



An enigmatic cap-shaped fossil from the Middle Cambrian of North Greenland

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Nyeboconus robisoni gen. et sp. nov., is described from the Middle Cambrian Henson Gletscher Formation of western North Greenland. Some authors have interpreted similar shells as chondrophorine hydrozoans or invertebrate fossils of uncertain systematic position. The coiled, cap-shaped shell and the presence of an internal plate, or pegma, suggest, however, that this new form is the second genus to be described of the Family Enigmaconidae MacKinnon, 1985 (Mollusca, Class Helcionelloida), otherwise known only from rocks of similar age in New Zealand.

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Lower and Middle Cambrian strata yield a variety of mainly small cap-shaped shells which are not readily assigned to molluscan classes, such as the Gastropoda or Tergomya, living at the present day (Peel, 1991a, b). Notable amongst these small fossils are shells of the Class Helcionelloida which are characterised by a bilaterally symmetrical (isostrophic) cap-shaped form, usually coiled through less than one whorl (Peel, 1991b).

Helcionelloids are widespread and diverse (e.g. Rozanov *et al.*, 1969 (= Raaben, 1981); Runnegar & Jell, 1976; MacKinnon, 1985; Geyer, 1986; Yu, 1987; Peel, 1988, 1991b; Missarzhevsky, 1989; Bengtson *et al.*, 1990; Benton & Erwin, 1993) but their record in post-Middle Cambrian strata is uncertain, as is their relationship to the molluscan groups which survive them.

Reconstruction of helcionelloid anatomy is not without dispute; helcionelloids have been considered to be gastropods (i.e., torted molluscs) but at the present day there is general agreement that they were untorted. In a model strongly influenced by a search for the origin of the Bivalvia, Runnegar & Pojeta (1974; see also Pojeta & Runnegar, 1976; Runnegar & Pojeta, 1985) considered helcionelloids to be exogastrically coiled untorted molluscs (i.e., with the apex lying anteriorly) similar to tryblidiid Tergomya such as *Pilina*, *Tryblidium* and the extant *Neopilina*. Others have interpreted the apex in helcionelloids to lie at the posterior such that coiling of the shell is endogastric (Yochelson, 1978, 1979; Geyer, 1986; Peel & Yochelson, 1987; Peel, 1988, 1991a, b). Peel (1991a, b) asserted this view in formally separating the endogastric helcionelloids from the exogastric Tergo-

mya; both helcionelloids and tergomyans were regarded as untorted.

The contrasting reconstructions of helcionelloids both rely heavily on interpretations of the mantle cavity, in particular the pattern of presumed inhalant and exhalant respiratory water currents. Taking into account the general small size of most helcionelloids (cf. Runnegar & Jell, 1976; Runnegar & Pojeta, 1985), it can not be assumed that these interpretations are valid. Most of the minute helcionelloids were subject to different physical and biomechanical constraints than the significantly larger molluscs which formed the basis for the mantle cavity reconstructions. While refuting the exogastric reconstruction of helcionelloids proposed by Runnegar & Pojeta (1974), Peel (1991b, pp. 19–20) admitted that his preferred endogastric model accepted the same precept that water transport into and out of the helcionelloid shell was possible.

The cap-shaped shell form is not restricted to the Helcionelloida in the Lower and Middle Cambrian. Articulated halkieriids (Conway Morris & Peel, 1990; Peel, 1991c) from the Lower Cambrian of North Greenland preserve a calcareous cap-shaped shell at the anterior and posterior extremities and the latter, in particular, is not unlike some molluscan shells in gross form. A broadly similar spectrum of shell forms of problematic origin has been documented by Qian & Bengtson (1989) from the earliest Cambrian of China, demonstrating that a variety of organisms produced shells of this type. That such a morphology is not necessarily indicative of molluscan affinity is clearly demonstrated by suggestions that some

of these Cambrian fossils may represent chondrophorine hydrozoans (Yochelson & Gil Cid, 1984; Stanley, 1986; Babcock & Robison, 1988). Thus, the cap-shaped fossil in these forms is no longer interpreted by these authors as the external, calcareous, dorsal shell of a mollusc, but as an impression of the internal, organic, float (pneumatophore) of a medusoid cnidarian.

A single enigmatic fossil of Middle Cambrian age from the Henson Gletscher Formation of northern Nyeboe Land promotes a discussion of these possible interpretations, also the suggestion by Evans (1992) that similar fossils may represent an invertebrate of presently unknown affinity. The specimen is associated with a few non-trilobite fossils which were kindly brought to my attention by Richard A. Robison; it is described below as *Nyeboeconus robisoni* gen. et sp. nov. in his honour, in gratitude for his studies and advice concerning Greenland Cambrian fossils during the past decade.

