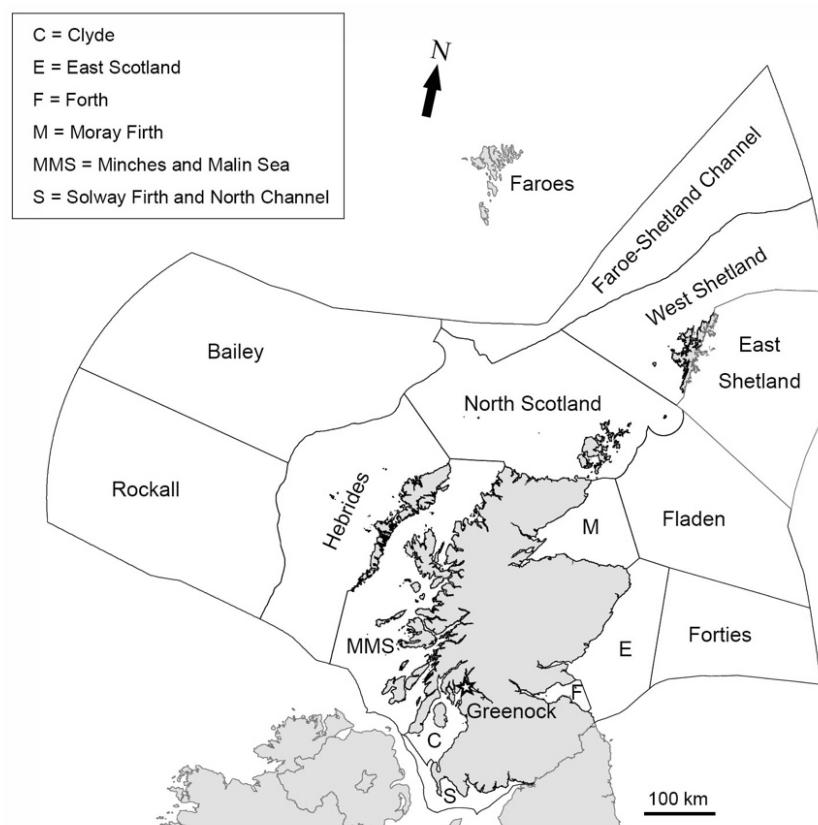


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## 1. Introduction

Concomitant with global warming and facilitated by human-related dispersal mechanisms, the last few decades have seen the expansion of the ranges of several bryozoan species into higher latitudes. These include warm-water fouling species, notably *Bugula neritina*, *Watersipora subatra* and *Schizoporella japonica*, which have begun to appear in harbours increasingly further north in the Atlantic waters of northwest Europe [1–3]. A further expectation is that the ranges of cold-water bryozoan species will have contracted polewards as sea temperatures increased, causing local extinctions. However, it is unclear whether any such range contractions have actually been documented.

Rapid climatic warming marked the end of the so-called Ice Age in the late Pleistocene [4]. Comparing the composition of fossil bryozoan faunas formed at this time with those of the present-day in the same region has the potential for identifying local extinctions of cold-adapted species. Unfortunately, very little has been published on bryozoans from the latest Pleistocene, especially in northern Europe. The presence in the Natural History Museum, London (NHMUK) of some latest Pleistocene bryozoans collected during the late 19th century from temporary exposures near the shore of the Firth of Clyde downstream of Glasgow at Garvel Park, Greenock (Figure 1), allows a glimpse of a bryozoan fauna that lived at a coastal site following deglaciation and sea-level rise. A few lists of bryozoan species from the Garvel Park have been published [5–7], but none of the species recorded have been described or figured. The current paper provides the first descriptions and figures of the Garvel Park bryozoans, some of which no longer live in Scottish waters but are present in colder waters further to the north, an example of ‘trailing-edge extirpation’ [8].



**Figure 1.** Regions of the sea around Scotland, based on work by Rouse and others [9], and the location (star) of the latest Pleistocene fossil bryozoan locality at Garvel Park, Greenock.

## 2. Materials and Methods

This taxonomic study is based entirely on historical material lodged in the fossil collections of the NHMUK. Some of these specimens were presented to the museum by D. Robertson on 4 November 1883, one is from the collection of J. Young and a few are from the collection of E. Jelly, who is known to have received bryozoans from other collectors and then redistributed them to her colleagues. The specimens donated by Robertson are labelled ‘Garvel Park, Greenock’. Other specimens, which were apparently collected at about the same time, probably came from the same locality or very nearby. Colonies are fragmentary but well preserved, allowing identification to species level in most instances.

Robertson [6] gave a detailed account of the Pleistocene geology of Garvel Park, Greenock, where the construction of a dry dock in 1870 and a wet dock in 1881 exposed boulder clay overlain by a sequence of clays and sands containing marine shells. These late glacial marine deposits came to become known as the ‘Clyde beds’ [10] or ‘Garvel Park Beds’ [7] but have since been given the formal name Clyde Clay Formation [11,12]. No permanent exposures exist at Greenock but temporary excavations both during the late 19th century and again in 1962 allowed the Clyde Clay Fm. to be seen in six small basins to a thickness of 10 m or more [10]. Unfortunately, the exact stratigraphical level (or levels) from which the bryozoans were collected is unknown. The Clyde Clay Fm. is a glaciomarine deposit considered to have been formed during the late Devensian (= late Weichselian) Marine Isotope Stage 2, about 13–10 ka BP [12,13].

After initial study with an optical microscope, the bryozoans were examined and imaged using a LEO 1455-VP scanning electron microscope. This instrument was operated in low vacuum mode, allowing the uncoated bryozoans to be imaged using a back-scattered electron detector. Species descriptions are based on the scanning electron micrographs obtained, and measurements were made from these calibrated micrographs. Abbreviated

synonymies are given for each species that include the first description, first referral to the currently accepted genus, and a modern description.

