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

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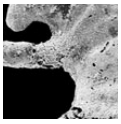

Five named species of the helcionelloid mollusc genus *Yochelcionella* Runnegar & Pojeta, 1974 are recognized from the lower Cambrian (Cambrian Series 2) of North America: *Yochelcionella erecta* (Walcott, 1891), *Y. americana* Runnegar & Pojeta, 1980, *Y. chinensis* Pei, 1985, *Y. greenlandica* Atkins & 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.

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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

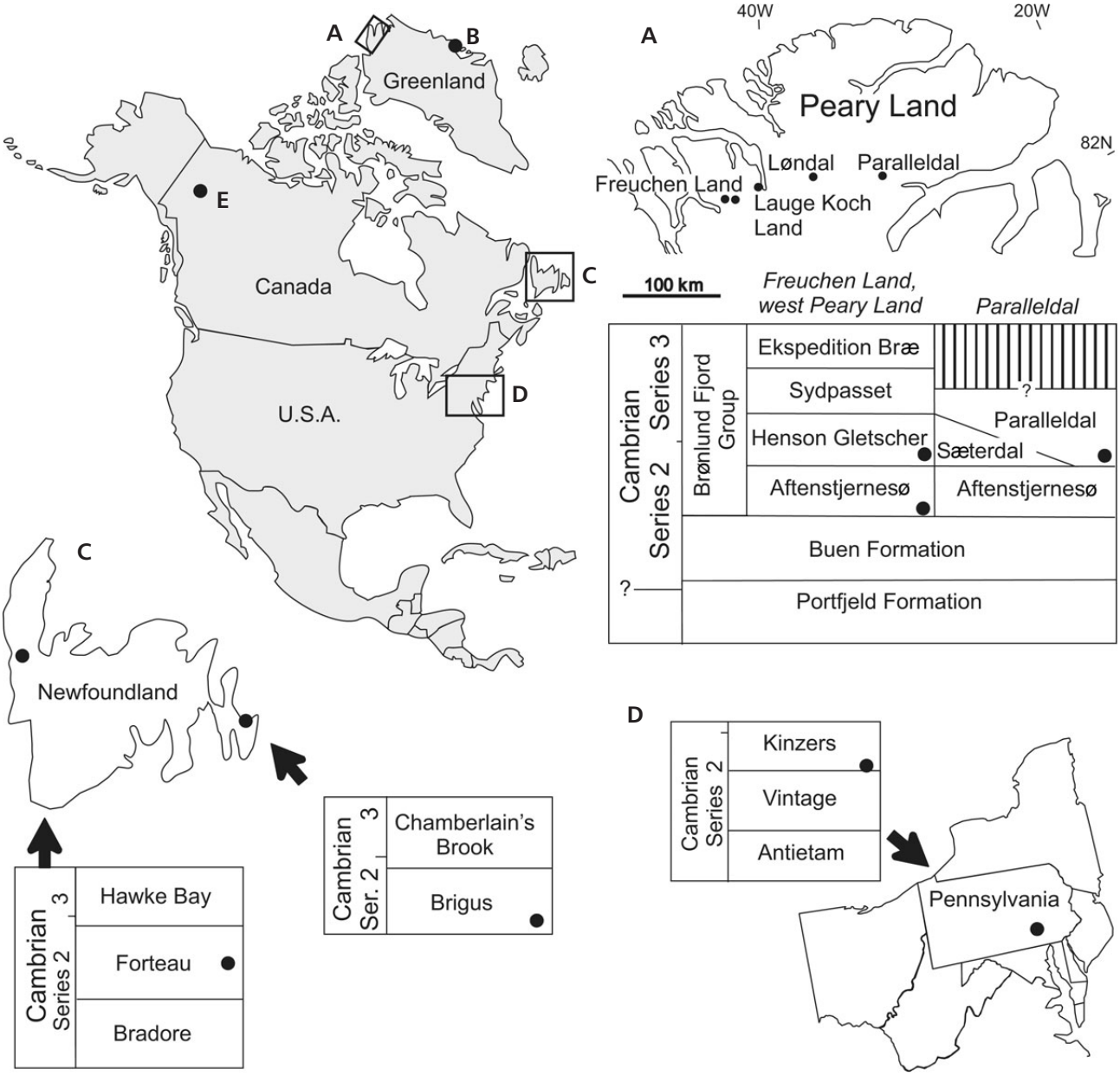

Figure 1. Map of North America showing localities and formations yielding *Yochelcionella*. • A – North Greenland. • B – North-East Greenland. • C – Newfoundland. • D – Thomasville, Pennsylvania, U.S.A. • E – MacKenzie Mountains, Northwest Territories, Canada. Black dots indicate occurrence of *Yochelcionella*.

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.

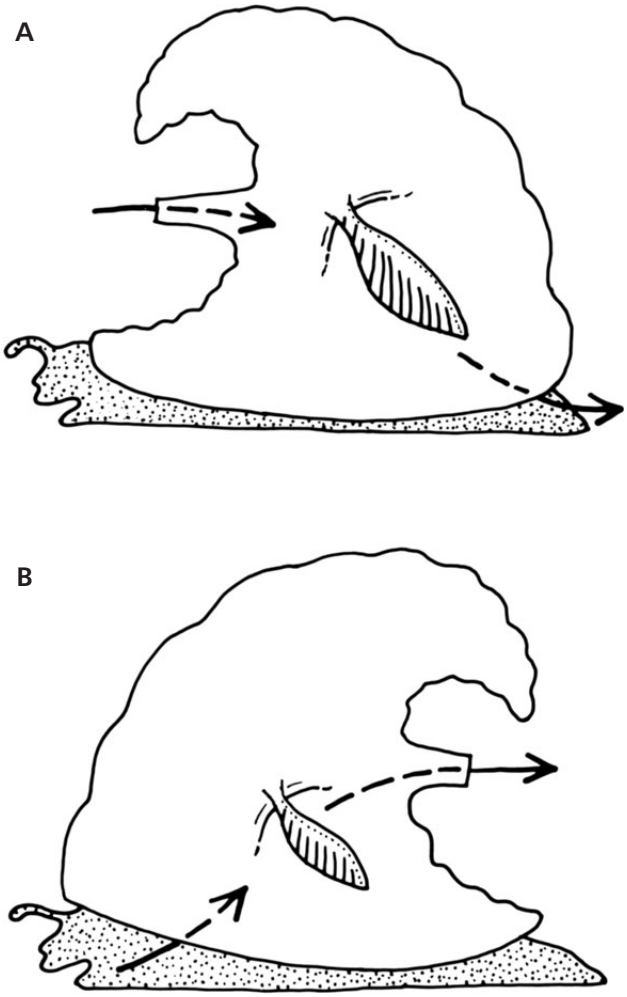

Figure 2. Alternative re-constructions of *Yochelcionella*. • A – exogastrically coiled, with the snorkel located anteriorly. • B – endogastrically coiled, with the snorkel located posteriorly; this is the orientation preferred herein.

