Yochelcionella (Mollusca, Helcionelloida) from the lower Cambrian of North America

Christian J. Atkins & John S. Peel

Five named species of the helcionelloid mollusc genus Yochelcionella Runnegar & Pojeta, 1974 are recognized from the lower Cambrian (Cambrian Series 2) of North America: Yochelcionella erecta (Walcott, 1891), Y. americana Runnegar & Pojeta, 1980, Y. chinensis Pei, 1985, Y. greenlandica Atkins & Peel, 2004 and Y. gracilis Atkins & Peel, 2004, linking lower Cambrian outcrops along the present north-eastern seaboard. Yochelcionella erecta, an Avalonian species, is described for the first time; other species are derived from Laurentia. A revised concept of the Chinese species, Y. chinensis, is based mainly on a large sample from the Forteau Formation of western Newfoundland and the species may have stratigraphic utility between Cambrian palaeocontinents. • Key words: Yochelcionella, Helcionelloida, Mollusca, lower Cambrian (Cambrian Series 2), North America.


Christian J. Atkins, Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden; Christian.Atkins@geo.uu.se • John S. Peel, Department of Earth Sciences (Palaeobiology) and Museum of Evolution, Uppsala University, Villavägen 16, SE-752 36 Uppsala, Sweden; John.Peel@pal.uu.se

DOI 10.3140/bull.geosci.2008.01.023

A fossil referable to the helcionelloid mollusc Yochelcionella Runnegar & Pojeta, 1974 was illustrated by Walcott (1891) from the lower Cambrian (Cambrian Series 2 in the proposed subdivision of the Cambrian, see Babcock et al. 2005) Avalonian succession of south-east Newfoundland (Fig. 1), but the genus was first proposed by Runnegar & Pojeta (1974) for species from the middle Cambrian of Australia (Cambrian Series 3). Yochelcionellids have been reported from Siberia, Laurentia, Baltica and Gondwana, and demonstrate potential for biostratigraphic correlation between Cambrian palaeocontinents (Gubanov et al. 2004). Their stratigraphic range spans the early and middle Cambrian (Cambrian Series 1–3).

Yochelcionellids are small, cap-shaped or coiled, bilaterally symmetrical helcionelloids characterised by a tubular snorkel located on the median line beneath the apex. The apex overhangs the snorkel in most species due to more rapid growth of the shell along the supra-apical margin. However, some species (such as Y. ostentata Runnegar & Jell, 1976, Y. aichalica Fedorov in Schabanov et al., 1987, Y. angustoplicata Hinz-Schallreuter, 1997 and Y. gracilis Atkins & Peel, 2004) undergo a reversal of coiling during growth such that the apex is oriented vertically, perpendicular to the plane of the aperture, or even overhanging the supra-apical margin.

The snorkel forms a conduit for fluid transfer between the mantle cavity and the surrounding environment, but there is debate about its precise function and the orientation of the shell. Yochelcionellids were initially considered to be exogastric by Runnegar & Pojeta (1974; see also Pojeta & Runnegar 1976 and Riedel 1996), with the snorkel located anteriorly on the sub-apical margin and forming a channel for the inhalation of oxygen-rich water (Fig. 2A). In this reconstruction, the coiled shell expands in a clockwise direction when viewed laterally. This reconstruction was challenged by Yochelson (1978), Berg-Madsen & Peel (1987), Peel (1991a, b), Hinz-Schallreuter (1997), and Atkins & Peel (2004), who considered the shell to be orientated endogastrically (Fig. 2B). In this interpretation the coiled shell expands in an anti-clockwise direction when seen in lateral view, with the anterior to the left; the snorkel is located posteriorly on the sub-apical wall and forms an exhalant conduit for de-oxygenated water. Peel (1991a) suggested that the snorkel of the endogastric Y. americana Runnegar & Pojeta, 1980 might have served for both inhalation and exhalation, in similar fashion to the dorsal perforation of scaphopods (Morton 1988, Reynolds 2002). The similarity between Yochelcionella and early growth stages of scaphopods was stressed by Peel (2004, 2006), who recognized a trend in Palaeozoic molluscs towards the scaphopod morphology, which he termed ‘scaphopodization’. Morphological comparisons between the coiling direction in Yochelcionella and the early growth stages of...
Scaphopods confirm that helcionelloids were endogastric in a similar fashion to living scaphopods (Peel 2006). Parkhaev (in Gravestock et al. 2001; Parkhaev 2002) controversially considered Yochelcionella to be a gastropod, with the shell oriented endogastrically and the posterior snorkel serving an inhalant function.