### 3. Results

#### 3.1. Systematics

Phylum Bryozoa Ehrenberg, 1831

Class Stenolaemata Borg, 1926

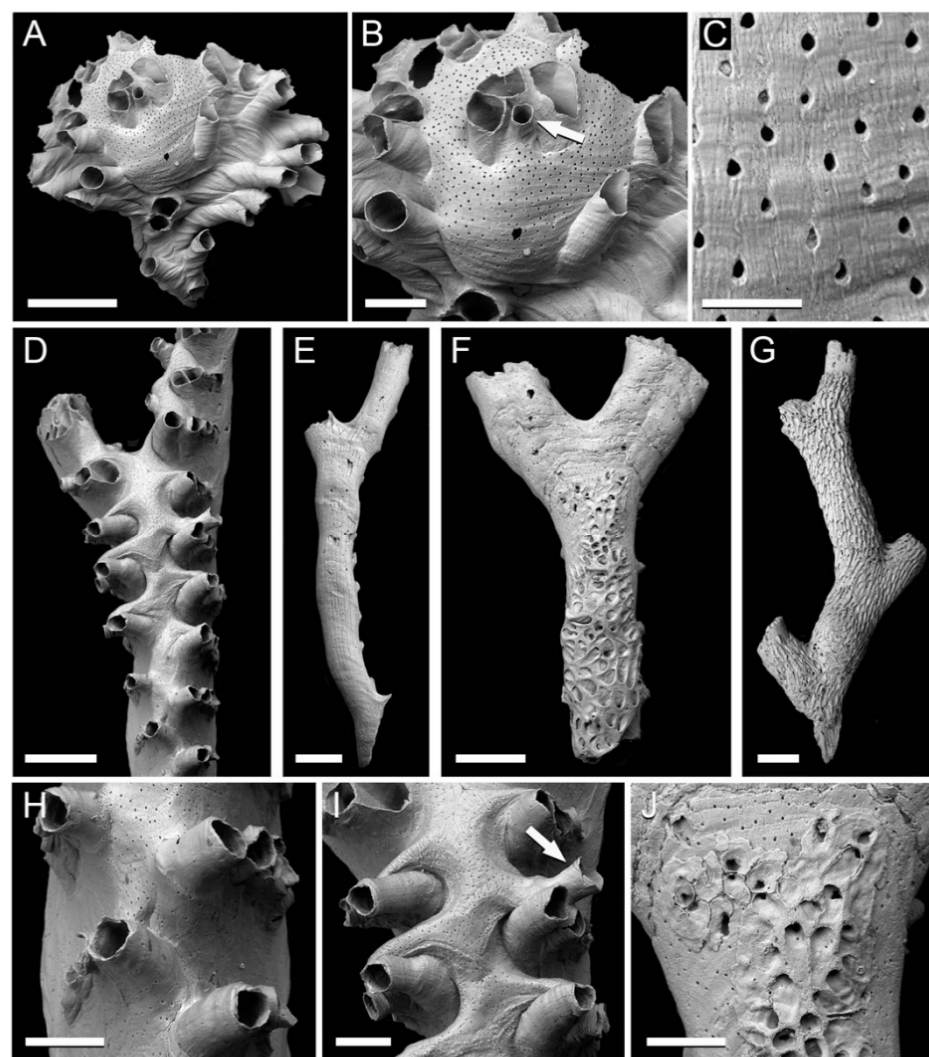
Order Cyclostomata Busk, 1852

##### 3.1.1. Family Tubuliporidae Johnston, 1837

Genus *Tubulipora* Lamarck, 1816

*Tubulipora* cf. *marisalbi* Gostilovskaja, 1955

Figure 2A–C



**Figure 2.** Cyclostome bryozoans from the Clyde Clay Formation of Garvel Park, Greenock, Scotland. (A–C) *Tubulipora* cf. *marisalbi* Gostilovskaja, 1955, NHMUK B1223e; (A) entire specimen; (B) gonozooid with oeciostome arrowed; (C), pseudopores on frontal surface of gonozooid. (D–J) *Idmidronea atlantica* (Forbes in Johnston, 1847); (D,H,I) fertile branch, NHMUK B1223a; (D) gonozooid occupying branch axis; (H) detail of autozooids on frontolateral sides of branch; (I) part of gonozooid with oeciostome arrowed; (E) abfrontal surface of branch lacking kenozooidal overgrowth, NHMUK

B1223d; (F,J) abfrontal surface of branch with kenozooidal overgrowth developing from the proximal end, enlarged pseudopores visible (upper left) at the bases of the kenozooids in (J), NHMUK B1223b; (G) branch abfrontal covered by an overgrowth of proximally directed kenozooids, NHMUK B1223c. Scale bars: A, D–G = 500 µm; B, H–J = 200 µm; C = 50 µm.

cf. 1955 *Tubulipora marisalbi* Gostilovskaja [14], p. 103, figs 5–6

cf. 1962 *Tubulipora marisalbi* Gostilovskaja: Kluge [15], p. 92, fig. 27

cf. 1978 *Tubulipora marisalbi* Gostilovskaja: Gostilovskaja [16], p. 51, fig. 13

Material examined. NHMUK B1223e. Robertson Collection.

Description. A single flabellate colony detached from its substrate, small, about 1.5 × 1.7 mm, comprising some 20 autozooids and a gonozooid. Autozooids proximally biserial, distally oligoserial, diverging from colony axis; frontal walls transversely wrinkled with sparse, teardrop-shaped pseudopores spaced about 60–100 µm apart; peristomes usually non-connate, except for those penetrating the gonozooid which are initially connate, apertures longitudinally elliptical, about 140 by 120 µm. Gonozooid ovoidal, 900 µm long by 800 µm wide, broken distally; roof bulbous, longitudinally striated, densely pseudoporous, pseudopores spaced about 20–30 µm apart; oeciostome located about two-thirds of the distance along the brood chamber, associated with three autozooidal peristomes that penetrate the brood chamber, a straight-sided tube, not distally flared; oeciopore almost circular, considerably smaller than an autozooidal aperture, about 70 µm in diameter.

Remarks. Seven species of *Tubulipora* have been recorded from the seas around Scotland [9], three from the Clyde region (Figure 1): *T. flabellaris*, *T. liliacea* and *T. lobifera*. However, the Clyde Clay Fm. specimen resembles none of these three and instead is closer in overall morphology to a fourth Scottish species [17] (*T. aperta*) not recorded from western Scotland but which has a funnel-shaped oeciostome and a larger oeciopore than the fossil species. A better match is with *T. marisalbi* Gostilovskaja, 1955 [14], in which the oeciopore is described as being smaller than an autozooidal apertures and the oeciostome appears not to be flared [16]. This species is known only from the White Sea where it is very rare (A.N. Ostrovsky, pers. comm. 20/3/2021). Pending a modern revision of the type material of *T. marisalbi*, the single Clyde Clay Fm. specimen can only be referred with some reservation to this Arctic species.