Biostratigraphy

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 Øleå, 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 Aftenstjernesø 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 Aftenstjernesø, Paralleldal 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 Aftenstjernesø 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 Aftenstjernesø Formation on the west side of Løndal, western Peary Land (Fig. 1A; J. S. Peel locality 19780714-1).

GGU samples 225711, 225712 and 225714 were also collected in Løndal, 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 Jungersen 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 Paralleldal Formation on the north side of Paralleldal, 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 Helcionelloida 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.

Remarks. – Assigned early-middle Cambrian (Series 1–3) species include: *Yochelcionella cyrano* Runnegar & Pojeta, 1974; *Y. daleki* Runnegar & Jell, 1976; *Y. ostentata* Runnegar & Jell, 1976; *Y. americana* Runnegar & Pojeta, 1980; *Y. recta* Missarzhevsky & Mambetov, 1981; *Y. stylifera* Missarzhevsky & Mambetov, 1981; *Y. chinensis* Pei, 1985; *Y. aichalica* Fedorov *in* Schabanov *et al.* 1987; *Y. delicata* Yu, 1987; *Y. pelmani* Vassiljeva, 1990; *Y. crassa* Zhegallo *in* Esakova & Zhegallo, 1996; *Y. parva* Zhegallo *in* Esakova & Zhegallo, 1996; *Y. erecta* (Walcott, 1891); *Y. angustoplicata* Hinz-Schallreuter, 1997; *Y. trompetica* Hinz-Schallreuter, 1997; *Y. fissurata* Hinz-Schallreuter, 1997; *Y. greenlandica* Atkins & Peel, 2004; *Y. gracilis* Atkins & Peel, 2004. Species in open nomenclature have been described by Geyer (1986), Berg-Madsen & Peel (1987), Hinz (1987), Dzik (1994), Kouchinsky (2000), Wrona (2003) and Skovsted (2004).

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- 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 orthoconic 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. chinensis* by its elongate, narrower, juvenile shell and uniform rate of expansion along the supra-apical margin. As illustrated, the snorkel is represented by a bulge, unlike the tubular structure seen in *Y. chinensis* 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. chinensis*.

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. chinensis* by the tall orthoconic shell, with the juvenile stage curved forward. The well-rounded protoconch overhangs the supra-apical margin, whereas it overhangs the sub-apical wall in *Y. chinensis*. 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 overhang of the sub-apical margin as in *Y. chinensis*. In similar fashion to *Y. chinensis* 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. chinensis* 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 supra-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. chinensis* 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. chinensis*, with a gradual reorientation of the aperture unlike the abrupt change observed in *Y. chinensis*. *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. chinensis*.

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. chinensis*. *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 overhanging the supra-apical wall and an upright, broadly flaring snorkel and apex, unlike *Y. chinensis*.

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. chinensis*. *Yochelcionella?* sp. B exhibits more continuous expansion along the supra-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 overhangs the supra-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. chinensis* by its reduced rate of lateral compression, more ovate aperture and fewer, lateral flaring rugae. While similar to *Y. chinensis*, *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. chinensis* by its tall almost orthoconic shell in which the apex slightly overhangs the supra-apical margin.

Species of *Yochelcionella* described in open nomenclature by Berg-Madsen & Peel (1987), Hinz (1987), Wrona (2003) and Skovsted (2004) are too poorly preserved to permit meaningful comparison with *Y. chinensis*.