In this paper the shell of Yochelcionella is considered to be endogastric. Oxygenated water generally passed up through the ventral aperture, drawn in by slight muscular contraction of the visceral mass, and moved over respiratory surfaces that are assumed to have been located on either side of the dorsal line below the snorkel. This created a series of discrete pressure pulses that established a positive pressure gradient through the shell into the snorkel. Deoxygenated water was expelled through the snorkel by a combination of continuous water pressure from the shell and forward flow by the negative pressure gradient created by the terminal flare of the snorkel (Runnegar & Jell 1980, Pei 1985, Hinz-Schallreuter 1997). The development of a snorkel and this pattern of water circulation may be seen as an adaptive strategy to avoid recycling deoxygenated water.

Two different morphological groups can be recognized within *Yochelcionella*. The first is clearly shown by the type species *Y. cyrano* Runnegar & Pojeta, 1974; expansion along the supra-apical margin creates a shell that is coiled through about one whorl. The apex lies posteriorly, when viewed laterally, and the shell expands anteriorly with uniform curvature. Species with this form also exhibit a relatively great amount of lateral compression when viewed dorsoventrally (e.g., *Y. americana*, Fig. 6). Members of the second morphological group show an increase in expansion along the sub-apical wall, which places the apex vertically or even inclined in a pseudo-exogastric sense over the supra-apical margin (e.g., *Y. ostentata* Runnegar & Jell, 1976, *Y. crassa* and *Y. parva* of Zhegallo in Esakova & Zhegallo, 1996, *Y. angustoplicata* Hinz-Schallreuter, 1997, *Y. gracilis* Atkins & Peel, 2004; see Fig. 8I–K). These forms also tend to have a more equidimensional aperture. Pokorny (1978) first noted these two groups and doubted that *Y. cyrano* and *Y. ostentata* were congeneric or even representatives of the same order. Runnegar & Jell (1980), however, remained confident of the integrity of the entire group. While maintaining a single genus, Geyer (1986) divided the second group into two, based on the position of the apex, and recognized a subgroup composed of *Yochelcionella*? sp. A and *Y. stylifera* Missarzhevsky & Mambetov, 1981. Hinz-Schallreuter (1997) considered placing her *Y. fissurata* into the second group but avoided erecting a separate generic name due to the high degree of intraspecific variation among many Cambrian groups and the lack of clarity as to which features were generically useful. More recently, Parkhaev (2002) raised the new genus *Runnegarella* to incorporate *Y. americana* based on the distinctive morphology of this species.

This separation of morphological groups of yochelcionellid species suggests two differing strategies for life, although they are generally inferred to be semi-infaunal or epifaunal detrital feeders or benthic grazers. The laterally compressed, more strongly coiled form with a narrow aperture (e.g., *Y. americana*, *Y. greenlandica*) is suggestive of a semi-infaunal mode of life (Peel 1991a, b), by comparison to bivalves (Stanley 1970). The wider, more ovate apertures of orthoconic and pseudo-exogastric species (*Y. ostentata*, *Y. recta*, *Y. gracilis*) imply a more epifaunal habit (Linsley 1977).

Coiled and erect species of *Yochelcionella* occur throughout the range of the genus. Furthermore, a tendency to be tightly coiled in the earliest growth stages and to uncoil or even reverse the direction of coiling during ontogeny occurs in many forms. On account of this, and the high variability seen in available large samples, we retain all species within the single genus *Yochelcionella*, regarding *Runnegarella* Parkhaev, 2002 as its junior synonym.

Since its first description *Yochelcionella* has proved to be widely distributed through the early to middle Cambrian (Series 1–3) on many palaeocontinents (Gubanov et al. 2004). The geologically oldest known species is *Yochelcionella pelmani* Vassiljeva, 1990, from the Tommotian (Series 1) of Siberia. The *Solenopleura brachymetopa* Zone, late middle Cambrian (Series 3) of Öleå, Bornholm has produced the youngest species yet known (Berg-Madsen & Peel 1986).

The Avalonian species *Y. erecta* is currently known only from eastern Newfoundland, but each of the other named species described herein occurs at several localities along the current north-eastern seabord of the Laurentian palaeocontinent. Following its original description from China, *Y. chinensis* is reported from the Forteau Formation of western Newfoundland and the lower Kinzers Forma-
tion of Pennsylvania. *Y. americana* is common in the lower Kinzers Formation of Pennsylvania and the Forteau Formation of western Newfoundland, but a single specimen is also described from the Aftenstjernes Formation of North Greenland. *Yochelcionella greenlandica* also occurs in these three areas and in New York State, Quebec and the MacKenzie Mountains. *Yochelcionella gracilis* is described from North Greenland and western Newfoundland. All these occurrences are of late Early Cambrian age (Cambrian Series 3, stage 4).

**Geological background and localities**

With the exception of *Y. erecta* from the Avalonian sequence of Conception Bay in south-eastern Newfoundland (Fig. 1), all the North American material described herein is derived from the Laurentian palaeocontinent.

