Bobellis oliveri gen. et sp. nov. from the Silurian of North Greenland (Laurentia) and the systematic position of pycnomphaline gastropods

John S. Peel

The gastropod *Bobellis oliveri* gen. et sp. nov. is described from carbonate mounds of the Samuelsen Høj Formation (early Silurian) within the Washington Land Group of North Greenland (Laurentia). It displays a profound adapertural swing of the growth lines across the upper whorl surface in the multi-whorled trochiform shell; the umbilicus is closed by a prominent funicle. *Bobellis oliveri* is assigned to the Family Pycnomphalidae (Ordovician–Devonian; *nom. transl*. Subfamily Pycnomphalinae Peel, 1984) which is transferred to the Euomphaloidea, alongside the morphologically similar Omphalotrochidae (Devonian–Permian). In pycnomphalids the umbilicus is usually partially or completely closed by a prominent circumbilical funicle while the umbilicus of omphalotrochids is generally open. • Key words: Silurian, North Greenland, Laurentia, Gastropoda, Pycnomphalidae.

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In most mobile marine gastropods the plane of the shell aperture is tangential to the final whorl and oriented parallel to the substrate in life. Tangentialism may be produced in several different ways (Wagner 2002) but it enables clamping of the shell down over the body when the animal is disturbed (Linsley 1977); it can be viewed as one of the earliest responses in gastropods to predation or environmental stress. In gastropods where the aperture is not tangential, the plane of the aperture lies along a radius from the shell coiling axis and the shell aperture cannot clamp down against the substrate (Linsley 1977, McNair *et al*. 1981). At the present day, gastropods with radial apertures are uncommon and include cemented and uncoiling forms such as the filter-feeding vermetids, where the shell aperture is closed by an operculum capable of regeneration (Hadfield 1970). In architectonicids the regularly coiled shell is attached to its cnidarian host with mucous threads and the animal feeds on the scleractinian corals with an unusually long, extensible proboscis (Robertson *in* Linsley 1977; Robertson 1967, 1970).

In contrast, gastropods with radial apertures are relatively common in the Palaeozoic, including groups such as the macluritoids and euomphaloids (Knight *et al.* 1960, Frýda *et al*. 2008, Frýda 2012, Bouchet *et al.* 2017), although Linsley & Kier (1984) suggested that these were not true gastropods (see also Bouchet *et al.* 2005, Frýda *et al.* 2008). Typically, such forms are low spired with an open umbilicus, a shell morphology that is common in the Palaeozoic (Wagner & Erwin 2006). Some are even open coiled (Yochelson 1971, Linsley & Yochelson 1973, Peel 1975, Linsley 1978). Many have been interpreted as filter feeders and often had a prominent operculum (Yochelson & Linsley 1972, Yochelson 1979, Rohr & Boucot 1984, Horný 1995, Rohr & Gubanov 1997, Rohr & Yochelson 1999, Rohr 2004, Rohr *et al*. 2004).

This paper describes a new gastropod, *Bobellis oliveri* gen. et sp. nov., from the lower Silurian of North Greenland (Fig. 1) in which the aperture is radial. Similar gastropods with a cyrtoconoid shell form and orthocline to opisthocline outer lip have been assigned to the Anomphalidae Wenz, 1938 and the Omphalotrochidae Knight, 1945 (Knight *et al.* 1960; Wagner 2002; Bouchet *et al*. 2005, 2017) and the description of *Bobellis* prompts discussion of the relationships of Palaeozoic gastropods that have been assigned to these families. *Bobellis* is closely related to *Grantlandispira* Peel, 1984, originally described also from the lower Silurian of North Greenland (Peel 1984; Fig. 2), and is readily placed together with the latter genus in the Subfamily Pycnomphalinae Peel, 1984. However, Pycnomphalinae is elevated herein to family status and removed from the trochoidean Anomphalidae. Pycnomphalidae and Omphalotrochidae are recognized as separate families with Euomphaloidea.