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-

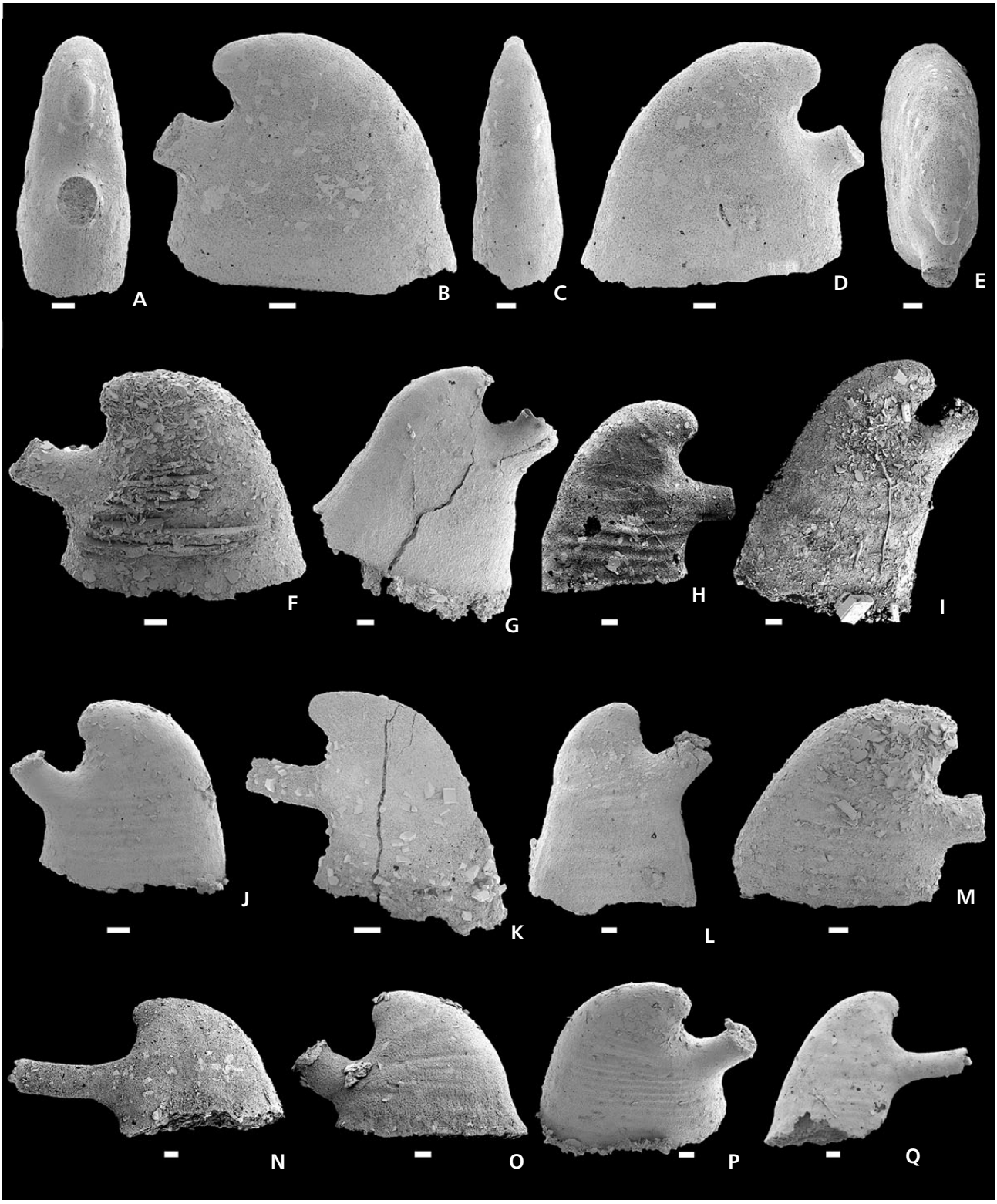

Figure 3. *Yochelcionella chinensis* Pei, 1985, internal moulds from the Forteau Formation, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada. • A–E – PMU 25000, sub-apical (A), right lateral (B), supra-apical (C), left lateral (D) and dorsal (E) views. • F – PMU 25001, right lateral view. • G – PMU 25002, left lateral view. • H – PMU 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.

trated by Pei (1985) in terms of outline but these lack ornamentation on the internal mould (Fig. 3A–E, G, M).

The apex of the type specimen illustrated by Pei (1985) is pointed with slight lateral compression. By comparison the Forteau material exhibits a spectrum of forms ranging from that of the type specimen to a low well-rounded boss with a distinct circumferential constriction (Fig. 4B, D). Also the shape and relative length of the sub-apical wall between the apex and snorkel affect the prominence of the apex (compare Figs 3L, N and 4E, F). In the holotype the snorkel is inclined upwards at an angle of about 20° to the plane of the aperture. This angle varies in the Forteau material from between 65° to –10°.

The teleoconch exhibits little variation in the degree of lateral compression and the outline of the aperture. However, during ontogeny the transition from coiled juvenile to orthoconic adult produces a flattening of the supra-apical surface, in lateral perspective, whereas the sub-apical wall, below the snorkel, may vary from concave to shallowly convex. A slight forward flaring of the margin in some specimens probably indicates the apertural margin in specimens where the shell interior is completely filled by the phosphate of the internal mould (Figs 3O, Q, 4C).

Specimen ornamentation varies from essentially smooth (Fig. 3A–E), to fine rugae (Figs 3O, P, 4A–D), and relatively coarse rugae (Figs 3H, 4J). It should be noted that all specimens are phosphatic internal moulds and that the expression of ornamentation on the shell exterior is not known.

Occurrence. – Xinji Formation, Henan Province, China; Forteau Formation, Newfoundland, Canada; lowest Kinzers Formation, Thomasville, Pennsylvania, USA. Early Cambrian (Cambrian Series 2, stage 4).

Yochelcionella cf. *chinensis* Pei, 1985

Figure 4L

Figured specimen. – PMU 25023, Forteau Formation, Newfoundland, Canada. Early Cambrian (Cambrian Series 2, stage 3).

Discussion. – Although otherwise similar to *Y. chinensis* this single specimen resembles *Y. americana* in its strongly coiled shell form. In lateral view the apex extends well beyond the posterior margin of the aperture.

Yochelcionella erecta (Walcott, 1891)

Figure 5

1891 *Stenotheca rugosa* var. *erecta* Walcott, p. 617, pl. 74, fig. 4.

1938 *Helcionella erecta* (Walcott, 1891). – Resser, p. 14, 23.

1997 *Yochelcionella erecta* (Walcott, 1891). – Hinz-Schallreuter, p. 111, fig. 4, table 1.