In North Greenland, species of *Yochelcionella* were collected by J.S. Peel from the Aftenstjernes, Parallelldal and Henson Gletscher formations of the Brønlund Fjord Group (Ineson & Peel 1997; Atkins & Peel 2004). GGU samples 271470 and 271471 were collected from the basal member of the Aftenstjernes Formation at its type locality on the western side of J.P. Koch Fjord, Lauge Koch Land, central North Greenland (Fig. 1A; Ineson & Peel 1997, pp. 39–46, figs 23, 24A, 25). GGU sample 271717 was collected from the basal member of the Aftenstjernes Formation on the west side of Lønddal, western Peary Land (Fig. 1A; J.S. Peel locality 19780714-1).

GGU samples 225711, 225712 and 225714 were also collected in Lønddal, from dark limestones of the Henson Gletscher Formation (Fig. 1A; see Blaker & Peel 1997, figs 8A, 11; GGU sample 225711 is from the same horizon as 225712). GGU sample 315092 is a dark limestone from a reference section through the Henson Gletscher Formation described by Ineson & Peel (1997, figs 32, 33) in southern Freuchen Land (Fig. 1A). 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. GGU sample 301354 is a talus block of the Henson Gletscher Formation collected from the easternmost nunatak on the northern side of the main, south-westward flowing, tributary glacier of Jungenersen Gletscher, southern Freuchen Land, about 5 km north-east of the previous sample (Atkins & Peel 2004; Fig. 1A).

GGU sample 274907 was collected from the lower part of the Parallelldal Formation on the north side of Parallelldal, central Peary Land (Fig. 1A). This is the same locality as GGU sample 274908 in Blaker & Peel (1997, fig. 8B), illustrated by Ineson & Peel (1997, pp. 78–81, fig. 75). The rich silicified fauna includes brachiopods described by Popov et al. (1997), helcionelloid and stenothecid molluscs and trilobites. Overlying dolomites of the same formation yield archaeocyathids of late Early Cambrian (Toyonian; Series 2) age (Debrenne & Peel 1986) and *Salterella* (Peel & Yochelson 1982).

In the Laurentian sequence of north-west Newfoundland, species of *Yochelcionella* were collected by J.S. Peel from the lower Cambrian (Cambrian Series 2) Forteau Formation, near the head of Dear Arm, Gros Morne (Fig. 1C; James & Stevens 1982, pp. 68, 69), from which locality Peel (1987) described *Yochelcionella americana*. The diverse associated fauna was described by Peel & Berg-Madsen (1988), Skovsted et al. (2004), Skovsted & Peel (2007). In the Avalonian sequence of south-eastern Newfoundland, specimens of *Y. erecta* described by Walcott (1891) are derived from the Manuels area of Conception Bay, from the lowest part of the Brigus Formation (Fig. 1C).

In Pennsylvania, *Yochelcionella* species were collected from the waterpipe section in Thomasville Quarry, 7 miles west of York (Fig. 1D). It is from this quarry that Runnegar & Pojeta (1980) described *Y. americana*, reportedly from the Vintage Dolomite. According to R.D.K. Thomas (written communication 1999), the current samples appear to have been derived from the lower part of the Kinzers Formation (see also Skinner 2005).

Illustrated specimens are deposited in institutions whose names are abbreviated in the text: PMU, Palaeontological collections of the Museum of Evolution, Uppsala University, Uppsala, Sweden; USNM, United States Museum of Natural History, Washington D.C., U.S.A.; GSC, Geological Survey of Canada, Ottawa, Canada; MGUH, Geological Museum, Copenhagen, Denmark. GGU indicates collections of the Geological Survey of Greenland (now part of the Geological Survey of Denmark and Greenland).

**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

*Yochelcionella* Runnegar & Pojeta, 1974  
Runnegarella Parkhaev, 2002

**Type species.** – *Yochelcionella cyrano* Runnegar & Pojeta, 1974, early middle Cambrian, (Ordian); Cambrian Series 3, New South Wales, Australia.

Yochelcionella chinensis Pei, 1985
Figures 3, 4A–K, M, N, 6K, 7A

1985 Yochelcionella chinensis Pei, p. 398, pl. 1a–d.
2007 Yochelcionella cf. chinensis Pei. – Skovsted & Peel, p. 736, fig. 4D.

Figured material. – PMU 25000–25022, 25035, early Cambrian, Cambrian Series 2, stage 4, Forteau Formation, Newfoundland, Canada; PMU 25036, early Cambrian, Series 2, stage 4, lowest Kinzers Formation, Thomasville, Pennsylvania, USA.