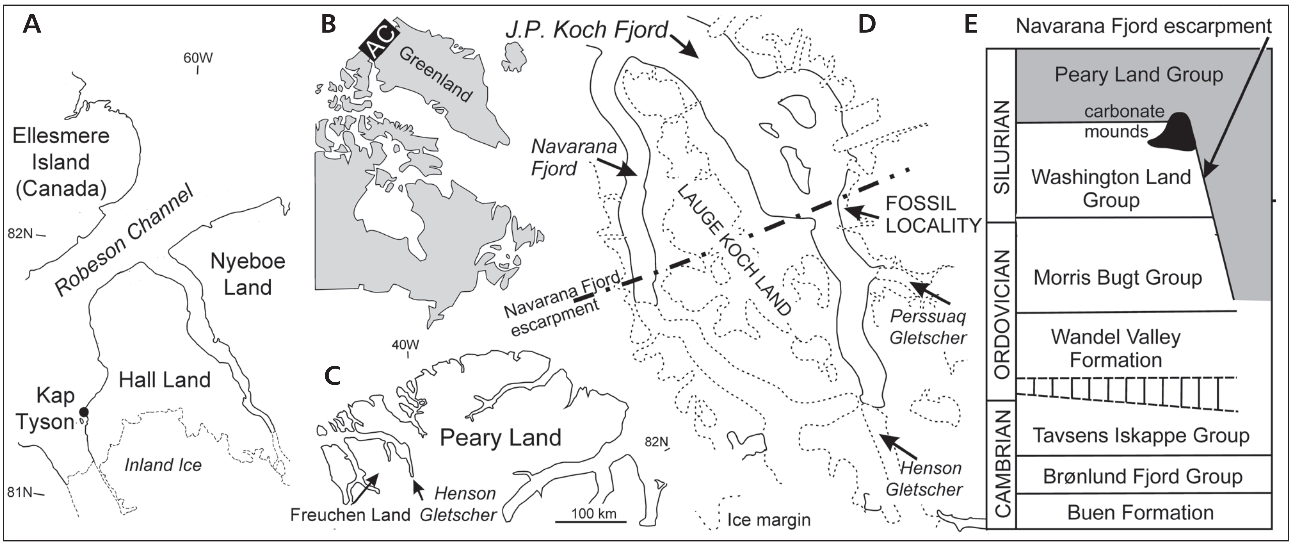

Figure 1. Derivation of samples. • A–D – maps showing the collection locality of *Grantlandispira christiei* Peel, 1984 at Kap Tyson in Hall Land (A) and of *Bobellis oliveri* gen. et sp. nov., east of J.P. Koch Fjord, Peary Land (D). • E – Cambrian–Silurian stratigraphic nomenclature around southern J.P. Koch Fjord locating carbonate mounds yielding *Bobellis oliveri*.

Derivation of material

All specimens of *Bobellis oliveri* gen. et sp. nov. are derived from GGU samples collected by J.S. Peel on 10th–12th August 1985, on the eastern side of J.P. Koch Fjord, Peary Land , North Greenland (82˚ 30´ N, 41˚ 16.5´ W, altitude about 600 m a.s.l.) from carbonate mounds of early Silurian age that occur at the top of the Washington Land Group (Fig. 1B–E). The mounds are located near the northern rim of a Cambrian–Silurian carbonate platform that terminates in a profound escarpment, the Navarana Fjord escarpment (Higgins *et al.* 1991). While representing a major down-to-basin tectonic feature in the geological evolution of North Greenland (Peel & Sønderholm 1991, Higgins *et al.* 1991, Surlyk 1991, Ineson & Peel 2011), the lineament shows little evidence of movement during the Late Ordovician and Silurian, although the geomorphological feature persisted as a steep scarp about 500 m in height. Trough siliciclastic sediments of the Peary Land Group accumulated rapidly against the face of the escarpment before drowning the southern carbonate platform in the late early Silurian. The associated fauna in the carbonate mounds consists of a rich assemblage of gastropods, corals and brachiopods; trilobites from the same locality were described by Hughes & Thomas (2015).

Institutional abbreviations. – GGU – Grønlands Geologiske Undersøgelse, the Geological Survey of Greenland, Copenhagen, Denmark; MGUH – the palaeontological type collection of the Natural History Museum of Denmark, Copenhagen, Denmark; PMU – the palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden.

Classification

Previous work. – The Family Omphalotrochidae Knight, 1945 was placed within the Superfamily Euomphaloidea (as Euomphalacea) de Koninck, 1881, Suborder Macluritina Cox & Knight, 1960 by Knight *et al*. (1960), while Anomphalidae Wenz, 1938 was located within the Superfamily Anomphaloidea Wenz, 1938 (as Anomphalacea) of the Suborder Trochina Cox & Knight, 1960.

Peel (1984) abandoned Anomphaloidea and placed Anomphalidae as a family within the Superfamily Trochoidea Rafinesque, 1815 (as Trochacea), following McLean (1981). He proposed a new Subfamily Pycnomphalinae within Anomphalidae to contain gastropods in which the outer lip varies from near orthocline to opisthocline, including *Pycnomphalus* Lindström, 1884 and a new genus, *Grantlandispira* Peel, 1984 from the lower Silurian of Greenland. Other anomphalid genera recognized by Knight *et al.* (1960) were placed by Peel (1984) within the Subfamily Anomphalinae on account of their generally prosocline outer lip.

Anomphalidae was recognized as a monophyletic family within Euomphaloidea by Wagner (2002) who followed Kase (1989) in suggesting that *Labrocuspis* Kase, 1989 and some genera assigned to Omphalotrochidae might belong here. Wagner (2002, p. 79) placed *Grantlandispira* as a synonym of *Trochomphalus* Koken & Perner, 1925. However, this genus was later considered to be a planitrochid in the on-line database Fossilworks, gateway to the Paleobiology Database (*http://www.fossilworks.org*), as updated by P.J. Wagner during 2017, while *Grantlandispira* was placed as a synonym of *Pycno-*

trochus Perner, 1903. *Turbocheilus* Perner, 1907 was synonymized with *Pycnomphalus*, as also (tentatively) were *Nematrochus* Perner, 1903, *Pycnotrochus* and *Isfarispira* Gubanov, Peel & Pianovskaya, 1995. The synonymies largely reflected Wagner's (2002) philosophy of eliminating monotypic genera from his phylogenetic classification of Lower Palaeozoic gastropods. Wagner (2002) commented that true omphalotrochids appear to have originated from within the Family Euomphalidae, although Knight *et al*. (1960) suggested their derivation from forms similar to the Silurian *Centrifugus* Bronn, 1834. Yochelson (1956, p. 201) commented that 'it is impossible to construct any meaningful family phylogeny at this time'.

Bouchet *et al.* (2005) considered Anomphalidae to be certainly basal Gastropoda but made no assignment to superfamily. In a study of Triassic fossils from Vietnam, Kaim *et al.* (2014) re-ranked Anomphalidae as the Subfamily Anomphalinae of the Family Turbinidae Rafinesque, 1815, a family which Knight *et al.* (1960) only recorded from Triassic–Recent, while *Anomphalus* Meek & Worthen, 1867 was originally described from the Carboniferous (Knight 1941). Nützel *in* Nützel & Nakazawa (2012) interpreted Anomphalidae as Turbinoidea Rafinesque, 1815 but Nützel & Ketwetsuriya *in* Ketwetsuriya *et al.* (2016) placed the family within Trochoidea. This latter placement was maintained by Bouchet *et al.* (2017, p. 337).

