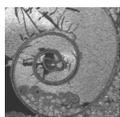# A new Early Jurassic gastropod from Ellesmere Island, Canadian Arctic – an ancient example of holoplanktonic gastropods

ALEXANDER NÜTZEL, SIMON SCHNEIDER, PETER HÜLSE, SIMON R.A. KELLY, LAURA TILLEY &
† REINHART VEIT

A new, most probably holoplanktonic gastropod genus and species, *Freboldia fluitans* Nützel & Schneider, is reported from the Early Jurassic (Pliensbachian) of Ellesmere Island, Canadian Arctic. Its shell is very thin, small, with a maximum diameter of 8 mm, inflated, planispiral and almost bilaterally symmetric, with deep umbilici. Hundreds of specimens of *Freboldia* occur in the matrix of transported siltstone concretions. In summary, these characteristics suggest a holoplanktonic lifestyle for *Freboldia*. Similar shells are present in the modern holoplanktonic gastropod family Limacinidae and in Cretaceous Bellerophinidae, and the new species is assigned to the latter family. The oldest records of holoplanktonic or pelagic gastropods are represented now by seven Early Jurassic genera: *Coelodiscus*, *Tatediscus*, *Costasphaera*, *Pterotrachea*, *Simoniceras*, *Globorilusopsis* and the new genus *Freboldia*. These are attributed to five different clades, which made their appearance at approximately the same time. We thus speculate that Early Jurassic anoxia triggered the rapid evolution of the holoplanktonic lifestyle in gastropods. • Key words: Jurassic, Canadian Arctic, pelagic holoplanktonic gastropoda, Pliensbachian, anoxia.

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Living holoplanktonic or pelagic snails are of moderate diversity (~ 140 species) but may be highly abundant and, owing to their lifestyle, widely distributed (*e.g.*, Lalli & Gillmer 1989). In places, particularly around ocean islands, above the aragonite compensation depth, dead shells of holoplanktonic gastropods may form a major component of the sediment, which is termed pteropod ooze (see Chen 1964, and references therein). A pelagic or planktonic lifestyle has evolved independently in Caenogastropoda and Heterobranchia and is probably polyphyletic even within these groups. Commonly these gastropods are considered to be planktonic although most of them are able to swim actively (Lalli & Gilmer 1989).

As summarized by Janssen & Peijnenburg (2013), the earliest certain members of the pteropods (planktonic Heterobranchia) are known from the late Palaeocene. Maubeuge (1998) discussed two Early Jurassic genera, *Globorilusopsis* and *Simoniceras*, including several species as being possibly related to the pteropods. However, while a holoplanktonic mode of life is possible in these Early Jurassic gastropods (see discussion below), an attribution to pteropods needs further testing.

Similarly, most modern heteropod families (planktonic Caenogastropoda) originate in the Cenozoic (see Janssen & Peijnenburg 2013 and Teichert & Nützel 2015 and references therein). However, a planktonic mode of life has been proposed for several Mesozoic gastropod genera, which were attributed to the heteropods. *Brunonia* and *Bellerophina* were reported from the Cretaceous (Destombes 1987, Dieni 1990). Additionally, several Early Jurassic gastropod genera, *i.e. Coelodiscus*, *Tatedicus*, *Pterotrachea* and *Costasphaera*, have been assigned to the heteropods (Bandel & Hemleben 1987, Nützel & Gründel 2015, Nützel & Teichert 2015).
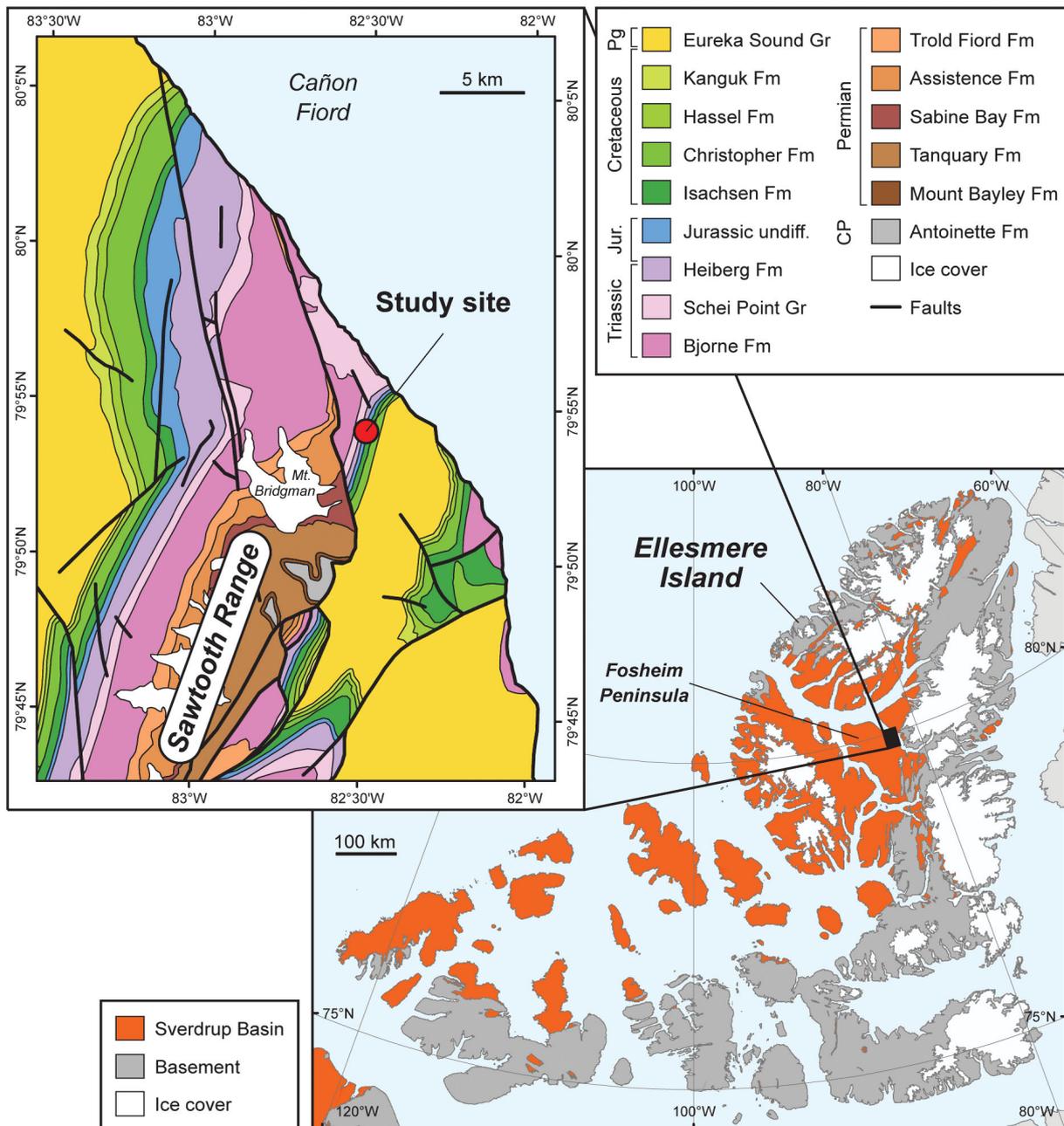
Figure 1. Geological overview of the Queen Elizabeth Islands, Arctic Canada (modified from Harrison *et al.* 2011) and the study area (inset map, modified from Thorsteinsson 1972). The study site is indicated by a red dot. Abbreviations: Gr = group; Fm = formation; undiff. = undifferentiated; Pg = Paleogene; Jur. = Jurassic; CP = Carboniferous to Permian.