Genus *Idmidronea* Canu and Bassler, 1920

*Idmidronea atlantica* (Forbes in Johnston, 1847)

Figure 2D–J

1847 *Idmonea atlantica* Forbes in Johnson [18], p. 278, pl. 48, fig. 3

1976 *Idmidronea atlantica* (Forbes in Johnson): Harmelin [19], p. 182, pl. 32

1985 *Idmidronea atlantica* (Forbes in Johnson): Hayward and Ryland [17], p. 90, fig. 31

Material examined. NHMUK B1223a–d. Robertson Collection.

Description. Colony erect, comprising narrow, about 0.6–1 mm wide, bifurcating branches of rounded triangular cross-section with zooids opening on the two frontolateral sides and lacking on the abfrontal side; branch abfrontal formed of pseudoporous exterior wall marked by traces of the basal outlines of the zooids; kenozooidal overgrowths often developing on branch reverse apparently originating from enlarged pseudopores. Autozooids arranged in transverse series comprising four or five zooids on each of the two frontolateral branch sides, alternating along the midline with series on the opposite frontolateral side; peristomes basally connate, becoming separated distally, particularly those of the most axial zooid; apertures circular to rounded quadrate, up to 100 µm in diameter; frontal walls slightly convex, irregularly and sparsely pseudoporous, 388–447 µm long (mean 418 µm; SD 18 µm; N = 10) by 82–106 µm wide (mean 85 µm; SD 7 µm; N = 10). Gonozooid elongate, brood chamber 2.6 mm long, located along the branch axis with lobes extending between autozooidal series, continuing into the two daughter branches at bifurcation; frontal wall densely covered with elliptical or teardrop-shaped pseudopores, sutured along the midlines of the main axis and lobes; oeciostome about midway along

length of brood chamber, attached to the distal side of an autozooidal peristome, oriented distolaterally, gently dilated distally, straight and tubular, distal end probably broken off; ooeciopore about the same diameter as an autozooidal aperture. Kenozooids developing on branch abfrontal side as patches or a more extensive proximally directed overgrowth; frontal walls lacking, apertures oblique, irregular in size and shape.

Remarks. *Idmidronea atlantica* is represented in the Clyde Clay Fm. by broken branches from what would originally have been erect colonies in the form of two-dimensional fans. Vine (1885, p. 214) [7] described this species as the ‘most important’ in the Garvel Park bryozoan fauna, possibly meaning that it is the most abundant or conspicuous. *Idmidronea atlantica* is a widely distributed species in the Atlantic and Mediterranean today, from the Arctic to the tropics [17]. However, taxonomic revision incorporating molecular data is needed to test whether this name has been applied to more than one species, which this broad latitudinal (and thermal) distribution would suggest. In Scotland at the present-day it is known from three regions (Minches and Malin Sea, Rockall and West Shetland) but has not been recorded from the Clyde region [9].

Class Gymnolaemata Allman, 1856

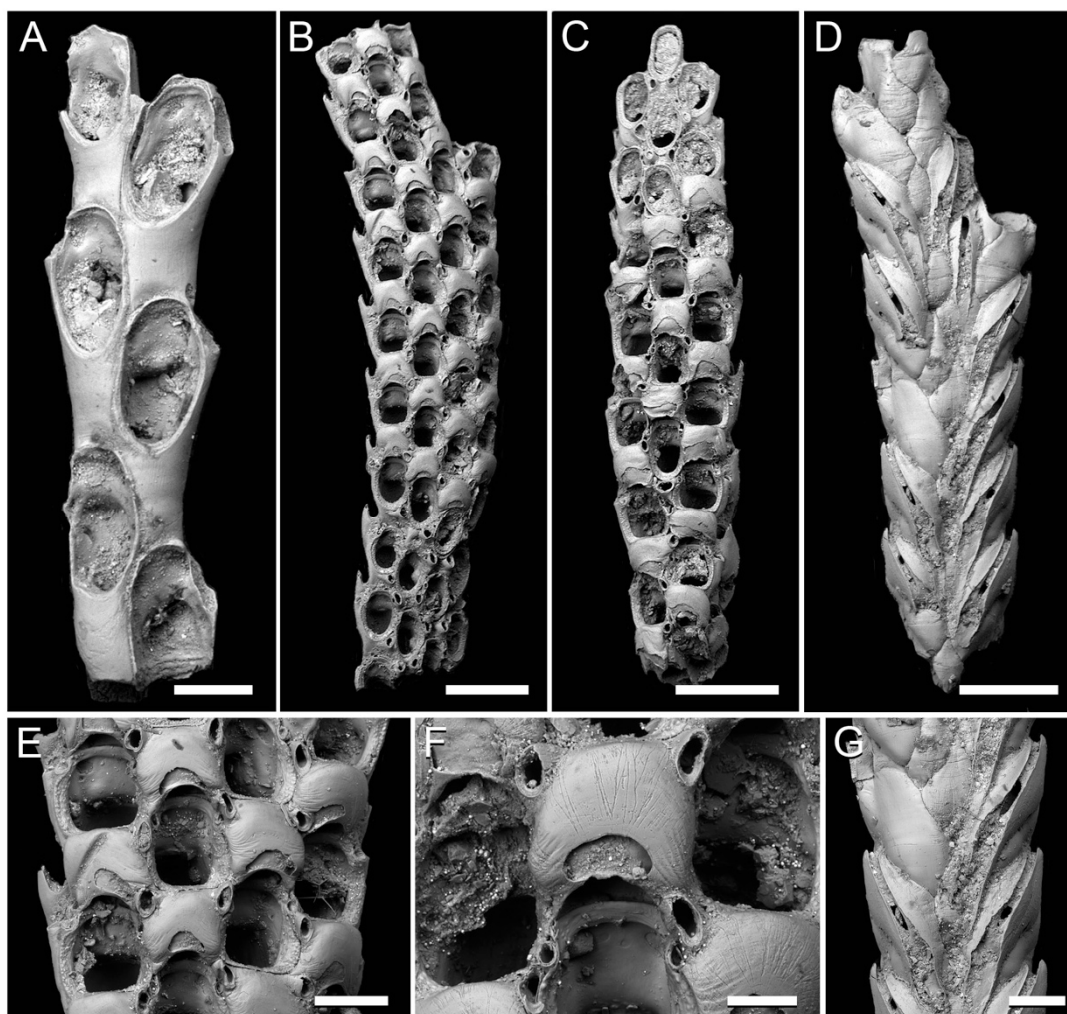
Order Cheilostomata Busk, 1852

3.1.2. Family Bugulidae Gray, 1848

Genus *Bugulopsis* Verrill, 1879

*Bugulopsis peachii* (Busk, 1851)

Figure 3A



**Figure 3.** Cheilostome bryozoans from the Clyde Clay Formation of Garvel Park, Greenock, Scotland. (A) *Bugulopsis peachii* (Busk, 1851), small branch showing biserial arrangement of autozooids on the frontal surface, NHMUK D1633.