The placement of Omphalotrochidae in the Superfamily Euomphaloidea (as Euomphalacea) of the archaeogastropod Suborder Macluritina by Knight *et al.* (1960) was accepted by Bouchet *et al.* (2005) but they considered euomphaloideans to be of uncertain position within the molluscs. This tentative interpretation as gastropods may have been a reflection of the placement of euomphaloideans within a new Class Paragastropoda by Linsley & Kier (1984). Bandel & Frýda (1998) elevated Euomphaloidea to a new Subclass Euomphalomorpha (not class as stated by Bouchet *et al.* 2005, p. 271), but Nützel (2002) did not maintain the subclass. In reviewing Palaeozoic gastropods, Frýda *et al.* (2008) considered Euomphalomorpha to be possibly ancestral to patellogastropods, although the origin and geological range of the latter clade is controversial (Lindberg 1988, Ponder & Lindberg 1997, Bouchet *et al.* 2005, Nakano & Ozawa 2007, Frýda *et al.* 2008, Frýda 2012, Aktipis & Giribet 2010). Bouchet *et al.* (2017, p. 333) regarded omphalotrochids as 'Palaeozoic basal taxa that are certainly Gastropoda', placing them within the Superfamily Euomphaloidea White, 1877.

The on-line databases Fossilworks, gateway to the Paleobiology Database and WMSDB – Worldwide Mollusc Species Database (*http://www.bagniliggia.it/WMSD/HtmFamily/OMPHALOTROCHIDAEL.htm*), placed respectively 13 and 14 genera within Omphalotrochidae, the only family placed within Omphalotrochoidea, but the reasons for including several of these genera, such as the holopeiform *Archaeosphera* Heidelberger & Bandel, 1999 (see also Heidelberger 2007), *Cinclidonema* Knight, 1945 and *Sylvestria* Heidelberger, 2001, close to *Omphalotrochus* are elusive.

In Fossilworks, Anomphalidae is listed as containing the Subfamily Pycnomphalinae with *Isfarispira*, *Pycnomphalus*, *Pycnotrochus*, (with *Grantlandispira* as a junior synonym) and *Turbocheilus* Perner, 1907, although *Isfarispira* is separately referred to Omphalotrochidae (placement cited as following Peel 2018). Peel (2018) considered *Isfarispira* to be a member of the pycnomphaline–omphalotrochid group and unrelated to anomphalines. To these genera, within Pycnomphalinae, WMSDB adds several genera included within Anomphalidae by Knight *et al*. (1960), Peel (1984, as Anomphalinae) and Fossilworks (as non-pycnomphaline anomphalids).

Discussion. – Three families are recognized herein. The placement of Anomphalidae within Trochoidea and Omphalotrochidae within Euomphaloidea reflects current opinions in published literature, discussed above. The fundamental difference in the nature of the outer lip noted by Peel (1984) promotes removal of Pycnomphalinae from Anomphalidae but the relationship between pycnomphalines and omphalotrochines is less clear. Both share the presence of a sub-sutural sinus in most constituent genera, although an emargination occurs in this position high on the upper whorl surface in several euomphaloideans and even in some unrelated pleurotomariiform, holopeiform and high spired gastropods (Knight *et al*. 1960, Harper 2016).

Pycnomphalinae is here elevated to a family, Pycnomphalidae (Ordovician–Devonian), and transferred to Euomphaloidea alongside Omphalotrochidae (Devonian–Permian). The rotelliform to cyrtoconoid shells of pycnomphalids usually develop a prominent funicle which restricts or closes the umbilicus. In omphalotrochids, the shell form is often gradate, even tending towards trochiform, and the umbilicus is usually open. Omphalotrochids are typically Permian in age but occur also in the latest Carboniferous (Yochelson 1956). However, several Devonian and Carboniferous taxa have been referred to the family but forms such as *Orecopia* Knight, 1945 *Bassotrochus* Tassell, 1978*, Labrocuspis* and *Pycnotrochus* are here placed within Pycnomphalidae. *Cinclidonema* Knight, 1945 is considered to be a holopeid, and *Trochonemopsis* Meek, 1873 is interpreted as a trochonematid, as suggested by Knight *et al.* (1960).

Of particular interest is *Pseudomphalotrochus* Blodgett, 1992, originally described from the Devonian of Alaska (Blodgett 1992, p. 141) as an omphalotrochid "but differing primarily [from *Omphalotrochus*] in the presence of a strong basal angulation bearing a prominent circumbilical ridge". Blodgett (1992) considered it likely that *Omphalotrochus* was derived from *Pseudomphalotrochus* but noted the significant stratigraphic gap between the two. The whorl profile of *Pseudomphalotrochus* is strongly gradate, with angular, almost perpendicular, transitions between the upper whorl surface, the outer whorl surface, the base and the umbilical wall. This, together with the open umbilicus which lacks the prominent funicle or callus seen in most pycnomphalids, argues against assignment of *Pseudomphalotrochus* to Pycnomphalidae. *Pseudomphalotrochus* is tentatively retained within Omphalotrochidae, although the supposed Devonian range of this late Carboniferous to typically Permian group (Yochelson 1956) is otherwise mainly based on *Orecopia*, following Knight (1945). *Orecopia* is regarded herein as a pycnomphalid. *Pseudomphalotrochus* may represent a separate, earlier, branch from euomphaloidean stock than *Omphalotrochus* and its immediate relatives such as *Babylonites* Yochelson, 1956 and *Coronopsis* Waterhouse, 1963.