Nyeboeconus robisoni is from the Henson Gletscher Formation, west of Hand Bugt, northern Nyeboe Land, western North Greenland (Fig. 1, locality 1). Several specimens of the helcionelloid *Latouchella* are also present in the same sample (GGU 298970), associated with elkaniid, acrotretid and orthoid brachiopods (Lars E. Holmer, personal communication, 1993), conodontomorphs and the mollusc *Pelagiella*. Pelagiellids also form a characteristic group of molluscs in Lower and Middle Cambrian strata. While possibly related to helcionelloids, they are readily distinguished by anisostrophic coiling which gives a superficial resemblance to the gastropod shell.

The most conspicuous fossils in the Henson Gletscher Formation at the collection locality are polymeroid and agnostoid trilobites described elsewhere in this volume by Babcock (1994a, b) and Robison (1994). An accompanying paper by Ineson *et al.* (1994) provides a stratigraphic and environmental background for these faunal descriptions.

Systematic description

Genus *Nyeboeconus* gen. nov.

Type species. *Nyeboeconus robisoni* gen. et sp. nov.

Derivation of name. From Nyeboe Land, North Greenland and *conus* (Latin), a cone.

Diagnosis. Cap-shaped fossil, slightly elongate in the plane of bilateral symmetry, in plan view; coiled through about one quarter of a revolution, with clearly distinguished sub-apical and supra-apical surfaces and a sub-central apex. Internal mould with prominent comarginal rugae on the supra-apical surface, crossed by sharply

defined radial grooves and varices; a prominent transverse groove on the internal mould represents a plate (pegma) on the sub-apical surface of the shell interior. Shell calcareous and seemingly thin, with an external ornamentation of radial ridges which correspond in their position to the grooves on the internal mould.

Discussion. In terms of the prominent pegma on the shell interior, *Nyeboeconus* closely resembles *Enigmaconus* MacKinnon, 1985 (Class Helcionelloida) from the late Middle Cambrian of New Zealand (MacKinnon, 1985, pp. 72–74, fig. 7). It is readily distinguished from this genus by its prominent ornamentation of rugae and radial grooves on the internal mould and less laterally compressed form; the internal mould (and consequently the shell interior) in *Enigmaconus* is smooth. The shell in *Enigmaconus* also appears to be taller, but this (together with some of the lateral compression) may in part reflect preservation of just the early part of the New Zealand shell as an internal mould; this is supported by comparison of *Enigmaconus* and *Nyeboeconus* in lateral aspect. In the former (cf. MacKinnon, 1985, fig. 7b, n), the most abapical part of the slot representing the pegma lies much closer to the latest preserved apertural margin than the corresponding point in *Nyeboeconus* (Fig. 2b).

The general similarity of *Nyeboeconus* to *Enigmaconus* in terms of shell form and the pegma warrants placement of the Greenland form within the Family Enigmaconidae MacKinnon, 1985. It should be noted that MacKinnon (1985, p. 72) considered the pegma to lie nearest to the shell anterior while this surface is here interpreted as posterior (cf. Peel, 1991a, b).

In terms of the unusual ornamentation of the inner surface of the shell, *Nyeboeconus* resembles *Marocella* Geyer, 1986 of uncertain systematic position which was proposed on the basis of specimens from the Cambrian of Morocco. Geyer (1986) assigned to this genus specimens described as *Scenella morenensis* sp. nov. by Yochelson & Gil Cid (1984) from the Cambrian of Spain, and interpreted as the floats of chondrophorine hydrozoans. *Nyeboeconus* differs from these specimens, and from additional material of *Marocella* described from Antarctica by Evans (1992), in possessing a prominent transverse pegma on the shell interior.

At first glance, *Nyeboeconus* bears some resemblance to the reconstruction (in dorsal aspect) presented by Conway Morris *et al.* (1991) of the problematic organism *Libodiscus ascitus* from the Upper Palaeozoic of Canada, showing a disc with concentric markings and some sort of transverse structure. The similarity, however, is quite superficial, although relevant in this context on account of the comparison between *Libodiscus* and supposed chondrophorines made by Conway Morris *et al.* (1991).