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,

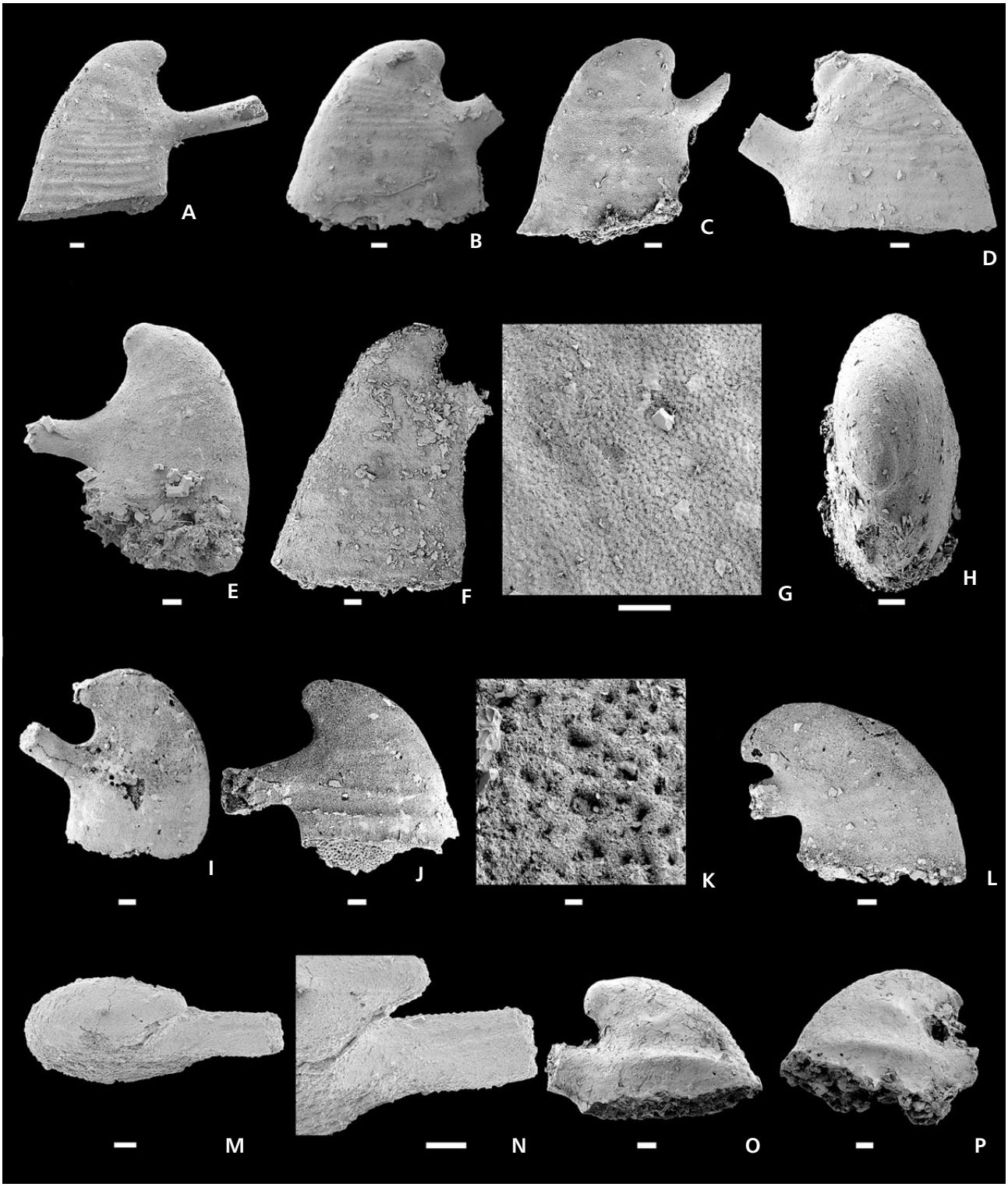

Figure 4. *Yochelcionella*, internal moulds from the Forteau Formation, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada. • A–K, M, N – *Yochelcionella chinensis* Pei, 1985. A – PMU 25013, left lateral view, B – PMU 25014, left lateral view, C – PMU 25015, left lateral view, D – PMU 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.

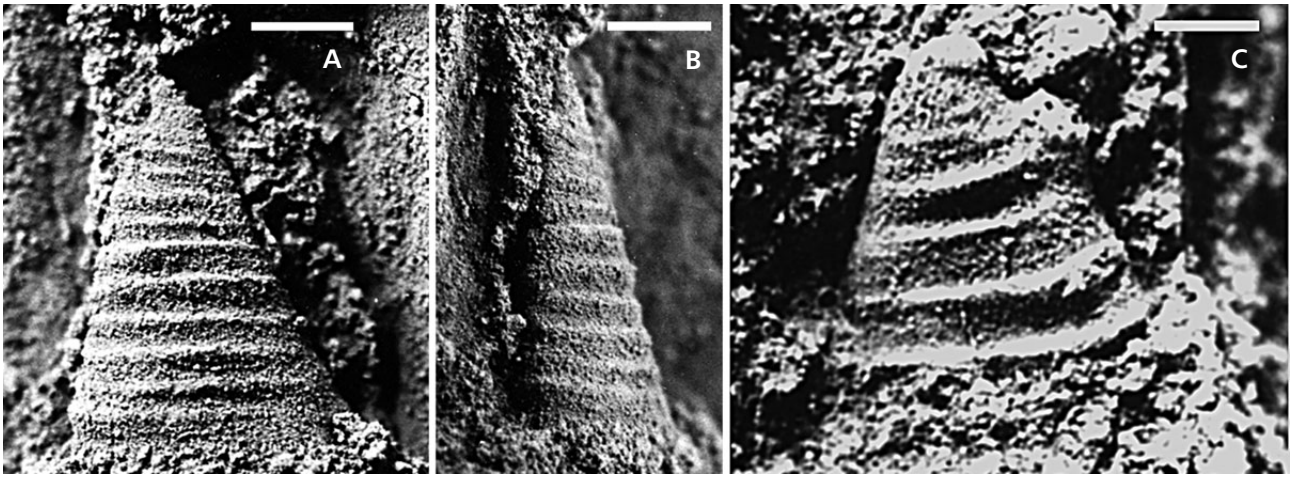

Figure 5. *Yochelcionella erecta* (Walcott, 1891), internal moulds from the Brigus Formation of Conception Bay, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada. • A, B – USNM 307721, right lateral (A) and postero-lateral (B) views. • C – USNM 307720, left lateral view. Photographs courtesy of Bruce Runnegar. All scale bars 1 mm.

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.

Occurrence. – Brigus Formation, Conception Bay, Newfoundland, Canada. Early Cambrian, Cambrian Series 2, stage 4.

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.
2002 *Runnegarella americana* (Runnegar & Pojeta). – Parkhaev, p. 33.
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 Aftenstjernesø 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-

