New species of *Yochelcionella* (Mollusca; Helcionelloida) from the Lower Cambrian of North Greenland

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The genus *Yochelcionella* Runnegar & Pojeta, 1974 contains small, coiled or cap-shaped, bilaterally symmetrical Cambrian molluscs that are distinguished by a characteristic tube-like snorkel located on the median line near the apex. The snorkel is located below the apex on the concave, sub-apical, surface of the coiled shell, but several species undergo a partial reversal of coiling direction during ontogeny such that the snorkel may appear to be located supra-apically. The snorkel is generally accepted as being associated with the transport of water between the mantle cavity and surrounding environment. There is debate, however, as to the orientation of the shell and the precise function of the snorkel. Runnegar & Pojeta (1974) considered the shell of *Yochelcionella* to be exogastric with the snorkel located anteriorly on the sub-apical wall and providing a conduit for the inhalation of oxygenated water. Pojeta & Runnegar (1976) put forward four possible interpretations for the function of the snorkel but re-stated their earlier conclusion (Rennegar & Pojeta 1974). This interpretation was challenged by Yochelson (1978), Geyer (1986), Peel & Yochelson (1987), Berg-Madsen & Peel (1987), Peel (1991a, b) and Hinz-Schalreuter (1997), who considered *Yochelcionella* to be endogastric with the snorkel placed posteriorly on the sub-apical wall as a pipe for the exhalation of de-oxygenated water. Riedel (1996) considered the shell to be exogastric, following Runnegar & Jell (1976), but suggested that the snorkel served the double function of inhalation and exhalation, an interpretation previously suggested by Peel (1991a, b) for the laterally compressed *Yochelcionella americana* Runnegar & Pojeta, 1980. A similar mechanism is employed by recent scaphopods (Morton 1988; Reynolds 2002). In the novel interpretation of Parkhaev in: Gravestock et al. (2001) and Parkhaev (2002), *Yochelcionella* is oriented with the apex and the snorkel located posteriorly, but it is interpreted as a gastropod. In this model, water is supposed to have entered the mantle cavity through the posterior snorkel prior to expulsion antero-laterally.

While broadly inferred to be vagile, epifaunal, or semi-infaunal benthic grazers or detrital feeders, the range of morphologies, from strongly coiled to orthoconic, displayed by species of *Yochelcionella* suggests a variety of modes of life. The narrow, laterally compressed, aperture in some yochelcionellids suggests a semi-infaunal mode of life (Stanley 1970; Peel 1991a, b), whereas the relatively wide apertures of other species may indicate an epifaunal habit (Linsley 1977).

*Yochelcionella* was first figured but not described by Walcott (1890) as *Stenotheca rugosa var. erecta* from the Lower Cambrian of Conception Bay, eastern Newfoundland. The genus itself was proposed by Runnegar & Pojeta (1974) for a new species, *Yochelcionella*...

Peel (1980) reported but did not describe **Yochelcionella** from the Cambrian of North Greenland. A supposed Upper Cambrian specimen was derived from the Cass Fjord Formation of western North Greenland, although subsequent re-arrangement of North American chronostratigraphic nomenclature by Robison (1988) indicated that the Dresbachian straddles the Middle – Late Cambrian boundary, and the record is thus of latest Middle Cambrian age. Unfortunately, the tiny specimen can not presently be located and the record is not confirmed. Skovsted (2004) described a poorly preserved specimen from the Lower Cambrian Bastion Formation of North-East Greenland.

In this paper, we propose two new species of **Yochelcionella** from the Lower Cambrian of North Greenland (Fig. 1): **Yochelcionella greenlandica** and **Y. gracilis**. All specimens were collected from the Brønlund Fjord Group during the North Greenland campaigns (1978–1985) of the Geological Survey of Greenland, now part of the Geological Survey of Denmark and Greenland (GGU sample prefix). Type and figured specimens are deposited in the type collections of the Geological Museum, Copenhagen, Denmark (MGUH specimen prefix).