(B–G) *Caberea ellisi* (Fleming, 1814), NHMUK Jelly Collection ‘GP1’; (B) frontal surface of branch (e) with proximal-most zooids infertile; (C) frontal surface of branch (b) with distal-most zooids infertile; (D) abfrontal surface of branch (a); (E) fertile autozooids and avicularia in branch (e); (F) ovicell in branch (c); (G) detail of abfrontal surface of branch (a) showing vibracula with long setal grooves. Scale bars: A, E, G = 200 µm; B–D = 500 µm; F = 100 µm.

1851 *Cellularia peachii* Busk [20], p. 82

1966 *Bugulopsis peachii* (Busk): Prenant and Bobin [21], p. 442

1998 *Tricellaria peachii* (Busk): Hayward and Ryland [22], p. 284, fig. 96

Material examined. NHMUK D1633. J. Young Collection.

Description. Small branch internode preserving 6 zooids arranged biserially, opening alternately on either side of the internode frontal side. Autozooids elongate pyriform, *c.* 700 µm long by 300 µm wide; proximal gymnocyst occupying slightly less than half of frontal surface, forming a short prolongation at the outer distal angle of the zooid, broken-off in the fossil to leave an elongate depression; cryptocyst narrow; opesia longitudinally elliptical, about 400 µm long by 200 µm wide. Avicularia lacking. Ovicells not developed in the single specimen studied, when present globose and with an uncalcified window in the ectoecium.

Remarks. Living examples of species are slender, tuft-like colonies consisting of articulated internodes of seven to nine zooids attached to the substrate by rhizoids. In the eastern Atlantic, the geographical range of *B. peachii* extends from the Yorkshire coast of England northwards to Shetland, Spitsbergen and the White Sea [22]. It has been recorded living in several regions around Scotland [9], though not on the west side of the country including the Clyde region.

### 3.1.3. Family Candidae d’Orbigny, 1851

Genus *Caberea* Lamouroux, 1816

*Caberea ellisi* (Fleming, 1814)

Figure 3B–G

1814 *Flustra ellisi* Fleming [23], p. 251

1880 *Caberea ellisi* (Fleming): Hincks [24], p. 59, pl. 8, figs 6–8

1998 *Caberea ellisi* (Fleming): Hayward and Ryland [22], p. 254, fig. 82

Material examined. NHMUK ‘GP1’, five branches (a–e) c mounted on a slide; E. Jelly Collection.

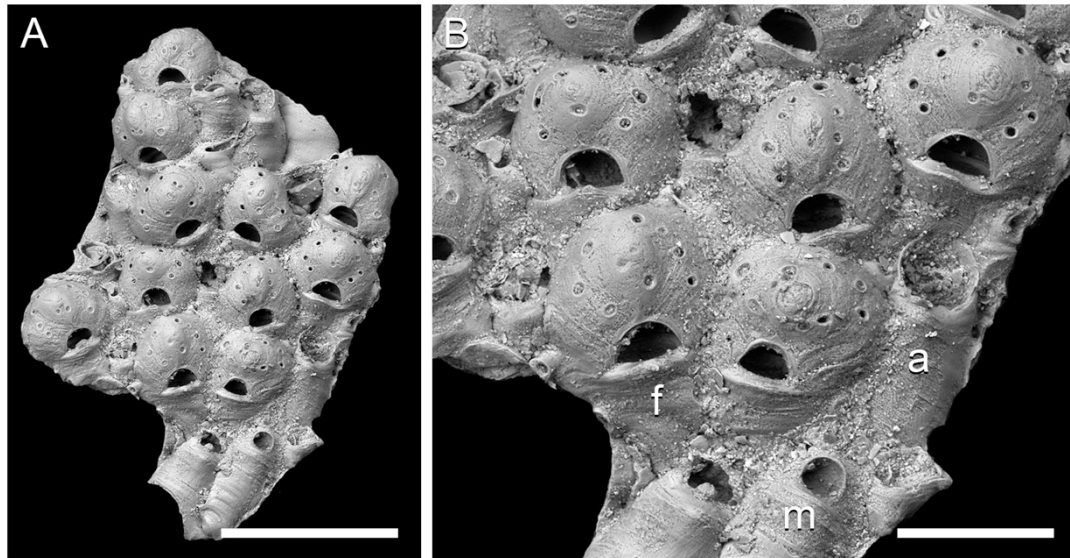
Description. Colony erect, preserved as internodes measuring 2 mm long by 0.4 mm wide. Autozooids opening on frontal surface of internodes in two to four series, rounded quadrangular, all examples ovicellate, including the ovicell 487–571 µm long (mean 526 µm; SD 31 µm; N = 7) by 213–276 µm wide (mean 240 µm; SD 24 µm; N = 7); gymnocyst lacking (or covered entirely by the ovicell) except in marginal zooids where a narrow lateral gymnocyst is evident; cryptocyst narrow, sloping steeply inwards, pustulose, not visible proximally due to the ovicell of the preceding zooid; opesia pear shaped, 225–267 µm long (mean 245 µm; SD 14 µm; N = 6) by 163–209 µm wide (mean 185 µm; SD 18 µm; N = 6); a pair of distolateral spine bases in medial zooids, two pairs in lateral zooids. Ovicells with rounded rectangular oecia, most slightly wider than long, 200–257 µm long (mean 218 µm; SD 20 µm; N = 10) by 200–267 µm wide (mean 233 µm; SD 22 µm; N = 10); ectoecium smoothly calcified, a crescentic window near the proximal edge. Avicularia situated at distolateral corners of the ovicells, small, oriented distally; rostrum arch shaped, tip subrounded; pivotal bar uncalcified. Abfrontal surface covered by vibracula with long setal grooves diverging from branch axis and open distally at branch margins.