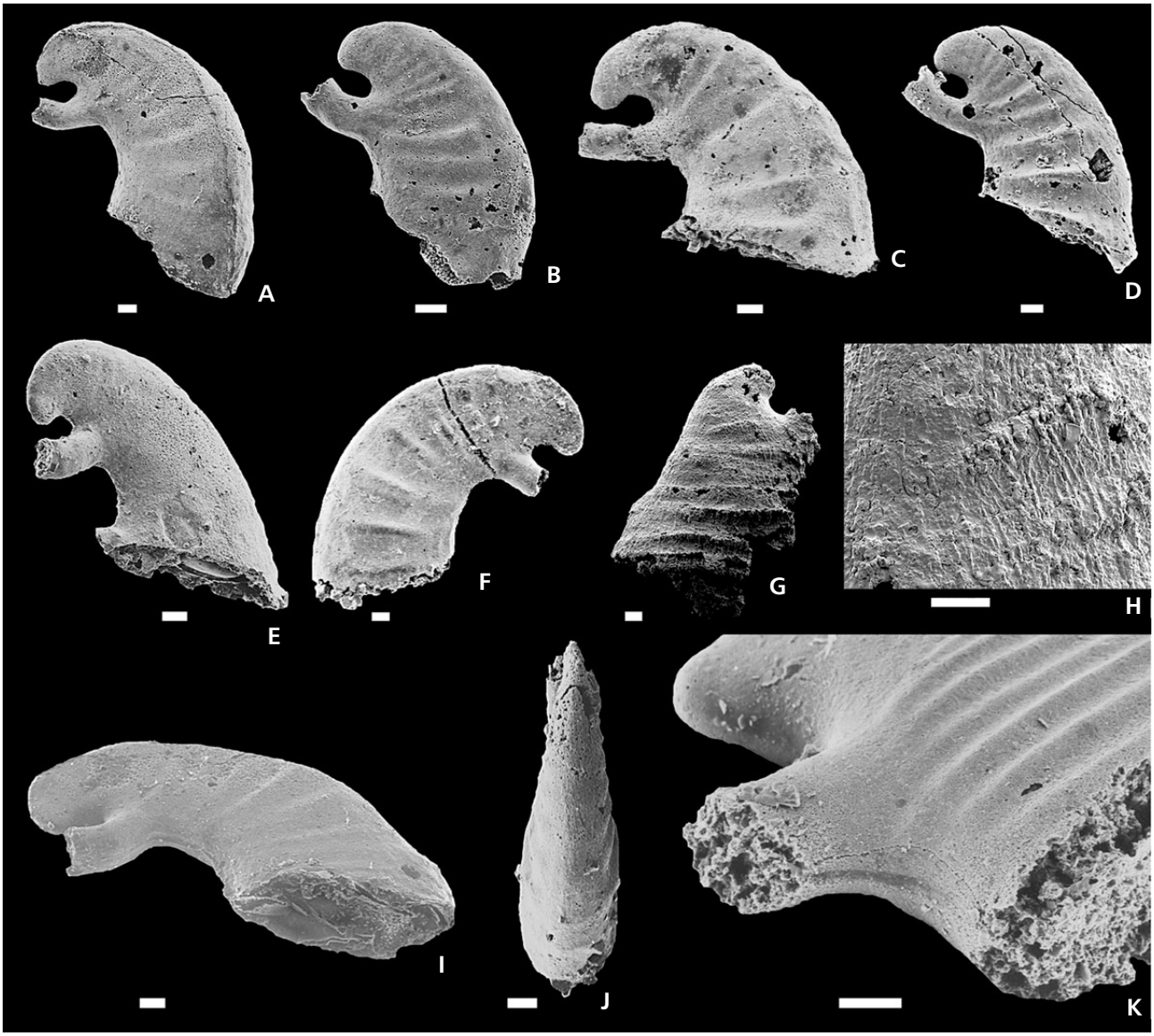

Figure 6. *Yochelcionella,* internal moulds from the Forteau Formation, early Cambrian (Cambrian Series 2, stage 4), Newfoundland, Canada. • A–F – *Yochelcionella americana* Runnegar & Pojeta, 1980. A – PMU 25026, right lateral view, B – PMU 25027, right lateral view, C – PMU 25028, right lateral view, D – PMU 25029, right lateral view, E – PMU 25030, right lateral view, F – PMU 25031, left lateral view. • G, H – *Yochelcionella gracilis* Atkins & Peel, 2004, PMU 25032, left lateral view (G) and detail of ornamentation (H). • I, J – *Yochelcionella americana* Runnegar & Pojeta, 1980. I – PMU 25033, oblique lateral view illustrating groove beneath snorkel, J – PMU 25034, supra apical view. • K – *Yochelcionella chinensis* Pei, 1985, PMU 25035, oblique right lateral view showing groove beneath snorkel. All scale bars 10 μm.

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

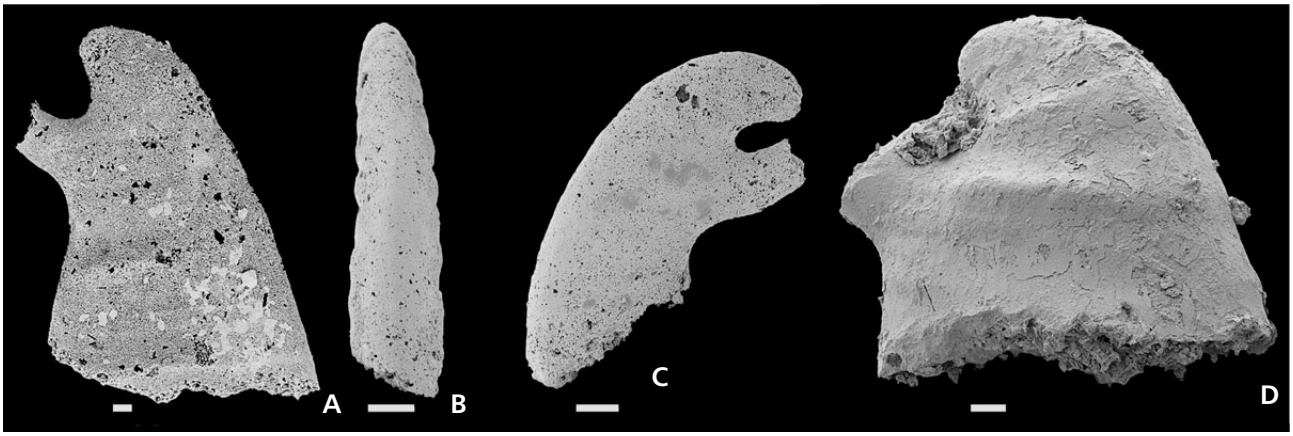

Figure 7. *Yochelcionella*, internal moulds from the Kinzers Formation, early Cambrian (Cambrian Series 2, stage 4), Thomasville, Pennsylvania, U.S.A. • A – *Yochelcionella chinensis* Pei, 1985, PMU 25036, right lateral view. • B, C – *Yochelcionella americana* Runnegar & Pojeta, 1980. B – PMU 25037, supra-apical view, C – PMU 25038, left lateral view. • D – *Yochelcionella greenlandica* Atkins & Peel, 2004, PMU 25039, right lateral view. All scale bars 10 μm.