**Geological background**

The Cambrian shelf stratigraphy of North Greenland has been fully described by Ineson & Peel (1997) who proposed a comprehensive stratigraphic nomenclature; see also Peel & Sonderholm (1991). The extensive Lower Cambrian trilobite faunas were described by Blaker & Peel (1997), who gave full details of localities. Information concerning the location of all samples described below is given with reference to these publications. Samples were collected from the Brønlund Fjord Group, a succession of Lower – Middle Cambrian dolomites, limestones and subordinate siliciclastics which accumulated in platform margin to outer shelf environments in North Greenland on the southern margin of the Franklinian Basin of Arctic North America. Eight formations were recognised within the Brønlund Fjord Group (Ineson & Peel 1997) and those occurring within the areas yielding **Yochelcionella** are indicated in Figure 1. The Henson Gletscher Formation is strongly diachronous within North Greenland. In southern Freuchen Land, it is entirely of Early Cambrian age, while in western Peary Land it extends up to the Ptychagnostus gibbus Zone of the Middle Cambrian. Early Cambrian faunas have not been located within the formation along the northern coast of North Greenland, where the Henson Gletscher Formation extends upwards to the latest Middle Cambrian (Ineson & Peel 1997, p. 50).

GGU samples 225711, 225712 and 225714 were collected by J. S. Peel (locality 19790715–2) from dark limestones of the Henson Gletscher Formation, Brønlund Fjord Group, in Løndal, western Peary Land (Fig. 1; see Blaker & Peel 1997, figs 8A, 11; GGU sample 225711 is from the same horizon as 225712).

GGU samples 271470 and 271471 are phosphatic dolomites which were collected from the Aftenstjernø Formation, Brønlund Fjord Group, on the west side of J. P. Koch Fjord, Lauge Koch Land, central...
North Greenland (Fig. 1; J. S. Peel locality 19780625–1). This is the type locality of the Aftenstjernesø Formation described by Ineson & Peel (1997, pp. 39–46, figs 23, 24A, 25). The two samples were collected in the basal member of the formation, 1 m below the base of a prominent breccia, the base of which is illustrated by Ineson & Peel (1997, fig. 27).

GGU sample 271717 was collected from the Aftenstjernesø Formation, Brønlund Fjord Group, in Londal, western Peary Land (Fig. 1; J. S. Peel locality 19780714–1). The sample of dolomitised limestone with phosphorite were collected at the top of the basal member of the formation, on the west side of Londal. The locality is about 200 m east of the point of intersection of the base of the Brønlund Fjord Group and the southernmost fault indicated by Ineson & Peel (1997, fig. 57A).

GGU sample 274907 is from silicified limestones of the Paralleldal Formation, Brønlund Fjord Group, collected on the north side of Paralleldal, central Peary Land (Fig. 1; collected by J. S. Peel on 26th July 1980 from J.R. Ineson locality 19800624–1). This is the same locality as GGU sample 274908 in Blaker & Peel (1997, fig. 8B).

GGU sample 301354 is a talus block of dark limestone from the Henson Gletscher Formation, Brønlund Fjord Group, collected by J. S. Peel 17th August 1985 from the easternmost nunatak on the northern side of the main, south-westward flowing, tributary glacier of Jungersen Gletscher, southern Freuchen Land (north easternmost outcrop of Brønlund Fjord Group in Ineson & Peel 1997, fig. 78). This is the easternmost of two localities in southern Freuchen Land indicated in Fig. 1; it is located about 7 km north-east of GGU sample 315092.

GGU sample 315092 is a dark limestone collected by J.S. Peel from the Henson Gletscher Formation, Brønlund Fjord Group, southern Freuchen Land (S.C. Wright and J. S. Peel locality 19840719–1). This is the same horizon as GGU sample 315093 of Blaker & Peel (1997, figs 8A, 10) and is located about 10.5 m above the base of the formation. It is the reference section through the Henson Gletscher Formation described by Ineson & Peel (1997, figs 32, 33).