Remarks. Living colonies of *Caberea ellisi* are fan-shaped and 2–3 cm in height [22]. The vibracula on the abfrontal surface have long setae that are serrated. In Britain, this distinctive and widespread species occurs today mostly in Scotland where it is recorded from two regions: North Scotland and West Shetland [9]. Its northerly range extends to Iceland [25] and the White Sea [16].

## 3.1.4. Family Hippothoidae Busk, 1859

Genus *Celleporella* Gray, 1848*Celleporella hyalina* (Linnaeus, 1767)

Figure 4



**Figure 4.** *Celleporella hyalina* (Linnaeus, 1767) from the Clyde Clay Formation of Garvel Park, Greenock, Scotland, NHMUK D1645; (A) colony fragment; (B) detail with examples of an autozooid (a), female zooid (f) and male zooid (m) labelled. Scale bars: A = 500  $\mu$ m; B = 200  $\mu$ m.

1767 *Cellepora hyalina* Linnaeus [26], p. 12861848 *Celleporella hyalina* (Linnaeus): Gray [27], p. 1281999 *Celleporella hyalina* (Linnaeus): Hayward and Ryland [28], p. 94, figs 20–21

Material examined. NHMUK D1645.

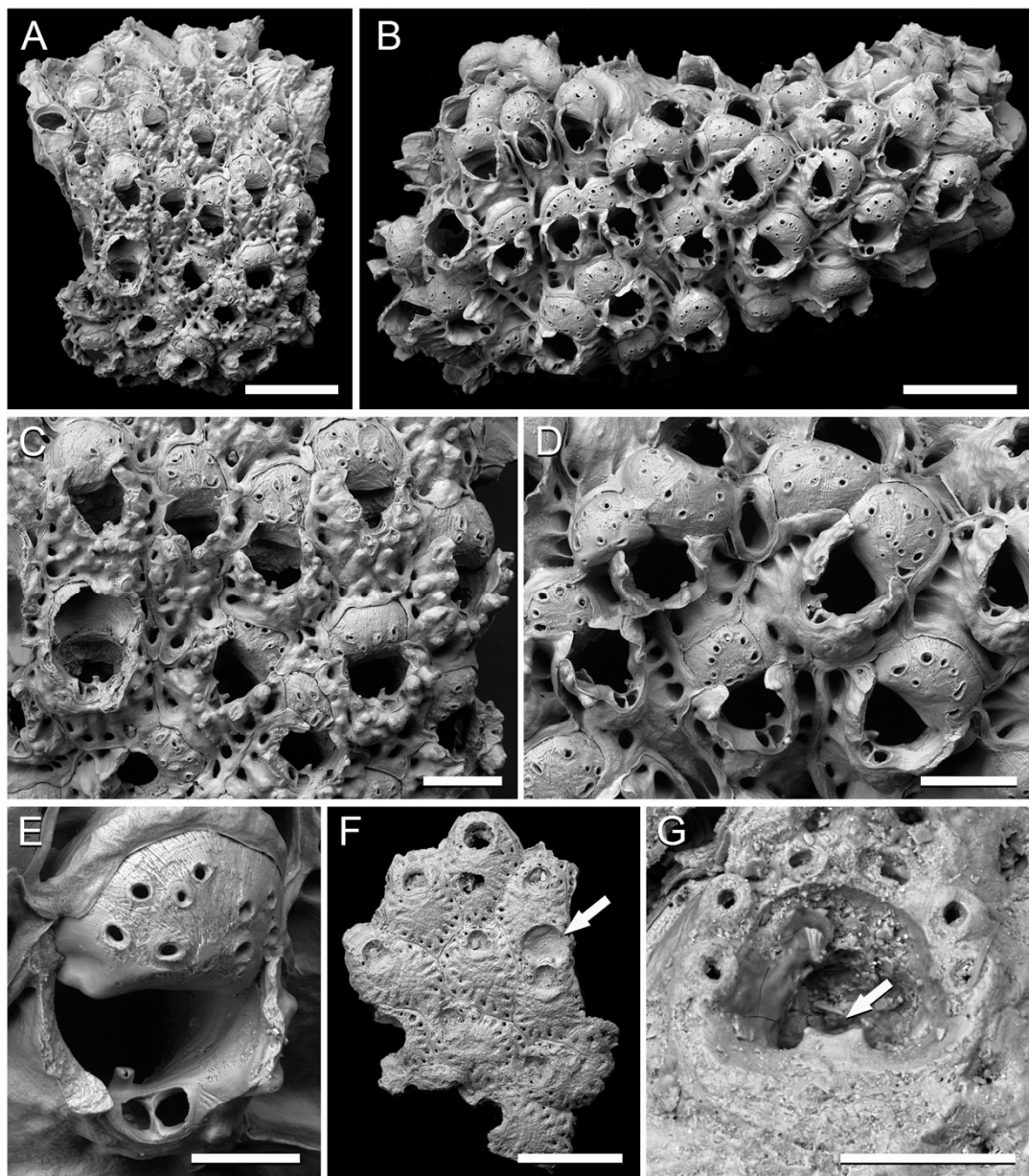
**Description.** Small fragment, 1.5 by 1.0 mm, consisting of about 20 zooids, detached from its substrate. Autozooids mostly overgrown; orifice about 100  $\mu$ m in diameter, with a broad sinus, an umbo located on the frontal shield proximally of the orifice. Male zooids distinguished by having a smaller orifice, about 50  $\mu$ m in diameter, three examples evident in the single specimen. Female zooids numbering 11, frontally budded onto the colony surface, orifice semielliptical, broad, 45–50  $\times$  70–90  $\mu$ m, overhung by a slight lip on the frontal shield; oecium globular, broad, 154–169  $\mu$ m long (mean 159  $\mu$ m; SD 8  $\mu$ m; N = 6) by 231–277  $\mu$ m wide (mean 254  $\mu$ m; SD 16  $\mu$ m; N = 6), with a prominent umbo encircled by about 8 circular or elliptical pores, often with one or two additional pores located more centrally.

**Remarks.** *Celleporella hyalina* forms a species complex of genetically distinct but morphologically indistinguishable lineages [29]. It occurs in sheltered areas of low intertidal to shallow subtidal habitats of cold-temperate and polar seas, usually as an epiphyte of macroalgae [28]. The example from the Clyde Clay Fm. probably grew on an alga which are known to be present in this formation [30].