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 25024–25025, Forteau Formation, Newfoundland, Canada; PMU 25039, lower Kinzers Formation, Thomasville, Pennsylvania, USA. Early Cambrian (Cambrian Series 2, stage 4).

Additional 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 and Newfoundland, 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)

Occurrence. – North Greenland, Eastern U.S.A., western Newfoundland, Quebec and MacKenzie Mountains, Canada. Early Cambrian (Cambrian Series 2, stage 4).

Yochelcionella gracilis Atkins & Peel, 2004

Figures 6G, H, 8E–G, I–K

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

Figured material. – Holotype, MGUH 27020 from GGU sample 225711, MGUH 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).

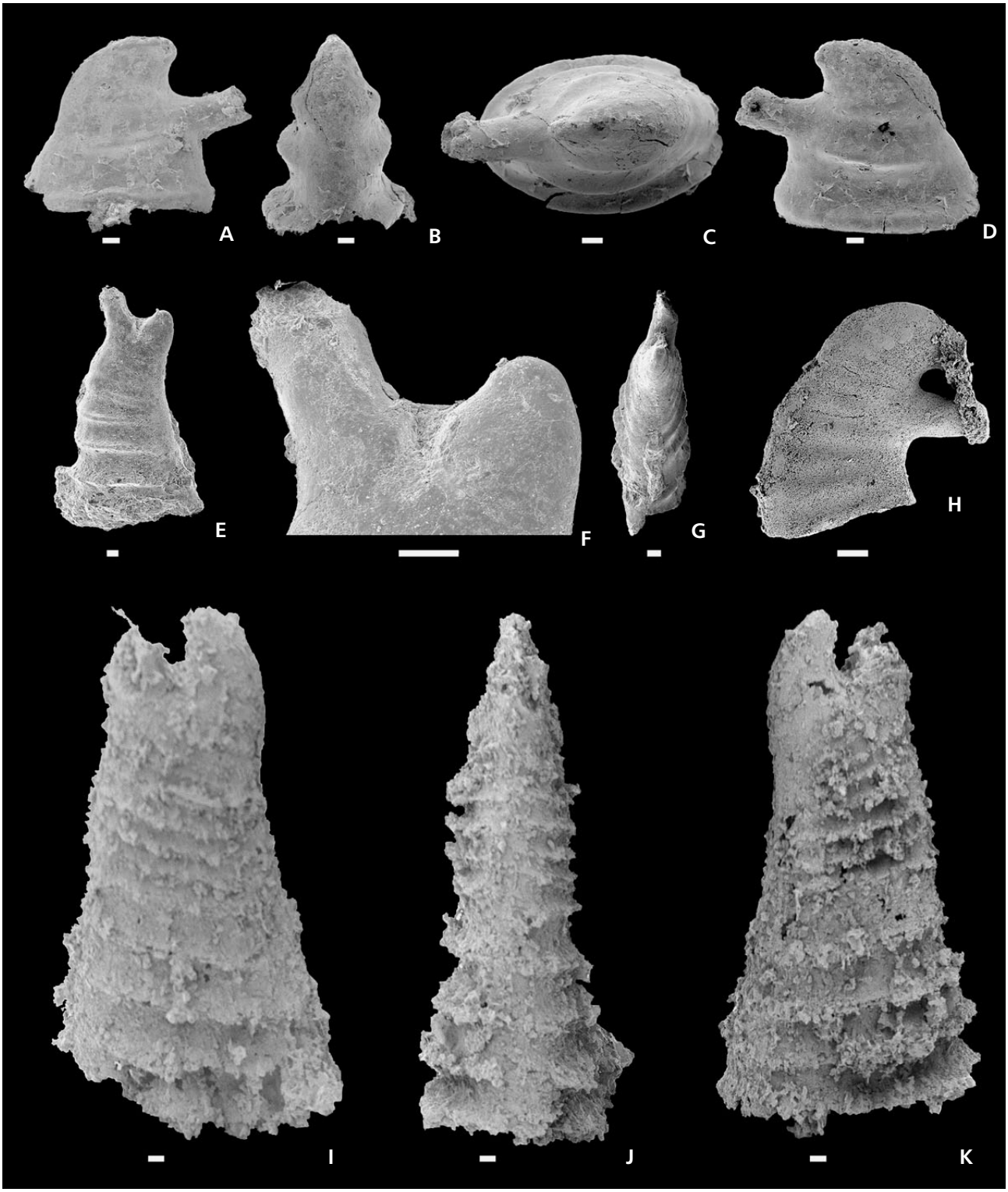

Figure 8. *Yochelcionella* from the early Cambrian (Cambrian Series 2, stage 4) of North Greenland. • A–D – *Yochelcionella greenlandica* Atkins & Peel, 2004, holotype, MGUH 27016 from GGU sample 271471, internal mould, Aftenstjernesø Formation, in left lateral (A), supra-apical (B), dorsal (C) and right 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, Aftenstjernesø 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 Paralleldal Formation (late Early Cambrian) of North Greenland, the comarginal rugae are frequently acutely flared and crossed by fine radial striations (Fig. 8I–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, Bastion 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.

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References

ATKINS, C.J. & PEEL, J.S. 2004. New species of *Yochelcionella* (Mollusca: Helcionelloida) from the Lower Cambrian of North Greenland. *Bulletin of the Geological Society of Denmark 51*, 1–9.

BABCOCK, L.E., PENG, S., GEYER, G. & SHERGOLD, J. 2005. Changing perspectives on Cambrian chronostratigraphy and progress towards subdivision of the Cambrian system. *Geosciences Journal 9,* 101–106.

BENGTSON, S., CONWAY MORRIS, S., COOPER, B.J., JELL, P.A. & RUNNEGAR, B. 1990. Early Cambrian fossils from South Australia. *Association of Australian Palaeontologists Memoir 9*, 1–364.

BERG-MADSEN, V. & PEEL, J.S. 1987. *Yochelcionella* (Mollusca) from the Late Middle Cambrian of Bornholm, Denmark. *Bulletin of the Geological Society of Denmark 36*, 259–261.

BLAKER, M.R. & PEEL, J.S. 1997. Lower Cambrian trilobites from North Greenland. *Meddr Grønland Geoscience 35*, 1–145.