Preservation. Specimens of Yochelcionella from GGU samples 225711, 225712, 225714, 271717, 271470, 271471 and 315092 are preserved as phosphatic internal moulds which were recovered by bulk acid dissolution of samples in buffered acetic acid (10%). Specimens from GGU samples 274907 and 301354 are preserved as silica replicas and were released from the rock using dilute hydrochloric acid.

Systematic Palaeontology

Phylum Mollusca Cuvier, 1797
Class Helcionelloidea Peel, 1991a
Order Helcionellida Geyer, 1994
Superfamily Helcionellacea Wenz, 1938
Family Yochelcionellidae Runnegar & Jell, 1976

Genus Yochelcionella Runnegar & Pojeta, 1974

Type species. Yochelcionella cyrano Runnegar & Pojeta, 1974, from the early Middle Cambrian, Coonigan Formation, New South Wales, Australia.

Yochelcionella greenlandica n.sp.

Holotype. MGUH 27016 from GGU sample 271471, Aftenstjernesø Formation, Brønlund Fjord Group, central North Greenland.

Additional Material. Aftenstjernesø Formation, GGU samples 271470 (34 specimens), 271471 (30 specimens) and 271717; Henson Gletscher Formation, GGU samples 225711, 225712, 225714 and 315092; Paralleldal Formation, GGU sample 274907.

Diagnosis. -A species of Yochelcionella with overhang- ing apex and well-formed symmetrical rugae on the lateral surfaces; the ruga concurrent with the lower (adapertural) margin of the snorkel has the same inclination as the snorkel, lying oblique to earlier and later rugae when viewed in lateral aspect. An ontogenetic increase in the rate of shell expansion, produces a sigmoidal curve on the supra-apical surface in lateral aspect.

Description. Bilaterally symmetrical, moderately lat- erally compressed helcionelloid mollusc with a prominent sub-apical snorkel. Protoconch represented on the internal mould by a rounded boss at the apex. Prior to the formation of the snorkel, the shell is relatively narrower than in later growth stages, with one prominent ruga on each lateral surface, and coiled
such that the apex overhangs the sub-apical wall. On the supra-apical margin, almost in line with the adapertural margin of the snorkel, a change in curvature in lateral view produces a slightly sigmoidal profile due to an increase in the rate of expansion of the supra-apical surface. Adult stage less coiled, almost orthoconic, laterally strongly rugose, with two or more co-marginal rugae on each lateral surface which continue across the supra-apical surface. The first of these rugae is inclined concordantly with the snorkel and does not pass around the sub-apical margin. The second, and subsequent rugae continue beneath the apex. Aperture oval with a length:width ratio of 3:2. Snorkel circular in cross-section, directed slightly upwards away from the shell; initially parallel sided, but flaring slightly outwards. A slight thickening of the shell at the base of the snorkel produces a corresponding depression on the internal mould. Shell thickness and ornamentation unknown.

Discussion. Specimens of *Yochelcionella greenlandica* n. sp. from the Aftenstjernesø and Henson Gletscher formations are phosphatic internal moulds, whereas the type species, *Y. cyrano* Runnegar & Pojeta, 1974 from the Middle Cambrian of Australia, is a silica replica (Runnegar & Jell 1976). *Yochelcionella greenlandica* has a taller shell than the type species, with more prominent rugae and a narrower snorkel. An internal mould tentatively referred to the type species by Runnegar & Jell (1976, fig. 11A, 1–3) lacks an overhanging apex and has a massively thickened snorkel. The type suite of *Y. cyrano*, however, shows similar curvature of the early growth stages to *Y. greenlandica*, although the allometric sigmoidal curvature of the latter is not developed.