## 3.1.5. Family Umbonulidae Canu, 1904

Genus *Rhamphostomella* Lorenz, 1886*Rhamphostomella radiatula* (Hincks, 1877)

Figure 5A–E



**Figure 5.** Cheilostome bryozoans from the Clyde Clay Formation of Garvel Park, Greenock, Scotland. (A–E) *Rhamphostomella radiatula* (Hincks, 1877); (A,C) NHMUK B1223f; (A) colony fragment with growing edge at top; (C) zooids; (B,D,E) NHMUK B1223g; (B) colony fragment; (D) group of ovicellate zooids; (E) ovicell, tooth-like lyrula and suboral avicularium. (F,G) *Escharella immersa* (Fleming, 1828); (F) fragment of a colony with broken ovicell (arrowed), NHMUK B1223m; (G) orifice with oral spine bases and lyrula (arrowed), NHMUK D1703. Scale bars: A, B, F = 500  $\mu\text{m}$ ; C, D = 200  $\mu\text{m}$ ; E, G = 100  $\mu\text{m}$ .

1877 *Lepralia radiatula* Hincks [31], p. 104, pl. 10, figs 9–14

1886 *Rhamphostomella radiatula* (Hincks): Lorenz [32], p. 13, pl. 7, fig. 9

2012 *Rhamphostomella radiatula* (Hincks): Winston and Hayward [33], p. 124, fig. 79

Material examined. NHMUK B1223f, B1223g, B1223h, B1223k, D. Robertson collection.

Description. Colonies encrusting, in one example attached to a branch of *Exidmonea atlantica*. Autozooids rounded hexagonal, separated by deep grooves, 453–600  $\mu\text{m}$  long (mean 505  $\mu\text{m}$ ; SD 52  $\mu\text{m}$ ; N = 9) by 200–347  $\mu\text{m}$  wide (mean 309  $\mu\text{m}$ ; SD 43  $\mu\text{m}$ ; N = 9); frontal shield covered by prominent, ‘knobbly’ tubercles, imperforate centrally, a series of areolar pores divided by buttresses around the edges; orifice submerged, distal margin rounded, proximal margin with a narrow, tooth-like lyrula; oral spine bases lacking. Ovicells developed in the majority of zooids, globular, 144–200  $\mu\text{m}$  long (mean 183  $\mu\text{m}$ ;



SD 20  $\mu\text{m}$ ; N = 9) by 189–240  $\mu\text{m}$  wide (mean 216  $\mu\text{m}$ ; SD 18  $\mu\text{m}$ ; N = 9), ectooecium uncalcified, entoecium pierced by up to about 10 pores varying in shape from circular to slit-like and with raised rims. Avicularia adventitious, small, about 80  $\mu\text{m}$  long, located on the proximal rim of the autozooidal peristome above and generally to one side of the lyrula, oriented transversely, a calcified pivotal bar dividing the opesia from a rostrum of approximately the same length but which is more pointed.

Remarks. This Arctic-Boreal species is not known to occur in the seas around Britain at the present-day. In Europe it has been recorded from the Barents Sea, White Sea, Iceland and northern Norway [34]. Elsewhere, it has been found in the Canadian Arctic, Labrador, western Greenland, Alaska and Hokkaido. However, neither *R. radiatula* nor any other species of *Rhamphostomella* have been recorded living in the seas around the British Isles at the present-day. The abundance of ovicells in the colonies found in the Clyde Clay Fm. imply that this species prospered in the latest Pleistocene at a latitude well south of its current range in Europe.

### 3.1.6. Family Romancheinidae Jullien, 1888

Genus *Escharella* Gray, 1848

*Escharella immersa* (Fleming, 1828)

Figure 5F,G

1828 *Lepralia immersa* Fleming [35], p. 533

1999 *Escharella immersa* (Fleming): Hayward and Ryland [28], p. 122, figs 35, 37A

2019 *Escharella immersa* (Fleming): Reverter Gil et al. [36], p. 17, fig. 4D

Material examined. NHMUK D1703, B1223j, B1223m.

Description. Three small fragments of encrusting colonies detached from their substrates, the largest preserving 10 zooid. Autozooids separated by narrow grooves, hexagonal, 400–577  $\mu\text{m}$  long (mean 507  $\mu\text{m}$ ; SD 41  $\mu\text{m}$ ; N = 12) by 345–422  $\mu\text{m}$  wide (mean 386  $\mu\text{m}$ ; SD 24  $\mu\text{m}$ ; N = 12); frontal shield convex, pustulose, imperforate centrally but with marginal areolar pores in one row, occasionally two, radially elongated; orifice semielliptical, wider (c. 120  $\mu\text{m}$ ) than long (c. 100  $\mu\text{m}$ ), an anvil-shaped lyrula present on the proximal edge; six stout oral spine bases around distolateral edge, four in ovicellate zooids. Ovicells visible in one colony, broken, about 200  $\mu\text{m}$  long by 230  $\mu\text{m}$  wide. No avicularia.