Additional material. – 400 specimens from the Forteau Formation, and 4 from the lowest Kinzers Formation, Thomasville, Pennsylvania.

Diagnosis. – Species of Yochelcionella with the apex overhanging the sub-apical wall and typically with fine rugae on lateral surfaces. Shell is coiled initially through about one quarter of a whorl but becoming orthoconic abapical of the tubular snorkel. Snorkel located at a distance of between once and twice its own diameter beneath the apex; it extends parallel to the plane of the aperture or may be inclined upwards away from the plane of the aperture.

Description. – Bilaterally symmetrical, laterally compressed species of Yochelcionella. Protoconch represented by a small round boss on the apex, separated from the juvenile shell by a slight circumferential constriction on the internal mould and overhanging the juvenile sub-apical wall. Juvenile stage coiled through about one quarter of a whorl. The adult stage is orthoconic with sub-apical and supra-apical margins well rounded. Snorkel, circular in cross section and extending parallel to the plane of the aperture or inclined upwards away from the apertural plane, often slightly flared. Lateral surfaces of internal mould covered by many fine rugae of similar amplitude that diminish towards the sub- and supra-apical margins, or occasionally smooth. Adult aperture has a width to length ratio of between 4 : 1 and 5 : 1, and is usually parallel-sided. However, on more complete, taller specimens a slight concavity of the lateral surfaces is apparent, producing a weak figure-of-eight-shaped aperture. As the material comprises only phosphatic internal moulds no information is available concerning shell thickness or ornamentation.

Discussion. – The degree of expression of the rugae on the shell exterior is not known, but such features are usually more subdued on the internal mould than on the shell exterior. The rugae might have resulted from periodic flaring of the shell aperture and, as such, their exterior expression can be as acute lamellae (cf. Gubanov et al. 2004, figs 6, 7). Slight thickening of the shell associated with the snorkel may be visible on the internal mould as constrictions or grooves (Figs 4M, N, 6K).

Yochelcionella chinensis Pei, 1985 was described on the basis of a single illustrated internal mould from the early Cambrian (Cambrian Series 2) Xinji Formation of China (Pei 1985). All specimens assigned herein to Y. chinensis are phosphatic internal moulds, whereas the type species, Y. cyrano from the middle Cambrian (Series 3) of Australia is preserved as a silica replica (Runnegar & Jell 1976). Y. chinensis has a taller, more orthocanic shell than the more strongly coiled type species. Runnegar & Jell (1976, fig. 11A1–3) figured an internal mould that was tentatively identified to the type species, but this lacks the overhanging apex of Y. chinensis and has a much more robust snorkel. Runnegar (in Bengtson et al. 1990) reported two incomplete steinkerns of Y. chinensis from the early Cambrian (Cambrian Series 2) of Australia, but the single illustrated specimen is not identifiable to species. Yochelcionella cf. chinensis of Steiner et al. (2004) from the Xihaoping Formation of China is clearly not referable to Pei’s (1985) species. It is strongly re-coiled such that the apex overhangs the concave supra-apical surface whereas the apex of Y. chinensis overhangs the sub-apical wall.

The earliest known representative of Yochelcionella, Y. pelmani Vassiljeva, 1990 from the early Cambrian (Tommotian; Cambrian Series 1, stage 2) of Siberia, was transferred by Vassiljeva (1998) to Eotebenna Runnegar & Pojeta, 1974. However, her illustrations indicate a true tubular snorkel of Yochelcionella type was developed, rather than the deep sinus in the sub-apical margin characteristic of Eotebenna (Vassiljeva, 1990). Yochelcionella pelmani can be distinguished from Y. chinensis by its cap-shaped shell and robust snorkel.
Missarzhevsky & Mambetov (1981) described Y. recta and Y. stylifera from the early Cambrian (Cambrian Series 2) of Maly Karatau, Kazakhstan. Yochelcionella recta differs from Y. chinesis by its elongate, narrower, juvenile shell and uniform rate of expansion along the super-apical margin. As illustrated, the snorkel is represented by a bulge, unlike the tubular structure seen in Y. chinesis and all other yochelcionellids (Missarzhevsky & Mambetov 1981). Yochelcionella stylifera has a more upright cap-shaped shell with fewer, more robust rugae that encircle the shell, unlike the finely rugose ornament of Y. chinesis.

Yochelcionella aichalica Fedorov in Schabanov et al. 1987 and Yochelcionella sp. of Dzik (1994), both from the early Cambrian (Atdabanian; Cambrian Series 2, stage 3) of Siberia, appear to be conspecific. Both can be differentiated from Y. chinesis by the tall orthoconic shell, with the juvenile stage curved forward. The well-rounded protoconch overlaps the super-apical margin, whereas it overlaps the sub-apical wall in Y. chinesis. Esakova & Zhegallo (1996) described two species from the Cambrian Series 2 of Mongolia. Yochelcionella crassa (see also Parkhaev 2004) has an upright protoconch with no overlap of the sub-apical margin as in Y. chinesis. In similar fashion to Y. chinesis and Y. greenlandica, Y. crassa also has rugae concordant with the snorkel. Yochelcionella parva appears to have an orthoconic juvenile stage unlike the coiled juvenile stage of Y. chinesis and the supra-apical surface becomes concave in subsequent growth.