Herein, we describe a new genus and species of putative Heteropoda, *Freboldia fluitans* Nützel & Schneider, from the Pliensbachian (Early Jurassic) of Ellesmere Island, Arctic Canada, which is assigned to the Bellerophinidae. The sudden appearance and considerable diversity of putative holoplanktonic gastropods in the Early Jurassic is noted, and potential underlying causes are discussed.

Geological setting

The fossils were collected along a river section northeast of Mount Bridgman (N 79° 54.209, W 82° 29.944), on the eastern side of the Sawtooth Range on Fosheim Peninsula, Ellesmere Island, Nunavut Province, Arctic Canada (Fig. 1). During the Early Jurassic, this area was part of the Sverdrup Basin, which is located in the Queen Elizabeth
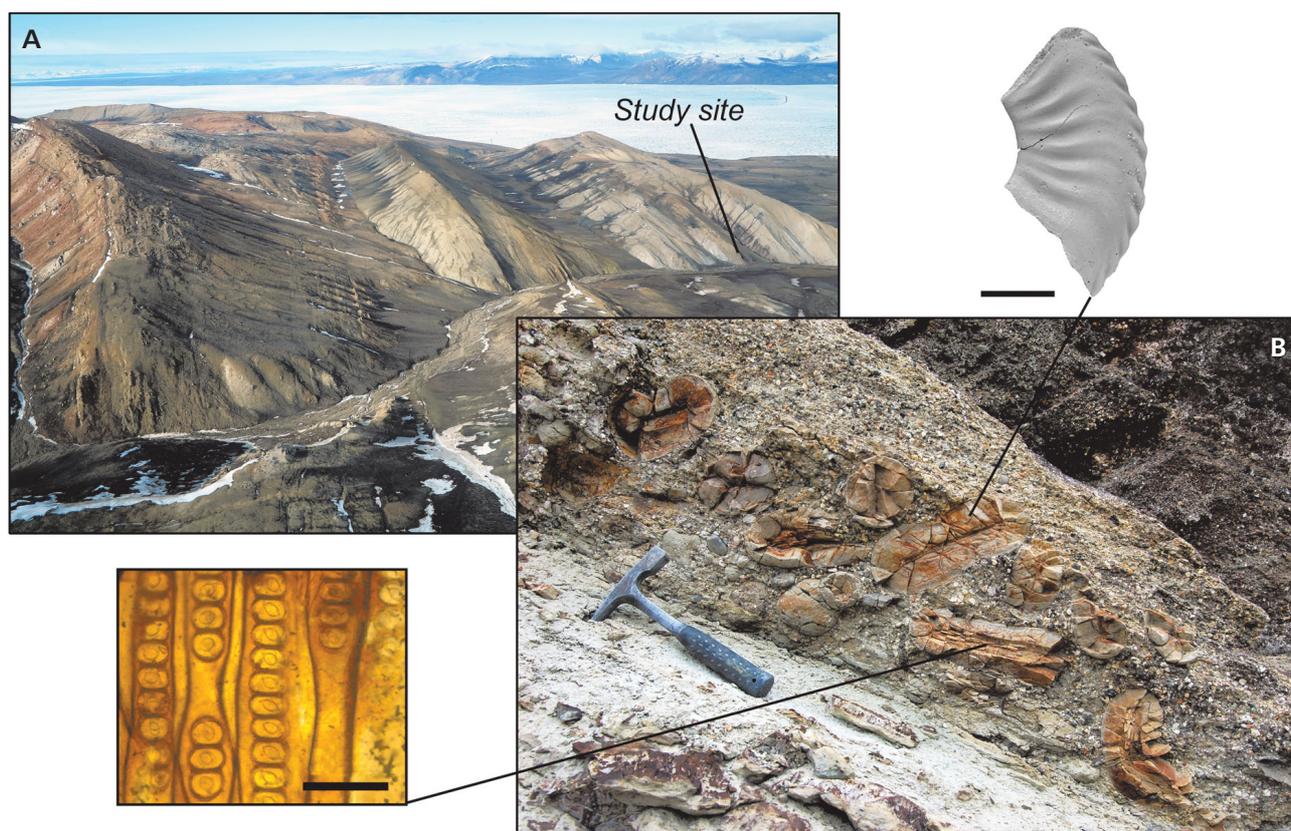
Figure 2. Outcrop. • A – river section east of Mount Bridgman, eastern slopes of Sawtooth Range, Fosheim Peninsula, Ellesmere Island. View from south, from helicopter. The position of the study site is indicated. Total width of photograph approximately 1.5 km. • B – siltstone concretions with pieces of fossilised wood as cores (early Late Pliensbachian in age), reworked into a polymictic conglomerate (Late Pliensbachian/Early Toarcian? in age); top part of Remus Member, Heiberg Formation. Length of hammer is approximately 40 cm. Upper right: *Amaltheus stokesi* (J. Sowerby), index fossil of the Stokesi subzone, CMN NUIF 419. Lower left: Radial longitudinal thin section of *Xenoxylon* sp. from the core of a concretion, CMN NUPB 464.

Islands and interisland channels (Nunavut and the Northwest Territories) and covers an area of approximately 300,000 km^2 (*e.g.* Schröder-Adams *et al.* 2014; Fig. 1). The study site was situated close to the eastern basin margin. Based on the palaeolatitude calculator of van Hinsbergen *et al.* (2015), a Pliensbachian palaeolatitude between 65° and 70° N can be assumed for this site.

The Sverdrup Basin is filled with up to 13 km of Carboniferous to Eocene sedimentary strata, which were deposited during eight major phases of development as proposed by Embry & Beauchamp (2008). These phases are characterised by distinct tectonic and depositional regimes and bounded by unconformities. The latest Triassic to earliest Cretaceous phase 5, characterised by widespread deposition of shallow offshore shelf deposits (Embry & Beauchamp 2008), is relevant to the present study. During the Rhaetian to Early Pliensbachian, the study area was part of an extensive delta plain, testified by the occurrence of massive, trough-cross-bedded sandstone beds with abundant plant material in the study section (Fosheim Member, Heiberg Formation; Embry 1983, Embry & Suneby 1995). Transgression in the Pliensbachian is repre-

sented by shallow-marine, partly sideritic sandstones, as demonstrated by intense bioturbation and the occurrence of shallow-marine bivalve and brachiopod assemblages (Remus Member, Heiberg Formation; Embry 1983). Outcrop is mediocre in this part of the section, and presumable mud- to siltstone intervals are covered by scree.