BROCK, G.A. 1998. Middle Cambrian molluscs from the southern New England Fold Belt, New South Wales, Australia. *Geobios 31*, 571–586. DOI 10.1016/S0016-6995(98)80045-4

CUVIER, G. 1797. *Tableau élementaire de l'historie naturelle des animaux*. 710 pp. Paris.

DEBRENNE, F. & PEEL, J.S. 1986. Archaeocyatha from the Lower Cambrian of Peary Land, central North Greenland. *Rapport Grønlands geologiske Undersøgelse 132*, 39–50.

DZIK, J. 1994. Evolution of 'small shelly fossils' assemblages. *Acta Palaeontologica Polonica 39*, 247–313.

ESAKOVA, N.V. & ZHEGALLO, E.A. 1996. Stratigrafiya i fauna nizhnego kembriya Mongolii. *Trudy, Sovmestnaya Rossiysko-Mongol'skaya paleontologicheskaya ekspeditsiya 46*, 1–213.

GEYER, G. 1986. Mittelkambrische Mollusken aus Marocco und Spanien. *Senckenbergiana lethaea 67*, 55–118.

GEYER, G. 1994. Middle Cambrian mollusks from Idaho and early conchiferan evolution, 69–86. *In* LANDING, E. (ed.) *Studies in Stratigraphy and Paleontology in Honor of Donald W. Fisher. New York State Museum Bulletin 481*.

GRAVESTOCK, D.I., ALEXANDER, E.M., DEMIDENKO, Y.E., ESAKOVA, N.V., HOLMER, L.E., JAGO, J.B., LIN, T., MELNIKOVA, L.M., PARKHAEV, P.Y., ROZANOV, A.Y., USHATINSKAYA, G.T., ZANG, W., ZHEGALLO, E.A. & ZHURAVLEV, A.Y. 2001. The Cambrian biostratigraphy of the Stansbury Basin, South Australia. *Russian Academy of Sciences, Transactions of the Palaeontological Institute 282*, 1–344.

GUBANOV, A.P. & PEEL, J.S. 2000. Cambrian monoplacophoran molluscs (Class Helcionelloida). *American Malacological Bulletin 15*, 139–145.

GUBANOV, A.P. & PEEL, J.S. 2003. The Early Cambrian helcionelloid mollusc *Anabarella* Vostokova. *Palaeontology 46*, 1073–1087. DOI 10.1111/1475-4983.00334

GUBANOV, A.P., KOUCHINSKY, A.V., PEEL, J.S. & BENGTSON,

S. 2004. Middle Cambrian molluscs of 'Australian' aspect from northern Siberia. *Alcheringa 28*, 1–20.

HINZ, I. 1987. The Lower Cambrian microfauna of Comley and Rushton, Shropshire/England. *Palaeontographica A 198*, 41–100.

HINZ-SCHALLREUTER, I. 1997. Einsaugstutzen oder Auspuff? Das Rätsel um *Yochelcionella* (Mollusca, Kambrium). *Geschiebekunde aktuell 13*, 105–122.

INESON, J.R. & PEEL, J.S. 1997. Cambrian shelf stratigraphy of North Greenland. *Geology of Greenland Survey Bulletin 173*, 1–120.

JAMES, N.P. & STEVENS, R.K. 1982. *Excursion 2B: anatomy and evolution of a continental margin, western Newfoundland*. 75 pp. 11th International Congress on Sedimentology, McMaster University, Hamilton, Ontario, International Association of Sedimentologists, Field Excursion Guide Book.

KOUCHINSKY, A. 2000. Shell microstructure in Early Cambrian molluscs. *Acta Palaeontologica Polonica 45*, 119–150.

LANDING, E. & BARTOWSKI, K.E. 1996. Oldest shelly fossils from the Taconic allochthon and Late Early Cambrian sea-levels in Eastern Laurentia. *Journal of Paleontology 70*, 741–761.

LANDING, E., GEYER, G. & BARTOWSKI, K.E. 2002. Latest early Cambrian small shell fossils, trilobites, and Hatch Hill dysaerobic interval on the Quebec continental slope. *Journal of Paleontology 76*, 287–305. DOI 10.1666/0022-3360(2002)076<0287:LECSSF>2.0.CO;2

LINSLEY, R.M. 1977. Some 'laws' of gastropod shell form. *Paleobiology* 3, 1039–1042.

MISSARZHEVSKY, V.V. & MAMBETOV, A.M. 1981. Stratigrafija I fauna pogranichnych sloev kembrija i dokembrija Malogo Karatau. *Trudy Geologicheskogo Instituta Akademii nauk SSSR 326*, 1–90.

MORTON, J.E. 1988. The pallial cavity, 253–286. *In* TRUEMAN, E.R. & CLARKE, M.R. (eds) *The Mollusca 11, Form and Function*. Academic Press, London.

PARKHAEV, P.Y. 2002. Phylogenesis and the system of the Cambrian univalved mollusks. *Paleontological Journal 36*, 25–36 (translation of *Paleontologicheskii Zhurnal 2002*, 27–39).

PARKHAEV, P.Y. 2004. Malacofauna of the Lower Cambrian Bystraya Formation of Eastern Transbaikalia. *Paleontological Journal 38*, 590–608 (translation of *Paleontologicheskii Zhurnal 2004*, 9–25).

PEEL, J.S. 1987. *Yochelcionella americana* (Mollusca) from the Lower Cambrian of Newfoundland. *Canadian Journal of Earth Science 24*, 2328–2330.

PEEL, J.S. 1991a. Functional morphology of the class Helcionelloida nov., and the early evolution of the Mollusca, 157–177. *In* SIMONETTA, A. & CONWAY MORRIS, S. (eds) *The early evolution of Metazoa and the significance of problematic taxa*. Cambridge University Press, Cambridge.

PEEL, J.S. 1991b. The classes Tergomya and Helcionelloida, and early molluscan evolution *Bulletin Grønlands Geologiske Undersøgelse 161*, 11–65.

PEEL, J.S. 2004. *Pinnocaris* and the origin of scaphopods. *Acta Palaeontologica Polonica 49*, 543–550.

PEEL, J.S. 2006. Scaphopodization in Palaeozoic molluscs. *Palaeontology 49*, 1357–1364. DOI 10.1111/j.1475-4983.2006.00599.x

PEEL, J.S. & BERG-MADSEN, V. 1988. A new salterellid (Phylum Agmata) from the Upper Middle Cambrian of Denmark. *Bulletin of the Geological Society of Denmark 37*, 75–82.