Yochelcionella delicata (Yu, 1987), from the early Cambrian (Cambrian Series 2) of the Yangtze region is distinguished by the increased expansion and inflation along its sub-apical margin, which rotates the apex over the super-apical field; a miniscule snorkel is recumbent on the sub-apical margin before diverging dorsally (Yu 1987).

Kouchinsky (2000) figured two internal moulds of Yochelcionella sp. from the early Cambrian (Cambrian Series 2) of Siberia, which have a less laterally compressed shell than Y. chinesis with an ovoid aperture and fewer, stronger rugae.

In addition to the type species, Runnegar & Jell (1976) described two further species of Yochelcionella preserved as silica replicas from the middle Cambrian (Cambrian Series 3) of Australia. Yochelcionella daleki Runnegar & Jell (1976, see also Brock 1998) is more strongly coiled than Y. chinesis, with a gradual reorientation of the aperture unlike the abrupt change observed in Y. chinesis. Yochelcionella ostentata Runnegar & Jell, 1976, also reported from Siberia (Gubanov et al. 2004), has a more orthoconic shell with a lower rate of lateral compression and a more oval aperture than Y. chinesis.

Hinz-Schallreuter (1997) described three new middle Cambrian (Cambrian Series 3) species: Y. angustoplicata from Bornholm, Denmark, and Y. fissurata and Y. trompetica from Queensland, Australia. Yochelcionella angustoplicata (see also Gubanov et al. 2004) is described from phosphatized shells with a partial outer phosphatic coating and internal mould. The apex is blunt, upright and has no overhang, unlike Y. chinesis. Y. fissurata is known from a phosphatic internal mould and is easily distinguished by the pegma-like structure between the vertically oriented snorkel and apex. Yochelcionella trompetica, also described from a phosphatic internal mould, has an apex overlapping the super-apical wall and an upright, broadly flaring snorkel and apex, unlike Y. chinesis.

Geyer (1986) described two poorly preserved species of Yochelcionella from the middle Cambrian (Cambrian Series 3) of Spain. Yochelcionella? sp. A has a more upright apex and greater expansion in the adult shell than seen in Y. chinesis. Yochelcionella? sp. B exhibits more continuous expansion along the super-apical margin; it is ornamented with continuous coarse rugae. Genus novum et species nova E of Geyer (1986) from the middle Cambrian (Cambrian series 3) of the Atlas Mountains of Morocco has a tall, cap-shaped, apex that overlaps the super-apical wall with the snorkel orientated vertically.

Yochelcionella erecta (Walcott, 1891) Hinz-Schallreuter, 1997 from the early Cambrian (Cambrian Series 2) of Conception Bay, eastern Newfoundland has a more slender shell with fewer rugae, which pass around the sub-apical margin and a tiny snorkel. The apex is missing in the holotype (USNM 18311), but is present in USNM 307720 and represented by an imprint on USNM 307721; it is more orthoconic in form.

Atkins & Peel (2004) described two new early Cambrian (Cambrian Series 2, stage 4) yochelcionellids from North Greenland. Yochelcionella greenlandica (Fig. 2A–Q; see also Landing & Bartowski 1996, Landing et al. 2002) can be distinguished from Y. chinesis by its reduced rate of lateral compression, more ovate aperture and fewer, lateral flaring rugae. While similar to Y. chinesis, Y. greenlandica has single rugae inclined concordantly with the snorkel. Yochelcionella gracilis (Fig. 8E–G, I–K) is known from both phosphatic internal moulds and silica replicas and is readily differentiated from Y. chinesis by its tall almost orthoconic shell in which the apex slightly overhangs the super-apical margin.


The 400 specimens recovered from the Forteau Formation clearly illustrate the high degree of morphological variation seen in some groups of Cambrian molluscs (e.g., Gubanov & Peel 2000, 2003; Skovsted 2004). Only three illustrated specimens closely resemble the specimen illus-
Figure 3. Yochelcionella chinensis Pei, 1985, internal moulds from the Forteau Formation, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada. • A–E – PMU 25000, sub-apical (A), right lateral (B), supra-apical (C), left lateral (D) and dorsal (E) views. • F – PMU 25001, right lateral view. • G–P M U 25002, left lateral view. • H–P M U 25003 left lateral view. • I – PMU 25004, left lateral view. • J – PMU 25005, right lateral view. • K – PMU 25006, right lateral view. • L – PMU 25007, left lateral view. • M – PMU 25008, right lateral view. • N – PMU 25009, right lateral view. • O – PMU 25010, right lateral view. • P – PMU 25011, oblique left lateral view. • Q – PMU 25012, left lateral view. All scale bars 10 µm.