The most prominent interval at outcrop is a more than five metres thick succession of polymictic conglomerates, composed of several individual beds, which are partly impregnated with siderite and form a distinct ridge in the section (Fig. 2A). The present interpretation is that the conglomerates were deposited during transgression in a nearshore environment. At the base of the lowermost horizon, 10 to 40 cm long oval mudstone to siltstone concretions, formed around pieces of fossilised wood, are present in the conglomerate (Fig. 2B). Several of these concretions preserve a single, up to 5 cm thick fossiliferous horizon, which yielded the fossil assemblage discussed herein. The different matrix of the concretions and the conglomerate, the random orientation of the concretions and the discontinuity of the fossil layer clearly indicate that the concretions are reworked into the conglomerate.
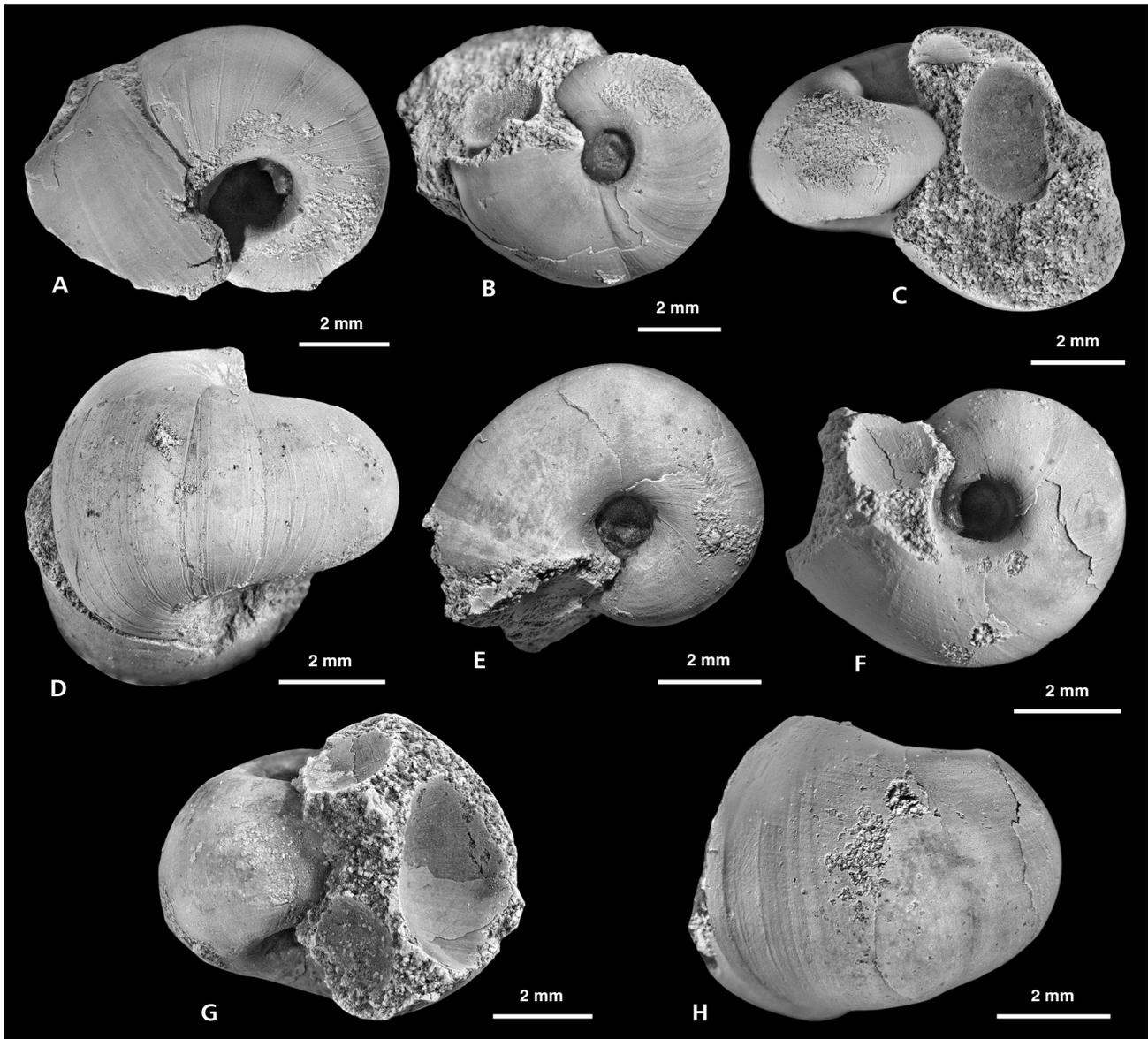
Figure 3. *Freboldia fluitans* gen. nov. sp. nov., coated with ammonium chloride for photographs. • A–D – paratype 1, CMN NUIF 1234. • E–H – paratype 2, CMN NUIF 1235. All scale bars 2 mm.

The reworked concretions and the enclosed fossil assemblage are accurately dated as earliest Late Pliensbachian by the occurrence of the ammonite *Amaltheus stokesi* (J. Sowerby, 1818), index species of the Stokesi Subzone of the Margaritatus Zone (*e.g.* Dommergues *et al.* 1997, Simms *et al.* 2004). Precise dating for the conglomerate layer itself is lacking. Assuming that it forms the top of the Remus Member, it should be latest Pliensbachian in age, but an (early) Toarcian age cannot be ruled out. With a significant interval of non-exposure, the conglomerates are overlain by intensely bioturbated mudstones, presumably of Toarcian age (Cape Canning Member, Jameson Bay Formation; Embry 1984, Embry & Johannessen 1992).

Two taxa of fossil conifer wood (*Cupressinoxylon* and *Xenoxylon*) have been identified from the fragments forming the cores of the concretions. Besides the supposedly holoplanktonic gastropods described herein, the fossil assemblage preserved in the matrix of the concretions yielded ammonites (*Amaltheus stokesi*, *Gemellaroceras*?), epi- and endobenthic bivalves (*Palaeonucula*, *Parvamussium*?, *Meleagrinella*, Limidae indet., *Liotrigonia*?, *Isotancredia*?, *Goniomya*), benthic gastropods (Pleurotomarioidea, Ataphridae), scaphopods (*Laevidentalium*) and a decapod fragment. The holoplanktonic gastropods occur *en masse*, comprising more than 90% of the specimens collected. The fossil assemblage, its palaeoecology and its peculiar taphonomy will be described in a separate study.
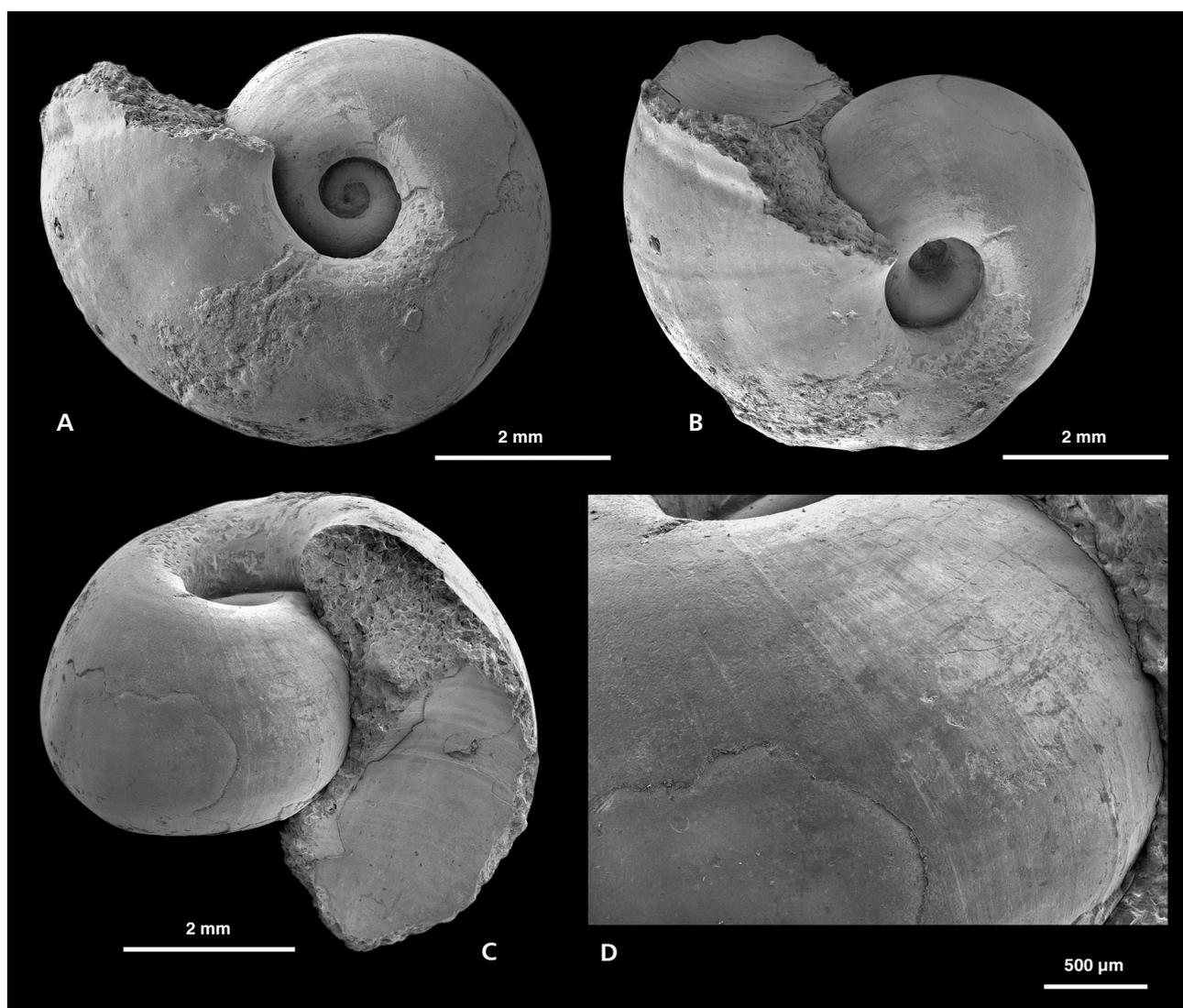
Figure 4. *Freboldia fluitans* gen. nov. sp. nov., holotype, SEM micrographs, CMN NUIF 422.