PEEL, J.S. & YOCHELSON, E.L. 1982. A review of *Salterella* (Phylum Agmata) from the Lower Cambrian in Greenland and Mexico. *Rapport Grønlands geologiske Undersøgelse 108*, 31–39.

PEI, F. 1985. First discovery of *Yochelcionella* from the Lower Cambrian of China and its significance. *Acta Micropalaeontologica Sinica 2*, 395–400 (in Chinese with English summary).

POKORNY, V. 1978. *Janospira*, a presumed archaeogastropod. *Lethaia 11*, 80. DOI 10.1111/j.1502-3931.1978.tb01220.x

POJETA, J. & RUNNEGAR, B. 1976. The paleontology of rostroconch molluscs and the early history of the phylum Mollusca. *Professional Papers of the U.S. Geological Survey 968*, 1–88.

POPOV, L., HOLMER, L.E., ROWELL, A.J. & PEEL, J.S. 1997. Early Cambrian brachiopods from North Greenland. *Palaeontology 40*, 337–354.

RESSER, C.E. 1938. Fourth contribution to nomenclature of Cambrian fossils. *Smithsonian Miscellaneous Collections 97(10)*, 1–43.

REYNOLDS, P.D. 2002. The Scaphopoda. *Advances in Marine Biology 42*, 137–236. DOI 10.1016/S0065-2881(02)42014-7

RIEDEL, F. 1996. Comments on "A new twist to the Garstang torsion hypothesis" by L.W. Buss. *Neues Jahrbuch für Geologie und Paläontologie 2*, 116–128.

RUNNEGAR, B. & JELL, P.A. 1976. Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. *Alcheringa 1*, 109–138.

RUNNEGAR, B. & JELL, P.A. 1980. Australian Middle Cambrian molluscs: corrections and additions. *Alcheringa 4*, 111–113.

RUNNEGAR, B. & POJETA, J. 1974. Molluscan phylogeny: the paleontological viewpoint. *Science 186*, 311–317. DOI 10.1126/science.186.4161.311

RUNNEGAR, B. & POJETA, J. 1980. The monoplacophoran mollusk *Yochelcionella* identified from the Lower Cambrian of Pennsylvania. *Journal of Paleontology 54*, 635–636.

SCHABANOV, Y.Y., ASTASHKIN, V.A., PEGEL, T.B., EGOROVA, L.I., ZHURAVLEVA, I.T., PELMAN, Y.L., SUNDUKOV, V.M., STEPANOVA, M.B. & SUKHOV, C.C. 1987. *Nizhniy paleozoy yugo-zapadnogo sklona Anabarskoy anteklizy*. 207 pp. Nauka, Novosibirsk.

SKINNER, E.S. 2005. Taphonomy and depositional circumstances of exceptionally preserved fossils from the Kinzers Formation (Cambrian), southeastern Pennsylvania. *Palaeogeography, palaeoclimatology, palaeoecology 220*, 167–192. DOI 10.1016/j.palaeo.2004.09.015

SKOVSTED, C.B. 2004. Mollusc fauna of the Early Cambrian Bastion Formation of North-East Greenland. *Bulletin of the Geological Society of Denmark 51*, 11–37.

SKOVSTED, C.B. & PEEL, J.S. 2007. Small shelly fossils from the argillaceous facies of the Lower Cambrian Forteau Formation of Western Newfoundland. *Acta Palaeontologica Polonica 52*, 729–748.

SKOVSTED, C.B., PEEL, J.S. & ATKINS, C.J. 2004. The problematic fossil *Triplicatella* from the Early Cambrian of Greenland, Canada and Siberia. *Canadian Journal of Earth Sciences 41*, 1273–1283. DOI 10.1139/e04-066

STANLEY, S.M. 1970. Adaptive themes in the evolution of Bivalvia (Mollusca). *Annual Review of Earth and Planetary Sciences 3*, 361–385. DOI 10.1146/annurev.ea.03.050175.002045

STEINER, M., LI, G. & QIAN, Y. 2004. Lower Cambrian small shelly fossils of northern Sichuan and southern Shaanxi (China), and their biostratigraphic importance. *Geobios 37*, 259–275.

VASSILJEVA, N.I. 1990. *Novye rannekembrijskie brjuchonogie molljuski Sibirskoj platformy i voprosy ich sistematiki,* 4–21. *In* NIKOLAEV, A.I. (ed.) *Mikrofauna SSSR, Voprosy sistematiki i biostratigrafii*. VNIGRI, Leningrad.

VASSILJEVA, N.I. 1998. *Melkaya rakovinnaya fauna i biostratigrafiya nizhnego kembriya Sibirskoi platformy*. 139 pp. VNIGRI, St. Petersburg.

VORONOVA, L.G., DROSDOVA, N.A., ESAKOVA, N.V., ZHEGALLO, E.A., ZHURAVLEV, A.Y., ROZANOV, A.Y., SAYUTINA, T.A. & USHATINSKAYA, G.T. 1987. Iskopaemye nizhnego kembriya gor Makkenzi (Kanada). *Trudy Paleontologicheskii Institut, Akademia nauk SSSR 224*, 1–88.

WALCOTT, C.D. 1891. The fauna of the Lower Cambrian or *Olenellus* Zone. *Tenth Annual Report U.S. Geological Survey*, 509–761.

WENZ, W. 1938–44. Gastropoda Teil 1: Allgemeiner Teil und Prosobranchia, 1639 pp. *In* SCHINDEWOLF, O.H. (ed.) *Handbuch der Paläozoologie 6*. Gebrüder Borntraeger, Berlin.

WRONA, R. 2003. Early Cambrian molluscs from glacial erratics of King George Island, West Antarctica. *Polish Polar research 24*, 181–216.

YOCHELSON, E.L. 1978. An alternative approach to the interpretation of the phylogeny of ancient mollusks. *Malacologia 2*, 165–191.

YU, W. 1987. *Yangtze micromolluscan fauna in Yangtze region of China with notes on Precambrian-Cambrian boundary. Stratigraphy and Palaeontology of systematic boundaries in China, Precambrian-Cambrian Boundary (1).* 275 pp. Nanjing University Publishing House, Nanjing.