**Figured material.** – Holotype, USNM 18311 (not illustrated), from the Brigus Formation, Manuel’s Brook, Conception Bay, Newfoundland. Early Cambrian (Cambrian Series 2, stage 3). USNM 307720 and 307721 from the same locality as the holotype.

**Diagnosis.** – Tall, slender, sub-orthoconic species of *Yochelcionella* with a tiny snorkel. The apex is upright with the tip slightly overhanging the sub-apical wall. In lateral perspective, after formation of the snorkel, the sub-apical wall becomes slightly convex, while the supra-apical wall is inclined and shallowly concave. Ornamented with coarse co-marginal rugae.

**Description.** – A bilaterally symmetrical moderately laterally compressed, sub-orthoconic *Yochelcionella* in which the protoconch forms a small apical boss, slightly overhanging the sub-apical line surface. The tiny snorkel is inclined at approximately 45° to the apertural plane; its length is unknown. In lateral view, the adult shell has a steep, shallowly convex, sub-apical surface while the supra-apical surface is inclined and becomes shallowly concave adaperturally. The aperture is poorly known, but apparently oval in large specimens. The surface of the internal mould is ornamented by a regular series of robust co-marginal rugae and fine striations.

**Discussion.** – *Yochelcionella erecta* is easily distinguished from *Y. chinensis* by its upright shell with no posterior displacement of the apex over the sub-apical margin and its tiny snorkel. The tall upright shell of *Y. erecta* readily distinguishes it from strongly coiled forms such as *Y. pelmani*, *Y. americana*, *Y. cyrano* and *Y. daleki* in which the apex overhangs the sub-apical margin. The alignment of rugae with the snorkel seen in *Y. erecta* (Fig. 5B) has been previously reported in *Y. greenlandica* by Atkins & Peel (2004) but this species is more strongly coiled with a more robust snorkel. Erect species such as *Y. recta*, *Y. stylifera*, *Y. crassa*, *Y. parva*, *Y. delicata*, *Y. gracilis*, *Y. ostentata*, *Y. angustoplicata*, *Y. trompetica* and *Y. fissurata* have a more pronounced sigmoidal form. The small size of the snorkel indicates a potential for confusion between poorly preserved *Y. erecta* and helcionelloids of similar overall shape but without a snorkel, e.g., *Mackinnonia taconica* (Landing & Bartowski, 1996), *Obtusoconus aberratus*, *O. magnus* and *O. brevis* of Zhegallo in Esakova & Zhegallo, 1996, *Anuliconus magnificus* and *A. trunctus* of Parkhaev in Gravestock *et al.*, 2001.

The illustration of the holotype given by Walcott (1891,
Yochelcionella, internal moulds from the Forteau Formation, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada.

- A–K, M, N – Yochelcionella chinensis Pei, 1985. A – PMU 25013, left lateral view, B – PMU 25014, left lateral view, C – PMU 25015, left lateral view, D – PMU 25016, right lateral view, E – PMU 25017, right lateral view, F–G – PMU 25018, left lateral (F) and enlargement of lateral area showing microstructure (G), H – PMU 25019, dorsal view, I – PMU 25020, right lateral view, J, K – PMU 25021, right lateral (J) and detail of possible encrusting epibiota (K), M, N – PMU 25022, dorsal view (M) and detail of dorsal groove on snorkel (N). • L – Yochelcionella cf. chinensis, PMU 25023, right lateral view. • O, P – Yochelcionella greenlandica Atkins & Peel, 2004. O – PMU 25024, right lateral view, P – PMU 24025, left lateral view. All scale bars 10 µm.

Figure 4. Yochelcionella, internal moulds from the Forteau Formation, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada.
pl. 74, fig. 4) indicates a slender cone with prominent rugae on the sub-apical surface decreasing in amplitude as they approach the supra-apical surface. The specimen itself is too poor to merit illustration but confirms this feature of ornamentation, although the narrowness of the shell is unclear. Both specimens illustrated herein have a more strongly expanded shell antero-posteriorly than Walcott’s illustration and the comarginal rugae pass around the shell with little change in the relief (Fig. 5). USNM 307720 has a more robust form than USNM 307721, and its blister-like protoconch is more prominent. However, in view of the scarcity and indifferent preservation of available material, the three discussed specimens are currently retained within a single species.