All fossil specimens from Ellesmere Island are stored in the collections of the Canadian Museum of Nature, Ottawa, Canada, (CMN) under collection numbers CMN NUIF 419 (*Amaltheus stokesi*), 422 (holotype of *Freboldia fluitans*), and 1234–1243 (paratypes and additional material of *Freboldia fluitans*), as well as CMN NUPB 464 (wood thin section).

Systematic palaeontology

Family Bellerophinidae Destombes, 1984

This family is based on the genus *Bellerophina* d'Orbigny, 1843 with its Early Cretaceous type species *Bellerophina minuta* (J. Sowerby, 1812). Except for *Brunonia*, it is the only putative holoplanktonic gastropod genus known from the Cretaceous. It is more or less bilaterally symmetrical with a diameter of up to 6 mm. Measurements of the shell thickness have not been provided, but according to published photographs (Destombes 1984, Tracey 2010), the shell is very thin, as can be expected for a holoplanktonic gastropod. Interestingly, already in the 19th century it was assumed that *Bellerophina minuta* was holoplanktonic (see Böhm 1918 for a discussion).

The new genus *Freboldia* is placed in Bellerophinidae because it shares an inflated bilaterally symmetrical shell shape with deep umbilici with *Bellerophina*.

Genus *Freboldia* Nützel & Schneider gen. nov.

Type species. – *Freboldia fluitans* sp. nov., by original designation herein.

Etymology. – In honour of Hans Frebold (1899–1983), German palaeontologist, for his remarkable contributions to the palaeontology of the Arctic, including the Early Jurassic of Arctic Canada (see Teichert 1984 for details).

Diagnosis. – Small, inflated, planispiral, bilaterally symmetrical shell with deep umbilici; aperture higher than wide, kidney-shaped with concave inner and convex outer lip; mature shell smooth, with fine, regular growth lines only; growth lines straight, orthocline at periphery and tangential towards umbilici; shell thin, approximately 25–50 μm in thickness.

Remarks. – *Freboldia* gen. nov. resembles the Early Cretaceous probably holoplanktonic genus *Bellerophina* Destombes, 1983 (type species *Bellerophina minuta*) in its globular shape and bilateral symmetry and in having a very thin shell. However, *Bellerophina* has a distinct reticulate ornament of axial and spiral lirae whereas *Freboldia* is smooth. The Pliensbachian to Aalenian probably holoplanktonic genus *Coelodiscus* Brösamlen, 1909 is not bilaterally symmetrical but has either a slightly elevated or faintly depressed spire (see Teichert & Nützel 2015). Moreover, *Coelodiscus* has a distinct, relatively dense spiral striation on the shell. The Early Jurassic genus *Tatediscus* resembles *Coelodiscus* in shape but differs from it and from *Freboldia* in having a conspicuous axial ornament.

Freshwater snails of the family Planorbidae, which ranges from the Jurassic to the Recent (Bandel 1991), hold forms that resemble *Freboldia*. However, they have shells of normal thickness, much thicker than in *Freboldia*, and a large protoconch with strong spiral cords (Riedel 1993). Moreover, *Freboldia* occurs in clearly marine sediment as indicated by the co-occurring mollusc fauna. Other Jurassic planispiral gastropods such as Discohelicidae differ from *Freboldia* in being widely phaneromphalous and disc-shaped instead of globular and involute.

Freboldia resembles the Palaeozoic to Early Triassic Bellerophontoidea in its bilaterally symmetrical shape, but this group is characterized by a median slit and selenizone and by having thicker shells.

The bilateral, planispiral, inflated shape of *Freboldia* also resembles the morphology of several Cenozoic to extant pteropods such as *Sphaerocina* Jung, 1971, *Heliconoides* d'Orbigny, 1835 and *Currylimacina* Janssen, 2003 (see *e.g.*, Cahuzac & Janssen 2010). However, these modern shells are distinctly more anisostrophically coiled (umbilici of unequal depth), and are sinistral especially in early whorls as is usual for coiled pteropod shells.

The possibility that *Freboldia* represents ammonitellas (early ontogenetic shells of ammonites) can be ruled out because internal moulds as well as thin sections revealed that septa are absent. Moreover, Mesozoic ammonitellas are much smaller than the present shells. De Baets *et al.* (2015, fig. 5.5) found that Jurassic ammonitellas are generally smaller than 1.5 mm.

Freboldia fluitans Nützel & Schneider sp. nov.
Figures 3–8

Holotype. – CMN NUIF 422 (Fig. 4).

Other material. – Eight illustrated paratypes, CMN NUIF 1234–1241 (Figs 3, 5–7); a thin section yielding several specimens, CMN NUIF 1242 (Fig. 8); and numerous additional specimens, CMN NUIF 1243.

*Type stratum*. – Remus Member, Heiberg Formation, Early Jurassic, late Pliensbachian, Stokesi subzone.

Type locality. – River section northeast of Mount Bridgman (N 79° 54.209, W 82° 29.944), on the eastern side of the Sawtooth Range on Fosheim Peninsula, Ellesmere Island, Nunavut Province, Arctic Canada.