Systematic palaeontology

This published work and the nomenclatural acts it contains have been registered in ZooBank: *http://zoobank.org/References/31053BC7-F67A-4871-BC10-0B7502CBF990.*

Phylum Mollusca Cuvier, 1797
Class Gastropoda Cuvier, 1797
Superfamily Euomphaloidea White, 1877
Family Pycnomphalidae Peel, 1984
nom. transl. Subfamily Pycnomphalinae Peel, 1984

Diagnosis. – Rotelliform to cyrtoconoid gastropods with the subradial aperture varying from near orthocline to strongly opisthocline on the upper whorl surface below a sub-sutural sinus. Umbilicus often partially or completely closed by a prominent circumbilical funicle extending adaxially from the base of the whorl (emended from Peel 1984).

Discussion. – Peel (1984) proposed Pycnomphalinae to include *Pycnomphalus*, his new genus *Grantlandispira* and possibly *Turbocheilus*, although the latter was considered to be a junior synonym of *Pycnomphalus* by Wagner (2002, p. 79).

The eponymous genus *Pycnomphalus* occupies a basal morphological position within the family in that neither the sub-sutural sinus nor the circumbilical funicle are strongly developed in the type species, *Pycnomphalus obesus* Lindström, 1884, from the Silurian of Gotland, Sweden. The latter is morphologically close to *Pycnomphalus borkholmiensis* Koken, 1897 from the Late Ordovician of Estonia. Thus, pycnomphalids range from the Late Ordovician into the Devonian where the family is represented by the well-known *Orecopia* which closely resembles *Grantlandispira* and *Bobellis* gen. nov., both from the lower Silurian of North Greenland. These three genera frequently show a decrease in the incremental angle through growth of the multi-whorled shell to produce a cyrtoconoid form in larger specimens.

Lindström (1884) described three species of *Pycnomphalus* from the Silurian of Gotland. Growth lines indicate that the essentially orthocline outer lip in the more rotelliform *Pycnomphalus obesus*, the type species, has a slight sub-sutural concavity (Knight 1941); the umbilicus is also partially closed by a broad funicle. The whorl periphery is well rounded, whereas it is acutely angular in *Pycnomphalus acutus* Lindström, 1884 [now assigned to ?*Grantlandispira acuta* (Lindström, 1884)] and *Pycnomphalus trochiformis* Lindström, 1884, also from the Silurian of Gotland. The periphery in ?*Grantlandispira acuta* is extended into a flange which recalls the supra-sutural cord of *Grantlandispira christiei* (Fig. 2B, C), although the former is lower spired and with a less prominent circumbilical funicle. *Pycnomphalus trochiformis* is similar in shell shape to *Bobellis oliveri* gen. et sp. nov., but lacks the prominent sub-sutural shoulder of the latter (Fig. 3B).

Pycnomphalus borkholmiensis, as illustrated by Koken & Perner (1925, pl. 32, figs 1–6, 9) from the Late Ordovician of the Baltic Region, has less inflated whorls than *Pycnomphalus obesus* and its funicle is more acute. Both species have fewer whorls than *Pycnomphalus colemani* Parks, 1915, from the lower Silurian of Canada which is rotelliform, but differs from the type species in its lower spired shell, greater number of whorls and the presence of a well-developed funicle. It is closely similar to the better known *Pycnomphalus solaroides* (Hall, 1852), as described by Whiteaves (1895, pl. 13, figs 3–8) from the Silurian Guelph Formation of southern Ontario, Canada. The latter has numerous slowly expanding whorls and the umbilicus is completely closed by the prominent circumbilical funicle. Growth lines on the upper whorl surface appear to be orthocline whereas those on the base are concave adapically, as in *Bobellis oliveri* (Fig. 3M).

Turbocheilus, as described by Knight (1941) from the Bohemian Silurian, is more globose and with fewer whorls than several species referred to *Pycnomphalus*. A slight sub-sutural sinus is developed and the umbilicus is completely closed by callus.

Grantlandispira has a cyrtoconoid shell in which the sides of the spire are uniformly convex in lateral profile (Fig. 2B, D). The growth lines forming the lower margin