Poorly preserved Lower Cambrian *yochelcionellids* described by Landing & Bartowski (1996, fig. 6.3–5) from the Browns Pond Formation, New York, U.S.A., and Landing et al. (2002, fig. 8.9), from the ‘Anse Maranda Formation’, Québec, Canada, closely resemble *Y. greenlandica* and probably represent the same species. All are fragmentary, although one specimen illustrated by Landing & Bartowski (1996, fig. 6.3) clearly illustrates the robust ruga paralleling the inclination of the snorkel, overhanging apex and curvature of the supra-apical wall characteristic of *Y. greenlandica*. A further specimen, interpreted by Landing & Bartowski (1996, fig. 6.4) as a phosphatised shell has generally smooth walls with a faint ruga in line with the snorkel, and an outline that closely resembles the internal moulds of *Y. greenlandica*.

*Yochelcionella pelmani* Vassilyeva, 1990, from the Early Cambrian (Tommotian) of Siberia is at present the earliest known yochelcionellid (Vassilyeva 1990). Vassilyeva (1998) transferred the species to *Eutebenna* Runnegar & Pojeta, 1974 but her illustrations suggest that the snorkel is developed as a closed tube, making assignment to *Yochelcionella* more likely. It can be distinguished from *Y. greenlandica* by its less coiled, cap-shaped shell and more steeply inclined, robust snorkel. The apical area above the snorkel in *Y. pelmani* is relatively much reduced, not overhanging, and the rugae are finer and more numerous. Esakova & Zhegallo (1996) described two species of *Yochelcionella* from the Lower Cambrian of Mongolia. *Y. crassa* Zhegallo in: Esakova & Zhegallo (1996, pl. 24, figs 1–7) has a more elongate and laterally compressed conch with more numerous and less robust rugae that continue around the sub-apical and supra-apical walls. Some specimens illustrate the change in rate of expansion on the supra-apical surface seen in *Y. greenlandica* (Esakova & Zhegallo 1996, pl. 24, figs 1, 2, 5). The apex and snorkel are both erect but appear to diverge on account of the lack of coiling of the apex. *Y. para* Zhegallo in: Esakova & Zhegallo (1996, pl. 24, fig. 8–10) has a tall narrow shell which is concave on the supra-apical surface due to pronounced allometry. The earliest growth stage appears straight and diverges strongly from the upright snorkel, unlike the coiled early growth stage of *Y. greenlandica*. Many fine rugae are continuous around the shell pass around the sub- and supra-apical surfaces.

*Stenotheca rugosa* var. *erecta* Walcott, 1891, from the Lower Cambrian of Conception Bay, eastern Newfoundland, was referred to *Yochelcionella* by Hinz Schallreuter (1997). It has a tall, slender, cap-shaped shell with many rugae and a tiny snorkel; the apex is missing in the holotype.

*Yochelcionella recta* and *Y. stylifera* were first described by Missarzhevsky & Mambetov (1981) from the Lower Cambrian of Maly Karatau Kazakhstan. *Yochelcionella recta* is distinguished from *Y. greenlandica* by its gently curving, elongate, and laterally compressed shell (Missarzhevsky & Mambetov 1981, pl. 10, fig. 8). The snorkel in their illustration is merely represented by a low bulge beneath the tall early growth stage. *Yochelcionella stylifera* has prominent rugae similar to those seen in *Y. greenlandica*, but the apex is upright with no overhang and the shell is not coiled. *Yochelcionella* sp. of Dzik (1994) from the Early Cambrian (Atdabanian) of Siberia may be conspecific with *Y. aichalica* Fedorov in: Shabanov et al. (1987, pl. 33, figs 11, 14) and can be differentiated from *Y. greenlandica* by the well rounded protoconch which is curved so strongly backwards as to overhang the supra-apical surface.

*Yochelcionella americana* Runnegar & Pojeta, 1980, from the late Early Cambrian of Pennsylvania, U.S.A. and Newfoundland (Runnegar & Pojeta 1980; Peel 1989), has a more gracile shell that is considerably

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more laterally compressed than that of Y. greenlandica. It is more strongly coiled, with the strongly overhanging apex directed down towards the snorkel. Yochelcionella chinensis Pei, 1985, from the Lower Cambrian of the North China platform (Pei 1985) and South Australia (Bengtson et al. 1990) has a more laterally compressed shell than Y. greenlandica with more numerous, but less prominent, rugae that are continuous around the shell. The apex is less tightly curved than Y. greenlandica.