Etymology. – From the Latin verb *fluitare*, meaning "drifting, floating", referring to the supposed planktonic style of living.

Description. – Shell small, with maximum diameter of 8 mm and maximum height of 6.3 mm; inflated, globular, planispiral, bilaterally symmetric, with deep umbilici. Aperture higher than wide in lateral view, kidney-shaped, with concave inner and convex outer lip. Mature shell smooth, with growth-lines only; growth lines straight, orthocline at periphery and tangential towards umbilici. Early ontogenetic shell with faint spiral striation and minute tubercles. Shell thin, approximately 25–40 μm in thickness.

Remarks. – Due to its bilaterally symmetrical shell, including umbilici of about the same depth and the overgrowth of the early whorls, it is unclear whether *Freboldia fluitans* has a dextral or sinistral mode of coiling. The smallest studied specimens (Fig. 7) have a diameter of about 1 mm. Their earliest visible whorl portions indicate no sign of sinistral coiling. Therefore, it is unlikely that *Freboldia* is

Figure 5. *Freboldia fluitans* gen. nov. sp. nov., SEM micrographs. • A–D – paratype 3, CMN NUIF 1236; D showing thin shell, partly peeled off. • E, F – paratype 4, CMN NUIF 1237, juvenile whorls showing faint spiral ornament.
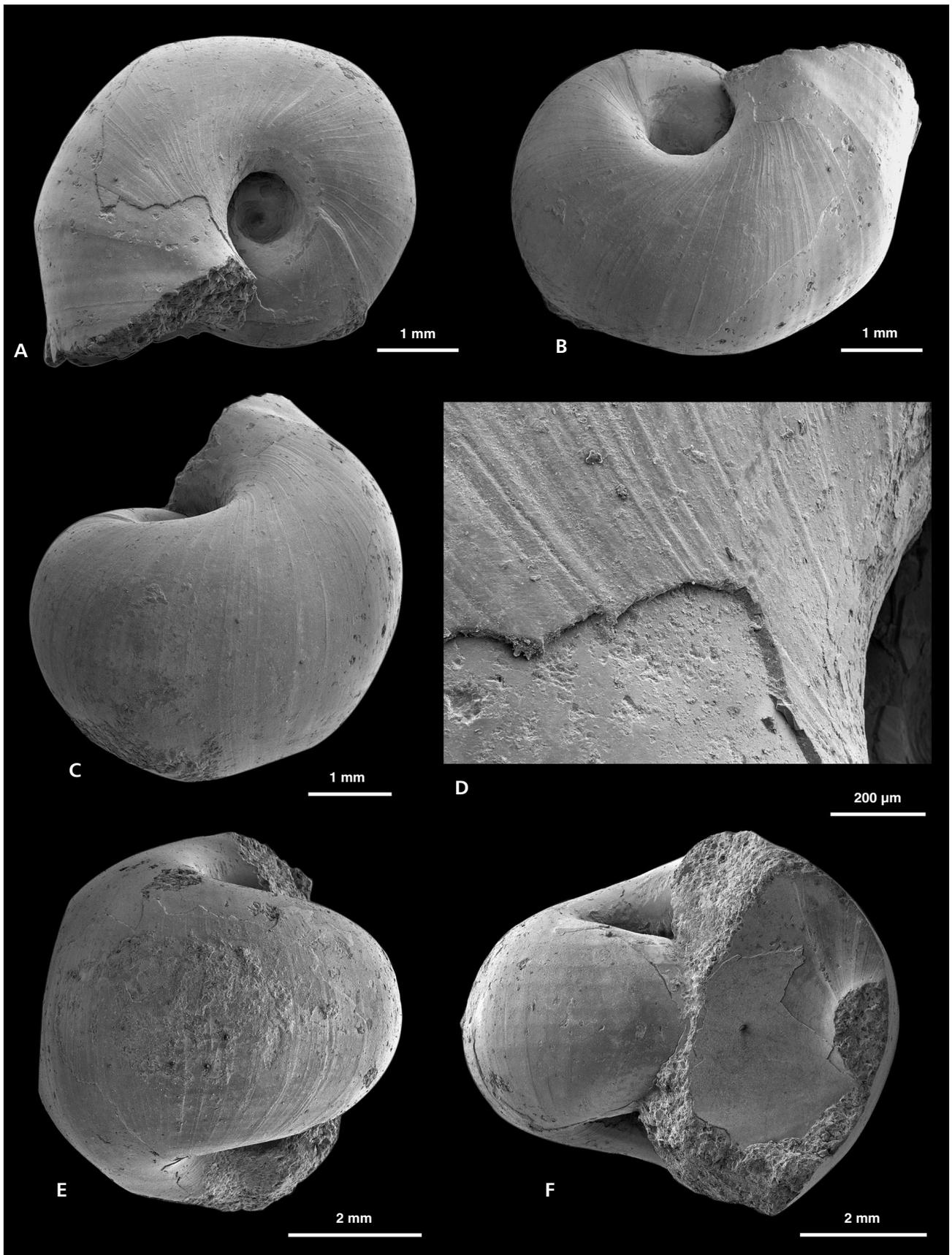
heterostrophic. However, the earliest portions of the whorls are covered by cement or matrix.

Since both the protoconch and the teleoconch are largely smooth, the transition from protoconch to teleoconch is indistinct, as is common in smooth-shelled fossil gastropods (see Nützel 2014). Whorls at a small shell size of distinctly less than 1 mm show a very fine micropunctation (Figs 6D–F, 7), which we could not detect in larger growth stages. We assume that this points to a larval shell of the planktotrophic type with fine micro-ornamentation. However, we were unable to document the termination of this possible larval shell and hence its exact size cannot be determined. To our knowledge, planispiral smooth larval shells with micro-punctation have not been reported from other holoplanktonic gastropods.

Discussion

The very thin shell, small size, bilaterally symmetrical shape and mass occurrence suggest a holoplanktonic life-style for *Freboldia fluitans* gen. et sp. nov. None of these arguments alone is unequivocal but overall, it is very likely that this gastropod had a planktonic lifestyle. The thin shell of 25–40 μm, in particular, represents important evidence for this hypothesis. Recent heteropods and pteropods have thin shells, which is undoubtedly an adaptation to the holoplanktonic lifestyle (weight reduction). Batten & Dumont (1976) investigated the holoplanktonic heteropods *Oxygyrus keraudreni* (Lesueur, 1817), *Protatlanta souleyeti* (Smith, 1888) and *Atlanta inclinata* with regard to shell structure and reported shell thicknesses of less than 50 μm for these species. Lalli & Gilmer (1989) summarized that in shelled pteropods the shell thickness ranges from 6 to 100 μm, being "unusually thin". The same authors reported a shell thickness ranging from 4 to 40 μm for atlantids (heteropods). Zhang *et al.* (2011) reported a shell thickness of 10 to 30 μm for the recent pteropod *Cavolinia uncinata*. Other recent holoplanktonic snails have reduced their shell completely or use cartilageous instead of mineralic material.