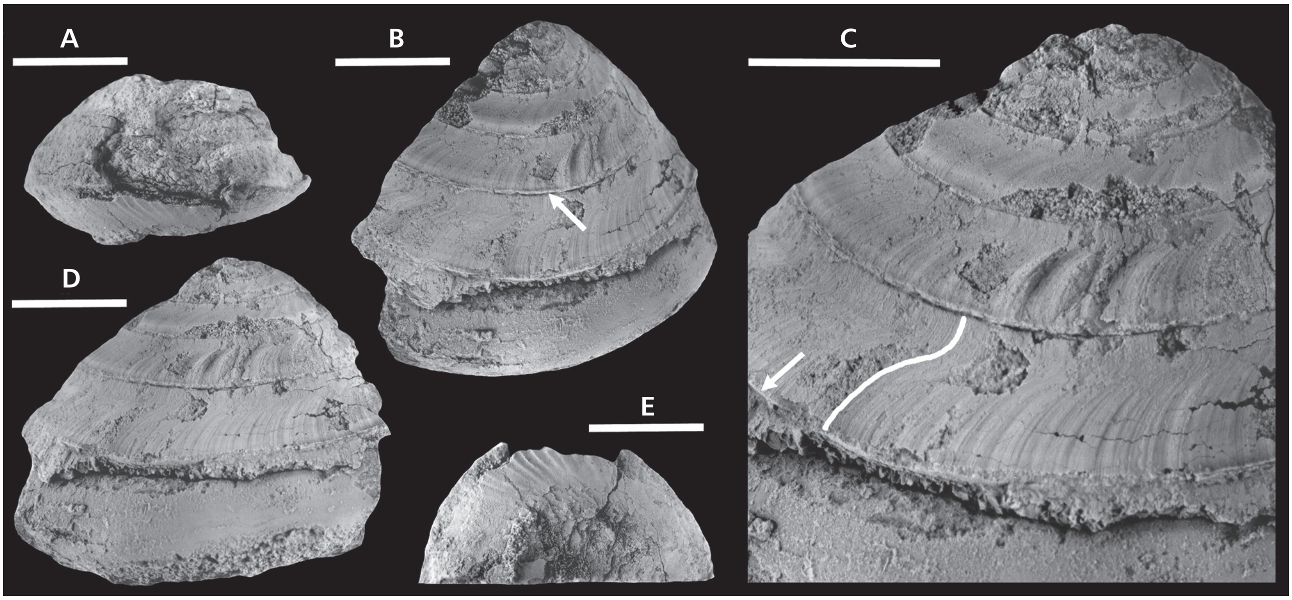

Figure 2. *Grantlandispira christiei* Peel, 1984. Silurian, Washington Land Group, Offley Island Formation, Kap Tyson, Hall Land, North Greenland; A, E – MGUH 16567 from GGU sample 82619, paratype, in lateral and basal views; B–D – MGUH 16566 from GGU sample 82626, holotype, in oblique lateral (B, C) and lateral views (D). Arrows indicate narrow peripheral cord, while the shape of growth lines on the upper whorl surface is inked in C. All specimens coated with ammonium chloride sublimate prior to photography. Scale bars = 10 mm.

of the sinus sweep strongly forward across the upper whorl surface in contrast to the near orthocline shape in *Pycnomphalus* and *Turbocheilus*.

The cyrtoconoid shell form and prominent circumbilical funicle (Knight 1945) motivate transfer of *Orecopia* to Pycnomphalidae. It is morphologically close to *Grantlandispira* and *Bobellis* gen. nov. but the sinus is broad and much less strongly asymmetrical than in the last two genera.

Other possible pycnomphalids include *Isfarispira*, from the Silurian of central Asia and Laurentia (Gubanov *et al.*1995, Peel 2018), *Labrocuspis* from the middle Devonian of Queensland and Japan (Heidecker 1959, Kase 1989), and *Fujispira* Kase & Nishida, 1986 from the middle Devonian of Japan (Kase & Nishida 1986).

Isfarispira septata Gubanov, Peel & Pianovskaya, 1995, from the Chorkuin Formation (Llandovery–Wenlock boundary) of the Pschemack Mountains, Kyrgyzstan, was tentatively assigned to Omphalotrochidae by Gubanov *et al*. (1995). In revising *Isfarispira perlata* (Hall, 1852) from the Guelph Formation of Laurentia, Peel (2018) left the position of *Isfarispira* unresolved within a pycnomphaline–omphalotrochid group. On account of its radial aperture, multi-whorled form and prominent circumbilical funicle *Isfarispira* is tentatively assigned herein to Pycnomphalidae.

Labrocuspis has a massively calcified shell in which the umbilicus appears to be completely closed by callus (Heidecker 1959). *Fujispira* is not well known but appears to be lower spired, trochiform, with relatively few whorls (Kase & Nishida 1986). The upper surface of the whorl seems to show a sinus high on the whorl, as in many pycnomphalids and omphalotrochids, but the widely phaneromphalous umbilicus suggests placement in Omphalotrochidae.

Pycnotrochus, from the upper Silurian of Bohemia, is inadequately known on account of its poor preservation, mainly as internal moulds from limestones of the Kopanina Formation, but it appears to be a pycnomphalid. A sinus is apparently present on the sub-sutural ramp and growth lines sweep strongly forward from this, across the upper whorl surface towards the periphery. The umbilicus is almost completely closed (Knight 1941).

Bassotrochus, from the lower Devonian of Victoria, Australia, was considered by Tassell (1978, p. 20) to be the oldest occurrence of the Omphalotrochidae described to date but it is here placed within Pycnomphalidae. The whorls vary from slightly adpressed to embracing the previous whorls below the periphery; a broad, shallow, sinus culminates high on the upper whorl surface and the whorl periphery may be extended into a broadly rounded flange. Tassell (1978) remarked that an umbilicus was apparently lacking, but general shell shape suggests that this may be the result of closure by a funicle.

Genus *Bobellis* gen. nov.

Type species. – *Bobellis oliveri* gen. et sp. nov., from the Samuelsen Høj Formation (early Silurian), Washington Land Group, North Greenland.

Etymology. – It is 50 years since I first met Ellis L. Yochelson (1929–2006) and Robert ('Bob') M. Linsley (1930–2006): my teachers, colleagues and friends. *Bobellis* commemorates their major contributions to the study of Palaeozoic gastropods.

Diagnosis. – Trochiform, with shallowly convex sides (cyrtoconoid) and a shallowly convex base. Umbilicus largely closed by a spiral funicle, the lower surface of which is confluent with the base of the whorl; parietal deposits forming the funicle extending variably out across the base, decreasing in thickness as the periphery is approached. Whorls strongly adpressed, embracing the previous whorl near the mid-height of the concave outer whorl surface which lies between the angular periphery and the prominent adpressed shoulder; sutures incised. Apertural cross-section sub-quadrate. Outer lip sinuate, the culmination of the sub-sutural sinus occupying the width of the adpressed shoulder; opisthocline growth lines representing the lower margin of the sinus cross the whorl surface towards the peripheral angulation without curvature. Base excavated, with concave growth lines passing from the peripheral angulation towards the funicle. A prominent tongue-like lobe of the apertural margin, corresponding to the peripheral angulation, is thus formed between the sinuses in the upper and basal whorl surfaces. Ornamentation of collabral growth lines with a tendency to become nodose on the shoulder and, to a lesser extent, also on the peripheral angulation.