Yochelcionella daleki Runnegar & Jell, 1976 and Y. ostentata Runnegar & Jell, 1976, from the Middle Cambrian of New South Wales, Australia, are both known from silica replicas (Runeqar & Jell, 1976, fig. 11, A11–19, C1–9). Yochelcionella daleki is laterally more compressed than Y. greenlandica and less strongly curved. Yochelcionella ostentata has a less laterally compressed shell with an ovoid aperture, and a less curved apex. The shell becomes concave on the supra-apical such that the snorkel is steeply inclined.

Yochelcionella angustiplicata Hinz-Schallreuter, 1997, from the Middle Cambrian of Bornholm, Denmark, is known from phosphatised shells with a partial phosphatic coating and internal mould. The apex is blunt with no overhang. The shell is more laterally compressed than Y. greenlandica but shares with this species the change in the rate of expansion commensurate with the base of the snorkel. At this point, Y. angustiplicata develops numerous fine comarginal plications. Hinz-Schallreuter (1997) described two additional new species from the Middle Cambrian of Queensland, Australia: Y. fissurata and Y. trompetica. Yochelcionella fissurata is characterized by a deep fissure between the upright snorkel and the apex. Yochelcionella trompetica differs from Y. greenlandica in that its juvenile shell overhangs the supra-apical wall due to strong sigmoidal coiling; its upright snorkel is also broadly flaring.

Geyer (1986) described two species of Yochelcionella from the Middle Cambrian of Spain and Morocco in open nomenclature. Yochelcionella? sp. A can be differentiated from Y. greenlandica by its less pronounced overhang of the apex, but is poorly preserved. Yochelcionella? sp. B of Geyer (1986) is superficially similar to Y. greenlandica but the damaged apex precludes closer comparison. Geyer (1986) also described a species very similar to Yochelcionella from the Atlas Mountains of Morocco as genus novum et species nova E. (Geyer 1986, pl. 4, fig. 61a, b). The apex in the tall shell overhangs the supra-apical margin due to change in the coiling direction and clearly distinguishes it from Y. greenlandica.

Hinz (1987), Berg-Madsen & Peel (1986) and Skovsted (2004) described Yochelcionella from the Lower Cambrian of Shropshire, England, the Middle Cambrian of Bornholm, Denmark, and the Lower Cambrian of North-East Greenland, respectively, but the specimens are too poorly preserved for meaningful comparison with Y. greenlandica.

Variation in Yochelcionella greenlandica results in some specimens, mainly from the Henson Gletscher and Paralleladal formations, having a less prominent apex with a less pronounced overhang of the supra-apical wall. The conch is more slender and a bulge in its lateral profile may be developed below the snorkel on the sub-apical wall due to the ontogenetic reversal of coiling. The rugae in some of these specimens may remain generally parallel through growth without the development of the prominent single ruga commensurate with the snorkel in Y. greenlandica.

Occurrence. Aftenstjerneso, Henson Gletscher and Paralleladal formations, Bronlund Fjord Group, North Greenland. Probably also from the Browns Pond Formation of New York State and the ‘Anse Maranda Formation’ of Quebec. Late Early Cambrian, Olenellus Zone, Dyran Stage of Laurentian (North American) usage. Botoman and Toyonian stages in terms of Siberian stratigraphic nomenclature.

Yochelcionella gracilis n. sp.

Fig. 3

Etymology. From the Latin gracilis, referring to the slender nature of the conch.

Holotype. MGUH 27020 from GGU sample 225711, Henson Gletscher Formation, Bronlund Fjord Group.

Other figured material. Paralleladal Formation, MGUH 27021 from GGU sample 274907; Henson Gletscher Formation, MGUH 27022 from GGU sample 301354, MGUH 27023 from GGU sample 225711.