The maximum shell size of less than 10 mm could also argue for a holoplanktonic lifestyle. Living atlantids and Pterotracheidae (the latter have only larval shells) as well as shelled pteropods usually have a shell diameter of less than 10 mm (Lalli & Gilmer 1989). As an exception, Carinariidae may have shells of more than 100 mm length. The Early Cretaceous (Barremian to Aptian) *Brunonia*

annulata (Yokoyama, 1890), which is the type species of *Brunonia*, has been placed in the planktonic heteropod family Carinariidae by Dieni (1990), who based his assumption mainly on the wide palaeogeographic distribution of this species. The limpet-shaped shell of *Brunonia annulata* is rather large, with distinct concentric annulations. Specimens from Japan reach 30 mm in diameter and specimens from Italy grew even as large as 6 cm. The rather capuliform shells of Recent *Carinaria* may reach a length of 140 mm (A.W. Janssen written communication including illustration), and thus this rather large size does not argue against a planktonic mode of life. However, additional evidence such as information about shell thickness would be desirable to corroborate a pelagic mode of life for *Brunonia*.

The almost bilaterally symmetrical, coiled shell of *Freboldia* could also point to a planktonic lifestyle. As discussed above, this morphology also occurs in several modern pteropods. Bilateral symmetry is also present in uncoiled pteropods and in *Cavolinia*. Richter (1973) interpreted the bilateral symmetry of pelagic gastropods as an adaptation to an actively swimming lifestyle.

To our knowledge, a holoplanktonic mode of life has not been reported for Palaeozoic and Triassic gastropods. Certain exclusively Palaeozoic groups such as the straight-shelled Tentaculita have been assigned to pteropods but this attribution is generally not accepted any longer, although some of these forms had probably a planktonic life-style (*e.g.*, Berkyová *et al.* 2007).

It is remarkable that there are no pre-Jurassic reports of pelagic gastropods. Putative holoplanktonic gastropods make their first appearance in the Early Jurassic, where the following seven genera are reported from Europe, South America and now the Canadian Arctic: *Coelodiscus* Brösamlen, 1909, *Costasphaera* Gründel & Nützel, 2015 (*in* Nützel & Gründel 2015), *Freboldia* gen. nov., *Globorilusopsis* Maubeuge, 1994, *Pterotrachea* Forsskål *in* Niebuhr, 1775 *sensu* Bandel & Hemleben (1987), *Simoniceras* Maubeuge, 1998, *Tatediscus* Gründel, 2001 (Table 1).

In all of these genera, evidence for a pelagic lifestyle is circumstantial, similar to that discussed for *Freboldia*. *Coelodiscus* and *Tatediscus* are closely related to each other and form the family Coelodiscidae Gründel, 2013 (*in* Schulbert & Nützel), which ranges from the Early Pliensbachian to the Early Aalenian (Schulbert & Nützel 2013, Teichert & Nützel 2015). They occur in oxygen-controlled environments in Central Europe and England (for

Figure 6. *Freboldia fluitans* gen. nov. sp. nov., SEM micrographs of early juvenile whorls. • A–C – paratype 5, CMN NUIF 1238; the pitted sculpture is not a shell ornament but represents impressions of a spherulithic A-cement that grew on the inner side of the of the peeled off shell. • D–F – paratype 6, CMN NUIF 1239; small specimen, early juvenile or larval whorl with punctate micro-ornamentation.
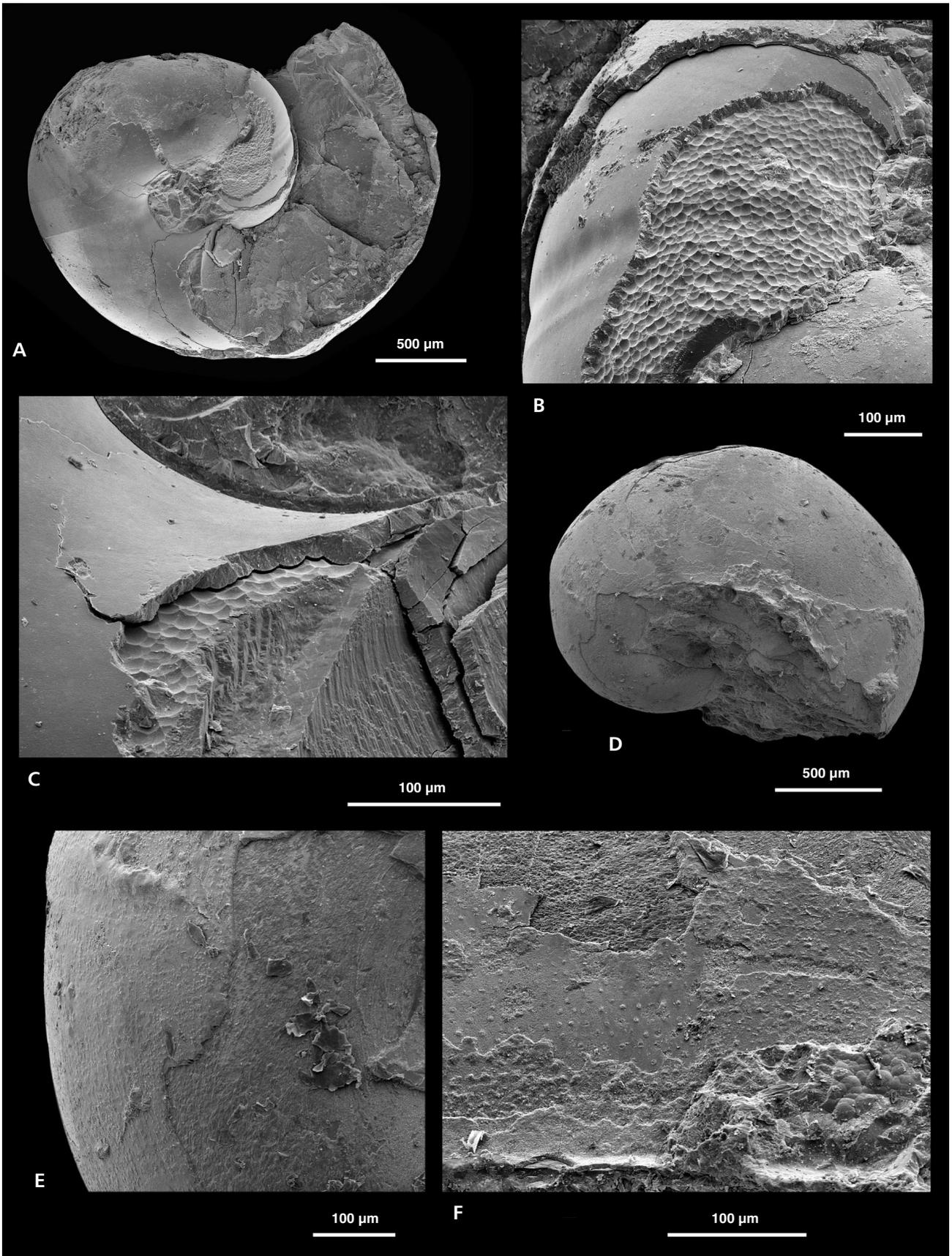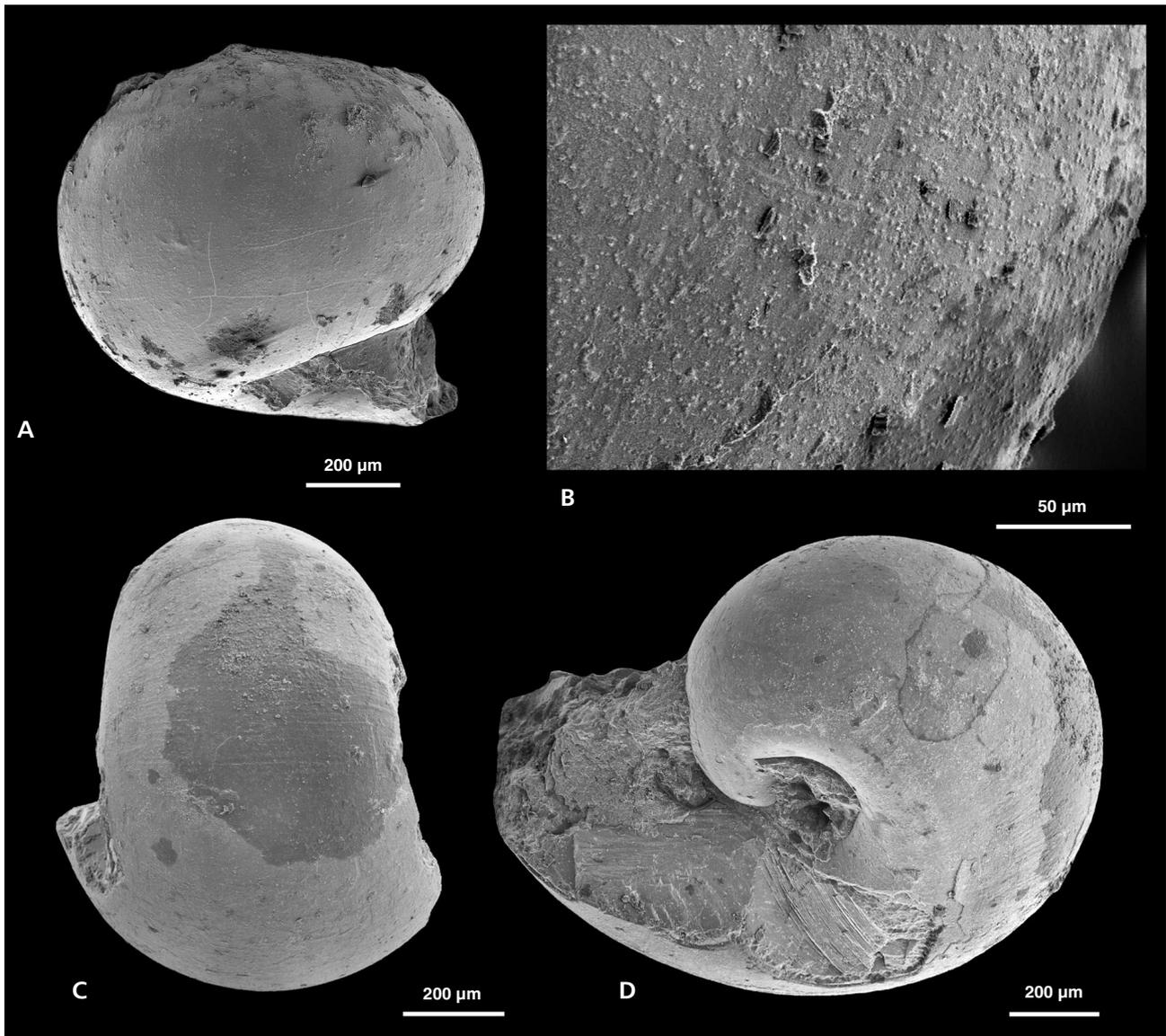
Figure 7. *Freboldia fluitans* gen. nov. sp. nov., SEM micrographs. • A, B – small specimen, probably larval shell with punctate micro-ornamentation. Paratype 7, CMN NUIF 1240. • C, D – CMN NUIF 1241, small specimen; earliest portions of whorls show no indication of heterostrophy.