Discussion. – *Bobellis* most closely resembles *Grantlandispira* from the lower Silurian of western North Greenland (Peel 1984; Fig. 2) and *Orecopia* from the Devonian of North America and Europe (Knight 1945, Pedder 1966). All three genera frequently show a decrease in the incremental angle through growth of the multi-whorled shell to produce a cyrtoconoid (beehive-shaped) shell in larger specimens (Knight 1945, pl. 80, figs 1a, g; Fig. 2A, C, D; Fig. 3B, L). Thus, juvenile shells often appear more lenticular than mature shells. Additionally, massive thickening at the umbilico-basal angulation produces a prominent circumbilical funicle (Fig. 4). Both of these features serve to reduce the relative width of the umbilicus and likely represent adaptations to counteract durophagous predatory attacks. The typically widely phaneromphalous umbilicus of euomphaliform gastropods is vulnerable to shell crushing attacks (Vermeij 1987, Lindström & Peel 1997, Alexander & Dietl 2003).

Bobellis is distinguished from *Orecopia* by its prominent sub-sutural shoulder and more pronounced trochiform shape, although the upper whorl surface may be concave above the periphery in both forms (Knight 1945; Fig. 3). The sinus is less asymmetric in *Orecopia* than in *Bobellis* and its culmination is lower on the upper whorl surface. *Grantlandispira* also lacks the prominent sub-sutural shoulder and peripheral angulation which are well developed in *Bobellis*. Additionally, growth lines forming the lower margin of the sinus are convex adaperturally and less strongly oblique in *Grantlandispira* than in *Bobellis*.

Bobellis resembles *Labrocuspis* from the middle Devonian of Australia and Japan but the type species, *Labrocuspis nodosa* Heidecker, 1959, from Queensland has a massively thick shell, fewer whorls and the umbilicus is completely closed by thickening of the umbilical wall (Heidecker 1959). The whorl profile in *Labrocuspis nodosa* is strongly shouldered, almost gradate, with prominent sub-sutural nodes in the early growth stages. *Labrocuspis kobayashii* **(**Kase & Nishida, 1986) from the middle Devonian Nakazato Formation of Japan **(**Kase & Nishida, 1986, Kase 1989) is less shouldered, more smoothly cyrtoconoid in shape, lacking the prominent, cord-like, sub-sutural shoulder of *Bobellis*. In this respect it resembles *Orecopia*, to which it was originally assigned by Kase & Nishida (1986). As in *Bobellis*, growth lines on the upper whorl surface in both species of *Labrocuspis* sweep strongly forward towards the aperture, although *Bobellis* is higher spired and has more whorls.

Fujispira is based on poorly preserved material from the middle Devonian of Japan (Kase & Nishida 1986). Few whorls are present and the umbilicus is widely phaneromphalous, suggesting placement within Omphalotrochidae. The upper surface of the whorl seems to show a sinus high on the whorl, as in *Bobellis*, *Grantlandispira* and *Orecopia*.

Other species. – Type species only.

Bobellis oliveri **sp. nov.**
Figures 3, 4B

Holotype. – PMU 34882 from GGU sample 301325, Samuelson Høj Formation, Washington Land Group, Peary Land, North Greenland.

Paratypes. – Figured: PMU 34883 and PMU 34888 from GGU sample 301325, PMU 34884 and PMU 34885 from GGU sample 301319, PMU 34886 from GGU sample 301324, PMU 34887 from GGU sample 301319. Same locality and horizon as the holotype.

Type horizon and locality. – Samuelsen Høj Formation (early Silurian), Washington Land Group, east side of J.P. Koch Fjord, westernmost Peary Land, North Greenland (Fig. 1).

Material. – More than 20 specimens from the same collections.