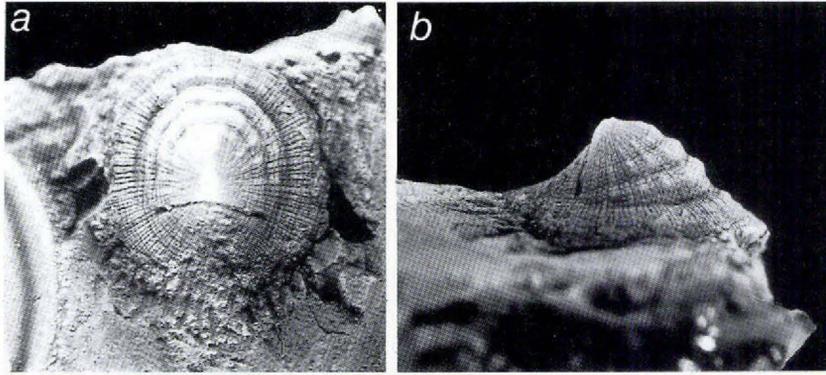


Fig. 2. *Nyeboeconus robisoni* gen. et sp. nov. MGUH 22.188 from GGU sample 298970, Henson Gletscher Formation, northern Nyeboe Land, western North Greenland (Fig. 1), internal mould, $\times 5$ (photo: R. A. Robison). a, apical view showing prominent comarginal rugae, radial ornamentation and the transverse groove representing the pegma. Fragments of shell with external ornamentation of radial ribs and growth lines occur on the supra-apical surface (top left) and around the apertural margins. b, lateral view showing the concave sub-apical surface (left) with pegma and the convex supra-apical surface with conspicuous comarginal rugae. Note the slightly protuberant apex which is slightly broken and the strong radial ornamentation.

Nyeboeconus robisoni gen. et sp. nov.

Fig. 2

Holotype. MGUH 22.188 from GGU sample 298970, Henson Gletscher Formation, northern Nyeboe Land, western North Greenland (Fig. 1, locality 1). GGU sample 298970 was collected at a height of 102 m in the section through the Aftenstjernesø, Henson Gletscher and Kap Stanton Formations at Hand Bugt (cf. Ineson *et al.*, 1994, fig. 4b and Babcock, 1994a, fig. 2). The specimen is preserved on the same small slab as a cephalon of *Lejopyge barrandei* (MGUH 21.416) illustrated by Robison (1994, fig. 23.1a, b).

Description. The only known specimen of this species is a cap-shaped fossil which, in dorsal view, is slightly longer in the plane of bilateral symmetry than wide; the apex is slightly excentric, lying closer to the apertural margin on the sub-apical surface. In lateral aspect, the shell is clearly coiled through about one quarter of a whorl, with a convex supra-apical surface and a concave sub-apical surface; shell height is almost two-thirds of shell length. Apex slightly protuberant on the internal mould, smooth. The dorsal surface carries strongly developed comarginal rugae which are most conspicuous on the supra-apical surface, but fade away across the lateral areas as the sub-apical surface is approached. These are crossed by closely spaced and sharply defined radiating grooves on the internal mould, presumably corresponding to sharp ridges on the shell interior; series of elongate radial nodes, or varices, cross the convex surfaces of the

rugae on the supra-apical surface. In the final preserved growth stage, comarginal rugae are absent and the planar aperture is slightly expanded.

A deep slot is present on the internal mould on the sub-apical surface, representing a plate (pegma) extending into the shell interior. The groove terminates near the base of the final prominent ruga on each lateral area; the bottom of the groove slopes up (adapically) from each lateral area towards the median plane of symmetry. Thus, the adapical surface of the pegma was probably arched and not a simple plate extending transversely straight across the shell interior from the lowest point of the groove on one side to the corresponding position on the other side.

Fragments on the supra-apical surface and near the apertural margin indicate that the shell is calcareous and thin; radiating spiral ridges on the shell exterior correspond in position to the radiating grooves on the internal mould.

Discussion. On account of the prominent ornamentation, casual examination suggests that the single specimen preserves the shell exterior and that this surface is ornamented with radiating cords separated by narrow grooves (Fig. 2). Closer scrutiny reveals, however, fragments of calcareous shell on the supra-apical surface with raised radial ribs and growth lines. The deep transverse slot largely filled with calcareous shell material, representing the pegma, also serves to confirm that this is an internal mould. Thus, the shell interior carries radial ridges which are reflected on the internal mould as deep grooves; the

thinness of the preserved shell fragments indicates that the coarse comarginal rugae affected both the outer and inner shell surfaces.

In view of the very small size of the preserved shell fragments it is difficult to assess if any exfoliation of shell material has taken place during separation of the fossil from the matrix. It remains possible, therefore, that the original shell thickness was somewhat greater than that preserved. The presence of clearly discernible radial ornamentation on the fragments of shell argues strongly that the calcareous shell material is not a secondary calcareous deposit.