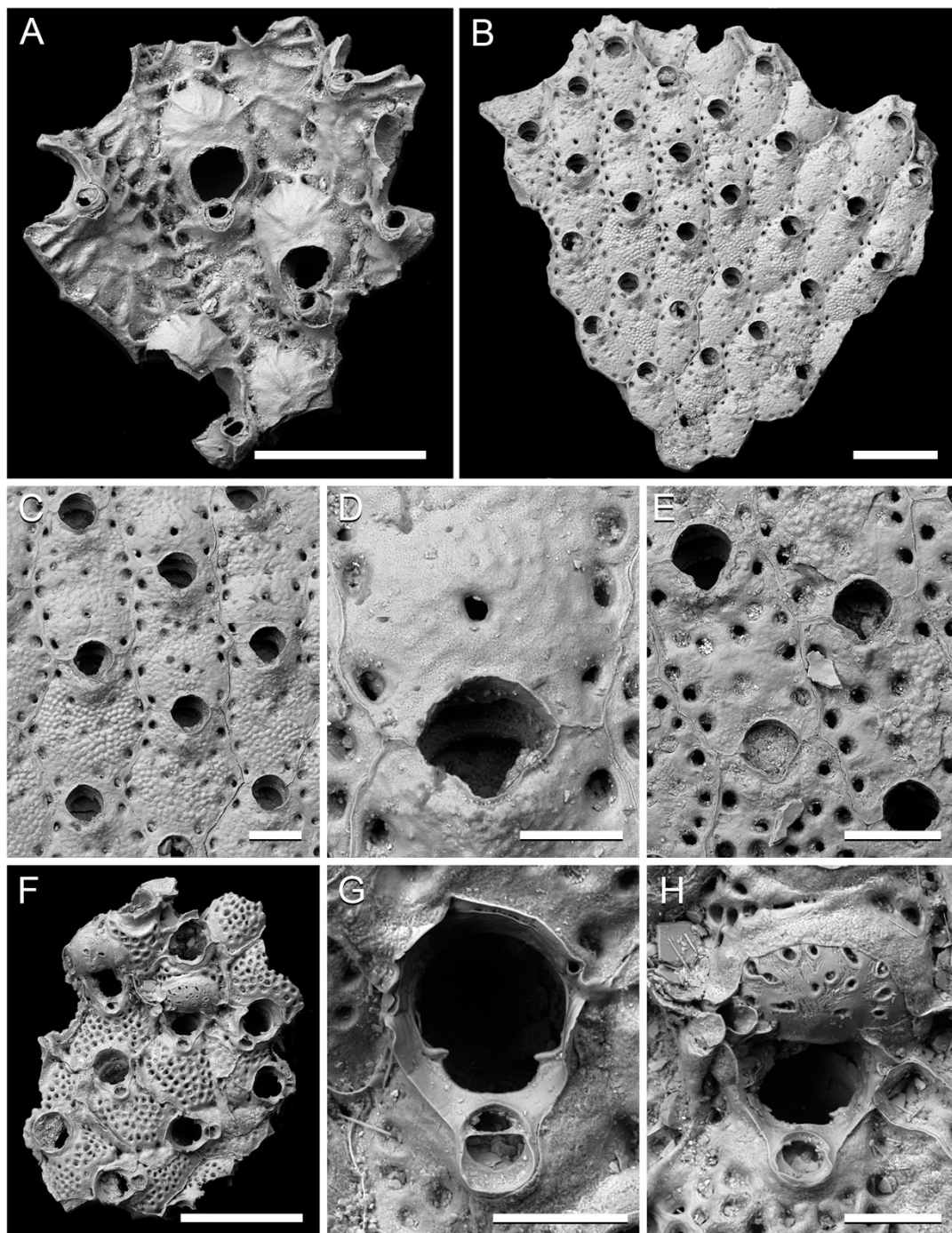
Remarks. This cold-water, Boreal-Arctic species is abundant today in the North Atlantic [28], recorded as far south as the Iberian Peninsula [36]. It has been reported from several Scottish regions, including the Clyde [9].

### 3.1.7. Family Bryocryptellidae Vigneaux, 1949

Genus *Porella* Gray, 1848

*Porella* cf. *alba* (Nordgaard, 1906)

Figure 6A



**Figure 6.** Cheilostome bryozoans from the Clyde Clay Formation of Garvel Park, Greenock, Scotland. (A) *Porella* cf. *alba* (Nordgaard, 1906), small fragment of colony showing zooids and ovicells, NHMUK B12231. (B–E) *Stomacrustula sinuosa* (Busk, 1860); (B–D) NHMUK D1311; (B) fragment of colony; (C) group of zooids; (D) ovicell and secondary orifice; (E) autozooids, NHMUK Jelly Collection ‘GP8b’. (F–H) *Schizomavella porifera* (Smitt, 1868), NHMUK B1223i; (F) colony fragment from early astogeny; (G) orifice of infertile zooid with suboral avicularium; (H) orifice and ovicell. Scale bars: A, B, F = 500  $\mu$ m; C, E = 200  $\mu$ m; D, G, H = 100  $\mu$ m.

cf. 1906 *Porella alba* Nordgaard [37], p. 25, pl. 3, figs 43–46

cf. 1999 *Porella alba* Nordgaard: Hayward and Ryland [28], p. 156, figs 54, 57B

Material examined. NHMUK B12231

Description. Tiny fragment consisting of one complete zooid surrounded by several broken zooids. Autozooids elongate, slender, about 600  $\mu$ m long by 250–300  $\mu$ m wide;

frontal shield with large areolar pores separated by buttresses prolonged as radial ridges towards the imperforate centre of the frontal shield; primary orifice not visible, hidden by the peristome; oral spines lacking. Ovicells globular, 200 µm long by 250 µm wide, oecium imperforate, crossed by similar radial ridges to those on the frontal shield. Avicularia adventitious, small, about 80 µm wide, suboral, oriented in a plane oblique to colony surface, directed proximally, rostrum rounded, pivotal bar calcified, usually broken.

Remarks. The single tiny specimen of this *Porella* is insufficient for the species to be identified with certainty. It does, however, show the greatest similarities with *P. alba* among the species of *Porella* recorded from British waters, although published figures of *P. alba* do not show the ridges on the ovicells that are so conspicuous in the Clyde Clay Fm. specimen. *Porella alba* is described as an Arctic-Boreal species distributed pan-globally [28]. Although present elsewhere in Scotland, it is unknown from the west coast including the Clyde region [9].

### 3.1.8. Family Fatkullinidae Grischenko, Gordon and Morozov, 2018

Genus *Stomatacrustula* Winston and Hayward, 2012

*Stomatacrustula sinuosa* (Busk, 1860)

Figure 6B–E

1860 *Lepralia sinuosa* Busk [38], p. 125, pl. 24, figs 2–3

1999 *Stomachetosella sinuosa* (Busk): Hayward and Ryland [28], p. 246, figs 105C, D, 107

2012 *Stomatacrustula sinuosa* (Busk): Winston and Hayward [33], p. 142, fig. 92

Material examined. NHMUK D1311, D1703, 'GP8b' (E. Jelly Collection).

Description. Colony encrusting, all three examples detached from their substrates. Autozooids hexagonal, 382–500 µm long (mean 481 µm; SD 48 µm; N = 10) by 289–409 µm wide (mean 346 µm; SD 49 µm; N = 10), boundaries marked by a narrow fissure; frontal shield thickly calcified, slightly convex, densely pustulose, areolar pores circular or elliptical, numbering about a dozen, a few frontal pores scattered elsewhere on the frontal shield; oral spines lacking; primary orifice hidden by low peristome, secondary orifice 127–136 µm long (mean 132 µm; SD 5 µm; N = 7) by 127–136 µm wide (mean 130 µm; SD 44 µm; N = 7), with a broad, shallow sinus. Ovicells common, about 180 µm long by 250 µm wide, subdued, calcification pustulose and continuous with frontal shield of distal zooid, a single pore at the centre. Avicularia lacking.