Fig. 3. Yochelcionella gracilis n. sp., A–C, holotype, internal mould, MGUH 27020 from GGU sample 225711, Henson Gletscher Formation. A, supra-apical, x 27, B, right lateral, x 27, C, enlargement of juvenile area right lateral showing pegma-like fissure, x 135. D–H, paratype, silica replica, MGUH 27021 from GGU sample 274907, Paralleladal Formation. D, enlargement of lateral area showing rugae with overlying vertical ribs, x 100, E, right lateral, x 48, F, supra-apical, x 48, G, left lateral, x 48, H, dorsal, x 66. I–K, paratype, silica replica, MGUH 27022 from GGU sample 301354, Henson Gletscher Formation. I, enlargement of right lateral area showing prominent rugae producing the distinctive outline of the sub-apical margin overlain by fine vertical ribs, x 75, J, right lateral, x 42, K, left lateral, x 42. L, paratype, MGUH 27023 from GGU sample 225711, Henson Gletscher Formation, right lateral, x 36.
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**Additional material.** Henson Gletscher Formation, GGU samples 225711 (2 specimens), 225714 (5 specimens) and 301354 (3 specimens); Paralleldal Formation, GGU sample 274907 (more than 200 specimens).

**Diagnosis.** Bilaterally symmetrical, moderately compressed helcionelloid with tall, almost orthoconic shell and an overhanging apex; snorkel steeply inclined separated from the sub-apical wall by a fissure on the internal mould. Protoconch represented on the internal mould by a rounded boss at the apex. Smooth, supra-apical margin becoming regularly concave; lateral areas commonly with prominent rugae which are conspicuous below the snorkel but fade somewhat on the supra-apical surface.

**Description.** Bilaterally symmetrical, laterally compressed species of *Yochelcionella* with a tall narrow shell. Protoconch represented by a small rounded boss on the apex of the internal mould. Apex in the juvenile shell overhangs the snorkel but reversal of coiling in the later shell causes the apex to overhang the supra-apical wall. A deep fissure on the internal mould separates the apex from the snorkel. Snorkel upright, increasing in angle of elevation with growth as the shell first reverses coiling and then becomes conical, with supra-apical wall showing steady expansion below the snorkel. Aperture sub-ovate, with width to length ratio of 4:1. Lateral surfaces ornamented with pronounced rugae that moderate in intensity around the supra-apical wall; rarely smooth. Rugae are acute on the shell exterior, separated by concave interareas with discontinuous radial cords.

**Discussion.** The tall, narrow shell and the fissure on the internal mould between the apex and the snorkel differentiate *Y. gracilis* n. sp. from *Y. greenlandica* n. sp. *Yochelcionella gracilis* closely resembles *Y. fissurata* from the Middle Cambrian of Bornholm (Hinz-Schallreuter 1997) which, as its name implies, also carries a prominent fissure on the internal mould of the only known specimen, although this fissure is narrower and deeper. The juvenile shell of *Y. fissurata* is more robust with no overhang of the supra-apical wall. Expansion of the shell in *Y. fissurata* is taken up on the supra-apical surface, such that the sub-apical surface is near vertical in contrast to the convex form of *Y. gracilis*.

The tall slender shell of *Y. gracilis* readily distinguishes it from more strongly coiled forms such as *Y. cyrano*, *Y. dalek*, *Y. pelmani*, *Y. americana* and *Y. chimensis*. With the exception of *Y. fissurata*, species exhibiting a similar shell form to *Y. gracilis* lack the distinctive fissure on the internal mould separating the apex from the snorkel (when these are known from internal moulds) and the ornamentation of acute rugae and spiral cords. *Yochelcionella aichalica* has a similar shell form to *Y. gracilis* but the blunt apex overlies the supra-apical surface.

**Occurrence.** Henson Gletscher and Paralleldal formations of the Brønlund Fjord Group. In terms of the Laurentian standard, these occurrences are late Early Cambrian, *Olenellus Zone*, Dyeran. Following the Siberian standard, the faunas are latest Early Cambrian, Toyonian.

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