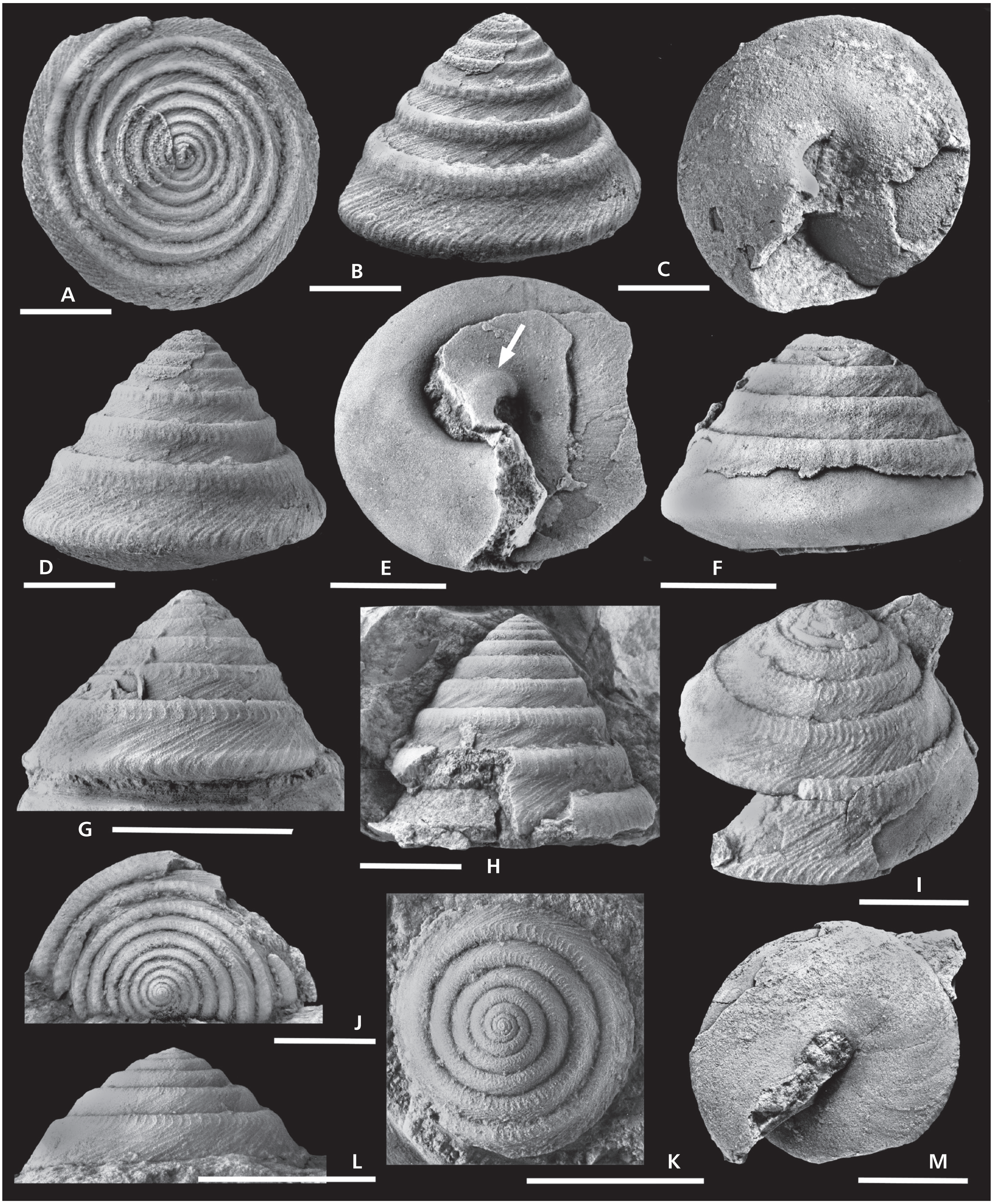

Figure 3. *Bobellis oliveri* gen. et sp. nov., Silurian, Washington Land Group, Samuelsen Høj Formation, east side of J.P. Koch Fjord, western Peary Land, North Greenland; A–D – PMU 34882 from GGU sample 301325, holotype in apical (A), oblique lateral (B), basal (C) and lateral (D) views; E, F – PMU 34883 from GGU sample from GGU sample 301325, paratype in oblique basal (E) and lateral (F) views, with arrow indicating funicular ridge; G – PMU 34884 from GGU 301319, paratype in lateral view; H, J – PMU 34885 from GGU sample 301319, paratype in lateral (I) and apical (J) views; I, M – PMU 34886 from GGU sample 301324, paratype in oblique lateral (I) and basal (M) views; K, L – PMU 34887 from GGU sample 301319, paratype in apical (K) and lateral (L) views. All specimens coated with ammonium chloride sublimate prior to photography. Scale bars = 10 mm.

Etymology. – For Oliver Jonathan Wilfred.

Diagnosis. – As for genus.

Description. – The type species of *Bobellis* with about 12 whorls. Shell form varies during ontogeny from high to low trochoidal, such that the height of the aperture ranges from about one third to one half of the total height; the known extremes of variation are illustrated (Fig. 2H, L). The shell is cyrtoconoid with the sides of the spire being shallowly convex, becoming increasingly so as the nucleus is approached; the incremental angle thus decreases during ontogeny.

The protoconch has not been observed directly, but it was not larger than about 0.2 mm. The following three whorls, up to a shell width of about 1.5 mm, are apparently smooth, after which the comarginal ornamentation gradually appears on the upper whorl surface, showing the same general shape as is present during later growth stages; as far as is discernible these earliest whorls only differ in shape from subsequent whorls in the absence of the sub-sutural shoulder (Fig. 2K, L).

The profile of later whorls is sub-quadrate; it is divided into upper and lower surfaces by a broad peripheral angulation located below mid-whorl height. The upper whorl surface is generally concave between the peripheral angulation and a prominent sub-sutural shoulder which represents the zone of adpression against the previous whorl. This band-like zone of adpression is almost half the height of the exposed whorl surface in the spire, and about one third of the height of the outer surface of the final whorl. The suture is therefore deeply incised in detail, almost canaliculate in some specimens. After slight concavity immediately adjacent to the peripheral angulation, the base is shallowly convex in profile as the umbilicus is approached. Delimitation of the floor of the whorl from the prominent circumbilical funicle is generally not possible (but see discussion of parietal deposits below). The umbilicus is essentially wide, but is partly closed by a massive circumbilical funicle extending almost to the axis of coiling in the later growth stages. The funicle is formed from parietal deposits which extend as a sheet across the base of the whorl, the thickness of the sheet decreasing as the whorl periphery is approached; its margin may be thickened and carry a small, rounded, tooth-like ridge (Fig. 3E, arrow).

The aperture is radial with a protruding tongue-like lobe, the adapertural termination of which corresponds to the peripheral angulation. A strongly asymmetric sinus is developed on the upper whorl surface, its culmination corresponding to the lower surface of the sub-sutural shoulder (Fig. 3G). The upper segment of the sinus is restricted to the narrow shoulder and is slightly prosocline. The lower segment extends from the base of the sub-sutural shoulder across the whorl face to the periphery; it is opisthocline, strongly oblique and without curvature. A narrow notch in the apertural margin may be present below the suture with the previous whorl, within the zone of the sub-sutural shoulder, but its absence from the transverse section (Fig. 4B) suggests that this was rapidly filled by shell deposition with subsequent growth. The basal lip is excavated, forming a shallow but uniformly concave (adaperturally) sinus extending from the periphery to the umbilicus (Fig. 3M).