Remarks. This Arctic-Boreal species has a wide distribution [28,33], and has been recorded living in the Clyde region [9].

### 3.1.9. Family Bitectiporidae MacGillivray, 1895

Genus *Schizomavella* Canu and Bassler, 1917

*Schizomavella porifera* (Smitt, 1868)

Figure 6F–H

1868 *Escharella porifera* forma *typica* Smitt [39], p. 9, pl. 24, figs 30–32

1968 *Schizomavella porifera* (Smitt): Powell [40], p. 253, pl. 3, fig. 9

2012 *Schizomavella porifera* (Smitt): Winston and Hayward [33], p. 131, fig. 85

Material examined. NHMUK B1223i, 'GP8a' (E. Jelly Collection).

Description. Colonies encrusting, both examples detached from their substrates. Autozooids hexagonal, 492–671 µm long (mean 578 µm; SD 70 µm; N = 7) by 224–353 µm wide (mean 289 µm; SD 51 µm; N = 7), boundary walls raised; frontal shield convex, areolar pores located at the corners of the zooid, large pseudopores covering the rest of the surface; orifice relatively large, 130 µm long by 120 µm wide, with a broad sinus demarcated from the rest of the orifice by a pair of prominent, horizontal condyles; peristome low, cormidial, with the distal edge formed by the distal autozooid; oral spine bases occasionally visible. Ovicells common, about 180 µm long by 270 µm wide, ectoecium uncalcified, entoecium with numerous irregularly shaped pores surrounded by raised rims, distal edge of ovicell overgrown by calcification of the distal zooid. Avicularia adventitious, suboral, included

within the calcification of the peristome, small, about 60 µm wide, oriented proximally, inclined obliquely to surface, rostrum spoon-shaped, rounded, pivotal bar calcified.

Remarks. Regarded as a pan-Arctic species, *S. porifera* lives today in the western Atlantic from Greenland south to the Gulf of Maine, and across the Arctic from Iceland to northern Norway, the White Sea and the Sea of Japan [33]. It has not been reported from the seas around Britain.

#### 4. Discussion

Pleistocene bryozoans from the late Devensian Clyde Clay Formation of Garvel Park, Greenock on the Firth of Clyde are described for the first time using historical material in the collections of the NHMUK. Two cyclostome and eight cheilostomes are identifiable. A recent checklist of Scottish bryozoans records seven of these ten species now living in the sea around Scotland. However, the Clyde Clay Fm. includes three species (*Tubulipora* cf. *marisalbi*, *Rhamphostomella radiatula* and *Schizomavella porifera*) that are unknown in the modern Scottish fauna, while a further four species (*Idmidronea atlantica*, *Bugulopsis peachii*, *Caberea ellisi* and *Porella* cf. *alba*) have not been recorded from the Clyde region. The three species currently unknown in Scotland are today distributed in colder, more northerly waters: their local extinction (extirpation) in Scotland is therefore consistent with warming of the sea around Scotland during the last 15,000 years. Thus, the Clyde Clay bryozoan fauna demonstrates the contraction towards the pole of the ranges of a few cold-water species as the Pleistocene icecaps receded.

Dealing only with the ten species identifiable in the collections of the NHMUK, this paper is not a comprehensive account of all of the bryozoan species from the Clyde Clay Fm. Faunal lists published during the 19th century name additional species. Vine [7] listed 15 species from Garvel Park, Robertson [6] the same number while noting the presence of a few more that were too imperfect for identification. Unfortunately, neither of these lists from the 1880s are accompanied by descriptions or figures, making the accuracy of the identifications impossible to evaluate. However, some of the species cited are unlikely to be among those described in the current paper, for example, *Cribrilina annulata*, *Crisia eburnea* and *Diastopora* [*Diplosolen*] *obelium* recorded by Vine [7] belong to distinctive genera quite unlike any of those described in the current paper.

Four species of non-calcareous algal fossils have been described from the Clyde Clay Fm. [30]. These extant species, together with an associated echinoid (*Strongylocentrotus drobachiensis*), have a wide latitudinal range at the present-day but predominantly inhabit cold seas. The algae live today between the low water mark and about 20 m depth, suggesting a similar depth of deposition for the Clyde Clay Fm. Most of the Clyde Clay Fm. bryozoans that are encrusting lack substrates and it is quite possible that they were epiphytic on algae no longer preserved. Indeed, algae are the most common substrates today for one of the Clyde Clay bryozoans, *Celleporella hyalina* [28].

The Clyde Clay Fm. Garvel Park is well-known for its rich mollusc fauna, the most diverse Pleistocene fauna from Scotland according to Peacock [10]. This author noted similarities between the Clyde Clay Fm. mollusc assemblage and modern shallow water Arctic communities in northeast Greenland and Spitsbergen today, consistent with the existence of Arctic water rather than Atlantic water off western Scotland at the time of deposition. This is corroborated by the bryozoan fauna described here.

Research on Upper Pleistocene bryozoans in NW Europe has been woefully neglected. Faunal lists published in the 19th century make it clear that bryozoans do occur in coastal marine sediments of this age, yet none seem to have been studied in recent years. Scanning electron microscopy, an essential tool in the taxonomy of bryozoans with mineralized skeletons, seems not to have been applied prior to the current study. There are two compelling reasons why Upper Pleistocene bryozoans in NW Europe merit study. The first is that they can provide information on how species distributions have changed with rapid global warming and sea-level rise. This has clear relevance to contemporary global change and how the geographical ranges of species might be impacted. The second

is that knowledge of the composition of Late Pleistocene bryozoan faunas can help to assess which species are native to the biotas of particular regions. Although the fossil record is incomplete and will always fail to record the existence of many native species, especially those with weakly mineralized skeletons, fossils have the potential for furnishing positive evidence for the indigenous nature of those species that are preserved [41]. This is important because widespread anthropogenic dispersal of bryozoan species is known to have occurred through shipping [42], and this could date back to times when humans first undertook long distance sea voyages in wooden boats. Thus, while it is often easy to pinpoint species that have been introduced during the 150 or so years since scientific records have been kept, Upper Pleistocene bryozoan faunas have the potential to prove that other species were a component part of the native biota prior to the time when human activities perturbed natural distributions.

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