Yochelcionella americana Runnegar & Pojeta, 1980
Figures 6A–F, I, J, 7B, C, 8H

1980 Yochelcionella americana Runnegar & Pojeta, p. 636, fig. 1.
1987 Yochelcionella americana Runnegar & Pojeta. – Peel, p. 2328–2330, fig. 1A–D.
2007 Yochelcionella americana Runnegar & Pojeta. – Skovsted & Peel, p. 736, fig. 4E.

Figured material. – PMU 25026–25031 from the Forteau Formation, Newfoundland, Canada (Peel 1987); PMU 25037–25038 from the lowest Kinzers Formation, Thomasville, Pennsylvania; MGUH 28900 from GGU sample 271470 from the Aftenstjernes Formation, North Greenland. Early Cambrian, Cambrian Series 2, stage 4.

Additional material. – 20 specimens from the lowest Kinzers Formation, Thomasville, Pennsylvania, and 30 from the Forteau Formation, Newfoundland, Canada.

Diagnosis. – (Emended from Runnegar & Pojeta 1980). A strongly coiled, laterally compressed, species of Yochelcionella in which the apex and earliest growth stages prominently overhang the sub-apical wall and apertural margin.

Description. – The high degree of lateral compression and the strongly coiled shell characterize this species of Yochelcionella. The shell is relatively slowly expanding, producing a narrow coil in which the apex significantly overhangs the posterior apertural margin. The supra-apical surface is strongly convex in lateral profile, but flattens somewhat towards the adult aperture to produce a tall shell with a short aperture. The protoconch is represented on the internal mould by a small (80–100 µm) rounded boss at the apex, often delineated from the teleoconch by a slight constriction. Due to the strong curvature, the apex, is moderately to strongly hooked over the sub-apical wall, almost touching the snorkel. In many specimens, the adult stage is less coiled than the juvenile stage as the logarithmic shell spiral expands, but there is considerable variation in the antero-posterior dimension of the aperture. The aperture is narrow and parallel sided, uniformly convex at the supra-apical margin but sometimes acute subapically; it has a length : width ratio of 1 : 4 to 1 : 6. The characteristic snorkel is circular in cross-section and occupies the full width of the sub-apical wall. Lateral shell surfaces are ornamented by regularly spaced, symmetrical rugae that usu-
ally fade towards the smooth supra- and sub-apical. The presence of shallow terminal sinuses is indicated in some specimens by the adapical convexity of rugae on the lateral areas. Ornamentation, structure and thickness of the shell are unknown.

Discussion. – All available specimens are phosphatic internal moulds. Peel (1980) considered examples of *Y. americana* from the Forteau Formation to be indistinguishable from the material from Pennsylvania. It should be noted that Runnegar & Pojeta (1980) recorded their material from a bore core in the Vintage Dolomite, whereas the currently figured material is from the lower beds of the overlying Kinzers Formation. The single example from North Greenland is an internal mould showing a slight constriction in growth slightly prior to formation of the snorkel (Fig. 8H).

Variation within available specimens is shown by the degree of curvature of the apex, orientation and curvature of the snorkel, the degree of expression and shape of the rugae and the length of the aperture. Runnegar & Pojeta (1980) considered that the distinctive lateral compression might be due to tectonic deformation but Peel (1980) concluded that
the compression and curvature of the shell are characteristic of the species. The slight trace running down the sub-apical surface from the snorkel to the aperture in some specimens (Fig. 6I) is also seen in other species (Fig. 6K).

*Yochelcionella americana* is readily distinguished from all other species of *Yochelcionella* by its strongly coiled shell, which presumably motivated Parkhaev’s (2002) proposal, here discounted (see also Skovsted & Peel 2007, p. 736), of the new genus *Runnegarella*. 

**Occurrence.** – Early Cambrian (Cambrian Series 2, stage 4) of Pennsylvania, Newfoundland, and North Greenland.

*Yochelcionella greenlandica* Atkins & Peel, 2004

Figures 4O, P, 7D, 8A–D

1987 *Yochelcionella* sp., Voronova et al., pp. 45, 46, pl. XX, fig. 2.
1996 *Yochelcionella* sp., Landing & Bartowski, p. 754, figs 6.3–6.5.
2002 *Yochelcionella* sp., Landing et al., pp. 298, 299, fig. 8.9.
2004 *Yochelcionella greenlandica* Atkins & Peel, pp. 3–6, fig. 2.

**Figured material.** – Holotype: MGUH 27016 from GGU sample 271471, Aftenstjernesø Formation, North Greenland; PMU 25032, Forteau Formation, Newfoundland, Canada; PMU 25039, lower Kinzers Formation, Thomasville, Pennsylvania, USA. Early Cambrian (Cambrian Series 2, stage 4).