Ornamentation consists of comarginal elements of two orders. Widely spaced, more prominent ribs are slightly lamellose and separated by several finer, parallel, striations (Fig. 3H) which are not readily visible on all specimens. The lamellose ribs are often slightly nodose on the sub-sutural shoulder and peripheral angulation; the lamellae are not perpendicular to the whorl surface but are steeply inclined, almost parallel to the axis of coiling.

Ornamentation on the base is variably obscured by the sheet of parietal deposits which extends from the

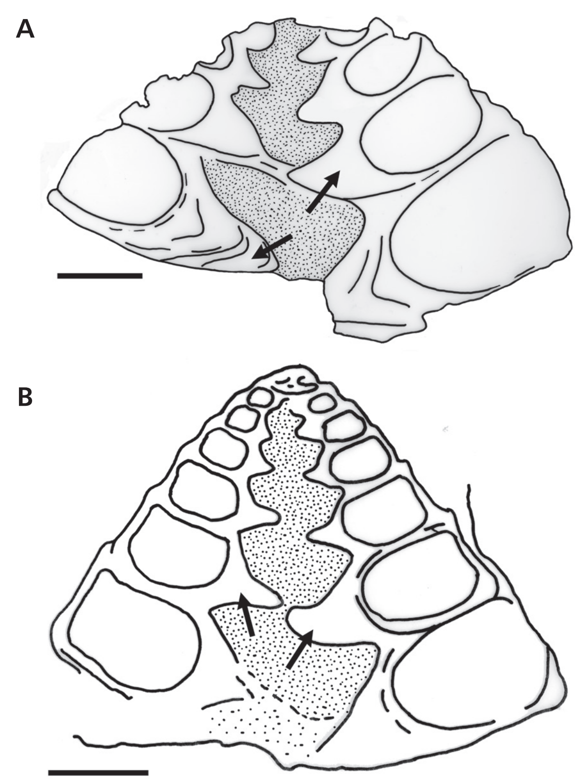

Figure 4. Axial sections with the sediment infilled umbilicus stippled; arrows indicate circumbilical funicles. • A – *Grantlandispira christiei* Peel, 1984, MGUH 16567 from GGU sample 82619, paratype, Silurian, Washington Land Group, Offley Island Formation, Kap Tyson, Hall Land, North Greenland. • B – *Bobellis oliveri* gen. et sp. nov., PMU 34888 from GGU sample 301325, Silurian, Washington Land Group, Samuelsen Høj Formation, east side of J.P. Koch Fjord, western Peary Land, North Greenland. Scale bars = 5 mm.

funicle towards the periphery (Fig. 3E), although the more prominent lamellose ribs may be discerned through this thin inductura.

The shell is relatively thin, but massively thickened in the vicinity of the funicle (Fig. 4B).

Discussion. – Specimens of *Orecopia mccoyi* (Walcott, 1884), the type species of *Orecopia* illustrated by Knight (1945), vary in profile from cyrtoconoid to somewhat gradate, but their periphery is more massive and rounded than in *Bobellis oliveri*. Additionally, the emargination on the upper whorl surface is more symmetrical than in *Bobellis*, where its lower margin projects more strongly, and with greater obliquity, towards the aperture (Fig. 3B, D, G). In this respect, the emargination in *Bobellis oliveri* closely resembles that in *Grantlandispira christiei* (Fig. 2C).

Bobellis oliveri is higher spired than *Orecopia cotei* Pedder, 1966 from the Devonian of British Columbia and Northwest Territories, Canada, and has a more pronounced sub-sutural shoulder and concave upper whorl surface. However, the shape of the apertural margin on the upper whorl surface of both species is similar (compare Fig. 3D, H with Pedder 1966, pl. 21, fig. 2). An additional specimen illustrated by Pedder (1966, pl. 21, fig. 7) from Northwest Territories, Canada, is somewhat atypical for the species in developing periodic node-like thickenings in the growth lines as they cross the shoulder, in which feature it resembles some specimens of *Bobellis oliveri* (Fig. 3G,L). *Bobellis oliveri* differs from *Orecopia kadzielniae* (Gürich, 1896), as described by Krawczyński (2002) from the Devonian (Frasnian) of Poland, in its greater number of whorls, concave upper whorl surface and the pronounced sub-sutural shoulder. *Orecopia murrayi* Tassell (1978) from the Lower Devonian of Victoria, Australia, is a low spired form without sub-sutural shouldering of the whorl or an angular periphery. The sinus on the upper whorl surface is much broader and shallower than in *Bobellis oliveri*. Tassell (1978) noted that a narrow umbilicus is sometimes present, suggesting the presence of an umbilical funcile, but the extent of this is not known.

Grantlandispira christiei lacks the prominent sub-sutural shoulder characteristic of *Bobellis* and its holotype develops a narrow peripheral cord (Fig. 2B, C, arrow) not present in *Bobellis*. Additionally, growth lines traversing the upper whorl surface are more strongly oblique in *Bobellis* than in *Grantlandispira christiei*. Species ?*Grantlandispira acuta* (Lindström, 1884, pl. 16, figs 1–6) from the Silurian Slite Beds of Gotland resembles *Bobellis* in its cyrtoconoid form but is lower spired, with a more acute periphery. It lacks the prominent sub-sutural shoulder and has less strongly inclined growth ornamentation below the sinus on the upper whorl surface. A circumbilical funicle is present but less strongly developed than in the *G. christiei* or *Bobellis oliveri*.

While similar in shell shape to *Bobellis oliveri, Pycnomphalus trochiformis* from Gotland lacks the prominent sub-sutural shoulder of the Greenland species (Fig. 3B).

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