Stratigraphic age. The only known specimen of *Nyeboeconus robisoni* is from the Henson Gletscher Formation at Hand Bugt, northern Nyeboe Land, western North Greenland (Fig. 1, locality 1). Agnostoid trilobites from the same collection (GGU 298970) are interpreted as belonging to the upper part of the *Ptychagnostus gibbus* interval-zone of the Middle Cambrian in an accompanying paper in this volume by Robison (1994). Co-occurring polymeroid trilobites are described in papers in this volume by Babcock (1994a, b). In the same section, the Henson Gletscher Formation ranges up into the *Ptychagnostus atavus* interval-zone of the Middle Cambrian, and possibly also to the latest Middle Cambrian at locality 3 (Fig. 1). In more southern outcrops in North Greenland, along the margin of the Inland Ice, the formation is mainly of Early Cambrian age (Higgins *et al.*, 1991a, b; Ineson *et al.*, 1994).

Chondrophore or mollusc?

In proposing *Marocella* as a mollusc-like shell of uncertain affinity, Geyer (1986) clearly indicated that this form is distinct from *Scenella* which he regarded as a tryblidiid monoplacophoran (= tergomyan of current usage, although the genus is now considered to be a helcionelloid, cf. Peel, 1991a, b.). Thus, the assignment of *Scenella* to the chondrophorine hydrozoans proposed by Yochelson & Gil Cid (1984) was refuted, an opinion also reiterated by Berg-Madsen & Peel (1986) and Landing & Narbonne (1992). The interior of the calcareous shell in *Scenella* is smooth, lacking the deep grooves seen in *Marocella* and *Nyeboeconus*.

Yochelson & Gil Cid (1984; see also Stanley, 1986) are probably correct in their assertion that many Cambrian and Ordovician fossils identified in collections or in the literature as *Scenella* may be chondrophores, but their extension of this concept to the type materials of *Scenella* as illustrated by Knight (1941) is inappropriate. Relevant non-chondrophorine features of these type specimens include the calcareous shell and the distinct spiral coiling.

The detailed description of *Marocella* by Evans (1992) demonstrates that the structure and ornamentation of the shell interior is seemingly without parallel in molluscs. In particular, the sharp ridges on the shell interior can not be reconciled with the normally smooth (or smoothed) internal surface of molluscan cap-shaped shells. There is some similarity in terms of ornamentation with the non-calcareous, internal float of the extant chondrophore *Porpita* which attains a size of up to 8 cm in diameter (Stanley, 1986), more than 10 times larger than *Marocella*. The float of *Porpita* is not coiled, however, and it is radially symmetrical about the central apex, whereas *Marocella* is clearly coiled with distinct sub-apical and supra-apical surfaces.

In terms of coiling, *Marocella* resembles *Nyeboeconus* but the general similarity in terms of ornamentation on the inner surface is less marked in detail. The latter genus has broad comarginal rugae and not the sharply defined rugae seen in *Marocella*; the spiral rugae of *Marocella* have not been discerned in *Nyeboeconus*.

Evans (1992) noted that shells of *Marocella* showed some similarity to the terminal plates of halkieriids (cf. Conway Morris & Peel, 1990; Peel, 1991c) but preferred to leave the affinity of the genus unresolved. The comparison of *Marocella* to the halkieriid shells may prove to be an attractive general model for future reconstructions but available data can not yet add further substantiation.

On balance, the calcareous shell and shell coiling of *Nyeboeconus* suggest that this genus is a mollusc and not a chondrophorine hydrozoan, although the ornamentation of the shell interior remains problematic. The high degree of similarity with *Enigmaconus* in terms of the sub-apical pegma is perhaps the most convincing indicator of molluscan affinities. Pojeta (1985) regarded the appearance of a pegma to be the delimiting character of the Class Rostroconchia from its helcionelloid ancestor, although Peel (1991a,b) has demonstrated that pegma-like structures are developed in a variety of helcionelloids. However, the pegma of *Nyeboeconus* compares well with the same structure in rostroconchs (cf. Pojeta & Runnegar, 1976), adding impetus to the suggestion of MacKinnon (1985) that *Enigmaconus* (and now *Nyeboeconus*) might be suitable ancestral forms to the Rostroconchia.

To summarise, while a possible Cambrian record for chondrophorine hydrozoans is acknowledged, *Scenella* and *Nyeboeconus* are considered to be helcionelloid molluscs, although the internal ornamentation of the latter genus is admittedly unusual. *Marocella* is not placed systematically, in agreement with Geyer (1986) and Evans (1992).

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MGUH denotes the type collection of the Geological Museum, Copenhagen. I am grateful to Lars Holmer and Søren Jensen (Uppsala University) for reviewing the manuscript.

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