**Addional material.** – 34 specimens from GGU sample 271470, 30 specimens from GGU sample 271471, and 15 specimens from 271717; all Aftenstjernesø Formation, North Greenland. 1 specimen from the lower Kinzers Formation, Thomasville, Pennsylvania, USA. Early Cambrian (Cambrian Series 2, stage 4).

**Discussion.** – A full description and discussion of *Y. greenlandica* was given by Atkins & Peel (2004). The upright, moderately laterally compressed, shell has lateral surfaces that are ornamented with up to three prominent rugae, the first of which is inclined concordantly with the snorkel.

In addition to the occurrences in Greenland, Pennsylvania, Newfoundland, and North Greenland, specimens now assigned to *Y. greenlandica* have been described in open nomenclature from the Sekwi Formation of the MacKenzie Mountains (Voronova et al. 1987), from the Browns Pond Formation of New York State (Landing & Bartowski 1996), and from the Anse Maranda Formation of Quebec (Landing et al. 2002).


*Yochelcionella gracilis* Atkins & Peel, 2004


2004 *Yochelcionella gracilis* Atkins & Peel, pp. 6–8, fig. 3.

**Figured material.** – Holotype, MGHU 27016 from GGU sample 225711, MGHU 27021 and 27022 from GGU sample 301354, all Henson Gletscher Formation, North Greenland; PMU 25032, Forteau Formation, Newfoundland, Canada. Early Cambrian (Cambrian Series 2, stage 4).
Figure 8. *Yochelcionella* from the early Cambrian (Cambrian Series 2, stage 4) of North Greenland. • A–D – *Yochelcionella greenlandica* Atkins & Peel, 2004, holotype, MGUH 27016 from GGU sample 271471, internal mould, Aftenstjernø Formation, in left lateral (A), supra-apical (B), dorsal (C) and right lateral (D) views. • E–G, I–K – *Yochelcionella gracilis* Atkins & Peel, 2004. E–G – holotype, MGUH 27020 from GGU sample 225711, internal mould, Henson Gletscher Formation, in right lateral (E) and dorsal (G) views with detail of pegma-like fissure (F). I–K – paratype, MGUH 27021 from GGU sample 274907, silica impressions, Paralleldal Formation, in oblique right lateral (I), supra-apical (J) and oblique left lateral (K) views. • H – *Yochelcionella americana* Runnegar & Pojeta, 1980, MGUH 28900 from GGU sample 271470, left lateral view of internal mould, Aftenstjernø Formation. All scale bars 10 µm.
Discussion. – A full description is given by Atkins & Peel (2004). In this erect, slender, species of Yochelcionella the apical area is inclined over the supra-apical margin due to a change in the direction of coiling during growth. Internal phosphatic moulds show development of a pegma-like structure between the snorkel and apex, a structure only seen elsewhere within this genus in Y. fissurata. In silica replicas from the Parallelidal Formation (late Early Cambrian) of North Greenland, the comarginal rugae are frequently acutely flared and crossed by fine radial striations (Fig. 81–K). Some co-existing specimens, however, are smooth, which may represent original variation and/or selective silification.

Although Y. gracilis shows the same sigmoidal morphology as Y. delicata Yu, 1987, the latter is distinguished by its low rounded apex, greatly inflated sub-apical wall and the recumbent initial stage of the snorkel. A single specimen (Fig. 6G) from the Forteau Formation does not have the apex fully placed over the supra-apical margin. In all other respects it closely matches material from the type locality including the fine radial cords draped over the lateral rugae.

Occurrence. – North Greenland and Newfoundland. Early Cambrian (Cambrian Series 2, stage 4).

Yochelcionella sp.

2004 Yochelcionella sp. Skovsted, p. 29, fig. 7Q.

Material. – MGUH 27003 from GGU sample 314808, Bas-tion Formation, late Early Cambrian, Albert Heim Bjerge, North-East Greenland.

Discussion. – While the presence of a snorkel clearly indicates its position within Yochelcionella, the poor preservation of this single specimen prevents identification.

Occurrence. – North-East Greenland; early Cambrian, Cambrian Series 2, stage 4.

Acknowledgements

Financial support from the Swedish Research Council (Vetenskapsrådet) to J.S. Peel is gratefully acknowledged. Bruce Runnegar kindly provided the photographs of Yochelcionella erecta. Roger Thomas and the late Ellis Yochelson guided J.S. Peel in Thomasville, Pennsylvania. Terry Fletcher provided information concerning Newfoundland stratigraphy. Michael Streng and Ian Ove R. Ebbestad are thanked for technical help and discussion. Gary Wife is thanked for technical help. Reviews from two journal referees are acknowledged.

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DOI 10.1111/j.1475-4983.2006.00599.x


DOI 10.1126/science.186.4161.311