a discussion see Bandel & Knitter 1983, 1986; Bandel & Hemleben 1987; Teichert & Nützel 2015) and have also been reported from Argentina (Gründel 2001).

Globorilusopsis and *Simoniceras* comprise several small species from the late Early Jurassic of Luxembourg, which are uncoiled to a variable degree. Maubeuge (1998) discussed a possible relationship with modern thecosomate pteropods but classified both Jurassic genera as small conoidal shells of uncertain affinity. There can be little doubt that these shells represent gastropods, based on their helicoidally coiled initial whorls. Based on their small size and general morphology, a pelagic lifestyle seems plausible. However, further study of shell thickness and protoconch morphology, in particular, is required.

Costasphaera, recently described by Nützel & Gründel (2015), is a tiny, helicoidally coiled gastropod with strong ribbing pattern that was repeatedly reported from the Pliensbachian of southern Germany and England. The possibility that these shells represent larval shells of an unknown caenogastropod cannot be ruled out entirely, but so far they have never been found attached to adult shells although they occur in faunas with abundant benthic gastropods.

Pterotrachea is a living pelagic gastropod with a relatively large body that lacks an adult shell. However, it has a larval shell that is almost planispiral, either smooth or axially costate (Richter 1968). These larval shells are small and, according to published images, range from 0.4 to
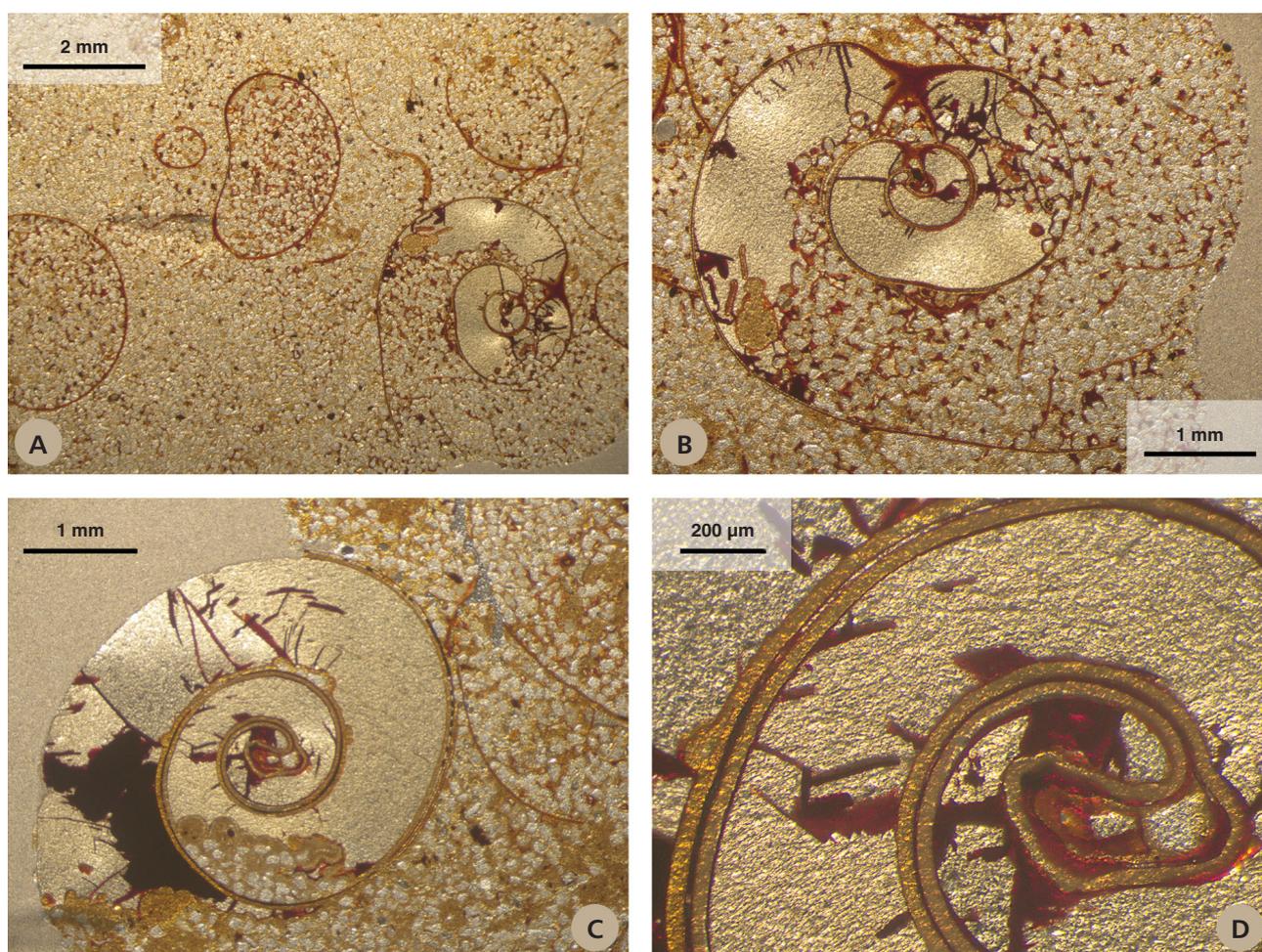
Figure 8. Thin section with *Freboldia fluitans* gen. nov. sp. nov., SEM micrographs. CMN NUIF 1242 (7634-41), scale bars A: 2 mm, B, C: 1 mm, D: 0.2 mm.

0.7 mm in diameter (Richter 1968, Janssen in Tree of Life Web Project, accessed October 2015). Bandel & Hemleben (1987) assigned the Toarcian "*Ammonites*" *ceratophagus* (alias *Pterotrachea liassica*) from Germany to the Recent heteropod genus *Pterotrachea*. We agree with the hypothesis that "*Ammonites*" *ceratophagus* is a pelagic gastropod, and a relationship with heteropods seems possible. However, Bandel & Hemleben (1987) reported that the shell of this species has a diameter of up to 3.5 mm; thus, it clearly does not represent a larval but an adult shell (see Nützel 2014). Therefore, a placement of these Jurassic shells in the Recent genus *Pterotrachea* is not justified, although the morphology of the Jurassic "*Ammonites*" *ceratophagus* and certain larval shells present in modern *Pterotrachea* is indeed similar.

As outlined above, the morphology of the new genus *Freboldia* is distinct from that of all other Jurassic putative pelagic gastropods and more similar to the Cretaceous *Bellerophina*. Jurassic pelagic gastropods also differ considerably from modern ones in shell morphology. Similar-

ities in some forms are probably rather the result of convergence according to a similar lifestyle. At present, we do not think that Jurassic pelagic gastropods are direct ancestors of the modern ones. We speculate that the fossil groups became extinct and that modern pelagic gastropods evolved much later. These assumptions need corroboration by new fossil finds. However, as outlined by Janssen & Peijnenburg (2013), the fossil record of holoplanktonic gastropods is hampered by their very thin aragonitic shells. In the discussed Jurassic forms, concretionary preservation plays a pivotal role because concretions are formed fast during early diagenesis and prevent compaction of the fragile shells.

This is also the case for *Freboldia*. Its shells were found accumulated in a single horizon within siltstone concretions that, apart from planktonic and nektonic elements, also preserve an autochthonous benthic fauna of various bivalves, scaphopods, small benthic gastropods and decapod crustaceans. These organisms testify a well-oxygenised sea bottom and upper sediment layer at moderately shallow

Table 1. Jurassic gastropod genera with a putative holoplanktonic life style, their stratigraphic range and geographic distribution. The higher systematic placements of these genera are largely unknown although some have been attributed to heteropods (Caenogastropoda) or pteropods (Heterobranchia). *The placement of Early Jurassic shells in the modern genus *Pterotrachea* is doubtful (see discussion).

Genus	Stratigraphic range	Geographic distribution
Coelodiscus	Pliensbachian–Aalenian	Germany, England, France, Switzerland
Costasphaera	Sinemurian–Pliensbachian	Germany, England
Freboldia	Pliensbachian	Arctic Canada
Globorilusopsis	Toarcian	Luxembourg
*Pterotrachea**	Toarcian–Recent	Germany
Simoniceras	Toarcian	Luxembourg
Tatediscus	Pliensbachian	England, Germany, Argentina

depths (several tens of metres). Most bivalves are preserved with attached valves, indicating little or no transport. Consequently, the accumulation of fossils may be related to winnowing by bottom water currents or to a phase of rather low sediment deposition. Certainly, early lithification of the concretions has promoted the preservation of undistorted shells in all the rather small molluscs recorded.

In summary, there are five known groups of Early Jurassic pelagic gastropods representing seven genera. Some of these gastropods are abundant and widespread. This earliest radiation of the pelagic lifestyle in Gastropoda is particularly remarkable, because pre-Jurassic pelagic gastropods are unknown.

During and after the end-Triassic biotic crisis, anoxic or dysoxic bottom waters were wide-spread, likely related to changing oceanographic patterns due to the breakup of Pangaea and the opening of the Atlantic Ocean (Hallam 1981, Hallam & Wignall 1997, van de Schootbrugge *et al.* 2013). Carbon cycle anomalies and recurrent anoxia persisted throughout much of the Hettangian (Bartolini *et al.* 2012), and further anoxic and dysoxic episodes are reported from the Sinemurian and Pliensbachian (van de Schootbrugge *et al.* 2013). Finally, the Pliensbachian–Toarcian Anoxic Event is well known as the most likely cause of the end-Pliensbachian extinction event. To sum up, oxygen deficiency was obviously a widespread phenomenon throughout much of the Early Jurassic.

Different scenarios have been proposed to explain this series of anoxia. However, increased input of organic matter from the continents has been generally suggested as a main driver. Bailey *et al.* (2003) suggested that global warming boosted continental weathering, freshwater runoff and the hydrologic cycle in general, resulting in a higher content of organic matter in the sea during anoxia. Van de Schootbrugge *et al.* (2013) also stated, "long-term ocean anoxia during the Early Jurassic can be attributed to greenhouse warming and increased nutrient delivery to the oceans" and hypothesized that this is "triggered by flood basalt volcanism".

The coincidence of repeated or long lasting anoxic or dysoxic conditions on the seafloor and the emergence of several pelagic gastropod groups within the Early Jurassic suggest that these phenomena might be causally linked. As hypothesized by Teichert & Nützel (2015) for the pelagic Early Jurassic gastropod *Coelodiscus*, the poor benthic living conditions during anoxia could have triggered the evolution of a planktonic life style in several gastropod lineages. As most marine gastropods undergo a planktonic larval stage, the prolongation of this condition into a holoplanktonic adult mode of life seems to be a relatively simple step. Mainly, it involves the partial or complete reduction of the adult shell, as can be seen in many modern representatives. Obviously, maintaining functional digestive and reproductive systems requires more space than is provided in many of these relic shells and large parts of the body are thus often unprotected in modern holoplanktonic gastropods. Several representatives also have completely reduced their shells. A similar development within several of the Early Jurassic holoplanktonic clades could explain their disappearance from the successive Mesozoic fossil record.

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