A TERGOMYAN MOLLUSC FROM THE UPPER CAMBRIAN OF WALES

by V. BERG-MADSEN *and* J. S. PEEL

ABSTRACT. *Bellerophon cambriensis* from the Upper Cambrian of North Wales is redescribed as the type species of the new genus *Telamocornu*. Unlike most similarly coiled molluscs of this age, apertural sinuses are present which permit both a functional morphological interpretation of it as an untorted mollusc with the apex of the shall oriented anteriorly, and directly support assignation of *Telamocornu* to the Order Cyrtonellida of the Class Tergomya.

THE Cambrian was a time of innovation within the Mollusca. From examination of the fossil record, Yochelson (1963) proposed that a radiation of molluscs in the Early Cambrian was eclipsed by a second great diversification near the Cambrian–Ordovician boundary, during which most of the major mollusc groups familiar to us at the present day arose. From the point of view of anatomy, however, others have suggested that two of these late-appearing, shell-bearing groups, namely the Monoplacophora and the Polyplacophora, were ancestral stocks appearing much earlier in mollusc evolution (Salvini-Plawen 1985; Wingstrand 1985). Stimulated by models of mollusc evolution developed originally by Runnegar and Pojeta (1974), the last two decades have seen attempts to extend the range of the major extant mollusc classes back to the earliest Cambrian (Runnegar and Pojeta 1985; Yu 1990). These efforts have met with some success but a complex of mainly Early to Middle Cambrian molluscs currently lies rather uncomfortably within accepted classifications. This complex includes forms such as the Helcionelloida, elevated to a class by Peel (1991*a*, 1991*b*), the Pelagiellida, the Onychochilida and the Stenothecoida. Most of these groups were placed within an extended Class Monoplacophora alongside the well-known *Neopilina* Lemche, 1957, and its relatives (Runnegar and Pojeta 1974, 1985; Runnegar and Jell 1976), although this expansion of the concept Monoplacophora has generated discussion concerning the usefulness of the term in systematics (Wingstrand 1985; see summary in Peel 1991*b*). Thus, Peel (1991*a*, 1991*b*) followed Wingstrand (1985), Haszprunar (1988) and Salvini-Plawen (1985, 1990) and abandoned the Class Monoplacophora. He introduced a Class Tergomya for members of the *Neopilina* group (based on the Subclass Tergomya Horný, 1965). Tergomyans are oriented with the shall apex in an anterior position, while in the second major group of Lower Palaeozoic untorted and bilaterally symmetrical molluscs, the extinct Class Helcionelloida, the apex is interpreted as posterior (Peel 1991*a*, 1991*b*).

Classification of molluscs within the Cambrian is clearly in a state of flux and this instability can be expected to persist for some time as current research continues to produce startling discoveries. Not least the recent description of articulated halkieriids from the Lower Cambrian of Greenland (Conway Morris and Peel 1990) and the re-interpretation of Cambrian 'scaly-shelled' molluscs by Bengtson (1992) open a new perspective to early molluscan evolution. The abundant microsclerites and the associated larger anterior and posterior plates in the halkieriids are shell features which find morphologic equivalents in the aplacophoran and polyplacophoran molluscs which Salvini-Plawen (1985) placed in the ancestry of the later shelled forms. Moreover, halkieriids occur in strata of suitable age; aplacophorans have no fossil record and that of polyplacophorans in the Cambrian is scant.

The group of isostrophically coiled forms referred to as the bellerophontiform molluscs has a

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geological range from Cambrian to Triassic (Knight *et al.* 1960; Yochelson and Yin 1985) and has traditionally occupied a central position in discussions of the origin of the gastropods (Knight 1952; Yochelson 1967; McLean 1984; Haszprunar 1988; Horný 1991*a*). Opinions are divided as to whether members of this group were gastropods (Harper and Rollins 1982) or untorted molluscs (Runnegar and Jell 1976; Runnegar and Pojeta 1985). Peel (1991*b*) and others (Yochelson 1967; Horný 1991*a*) considered the bellerophontiform molluscs to be a mixture of both torted and untorted forms. Forms interpreted as untorted were referred by Peel to the Order Cyrtonellida of the Class Tergomya, although some genera within the Class Helcionelloida also share this coiling style (e.g. *Protowenella* Runnegar and Jell, 1976, and *Coreospira* Saito, 1936). Supposedly torted bellerophontiform molluscs were assigned to the Class Gastropoda. Unfortunately, few Cambrian bellerophontiform molluscs are readily referred to one class or the other on the basis of morphological features. Features such as an apertural slit producing a median dorsal selenizone, although previously considered to be a reliable systematic tool, are potentially developed within unrelated stocks (Rollins and Batten 1968; Yochelson 1984; Haszprunar 1988; Peel 1991*b*).

In this paper we propose a new genus of bellerophontiform mollusc from localities in the Upper Cambrian of Wales (Text-fig. 1). Unlike most contemporaneous bellerophontiform species, apertural structures are present which permit a functional morphological interpretation of this genus as an untorted mollusc, thus strengthening the record of the Class Tergomya near the Cambrian–Ordovician boundary.

SYSTEMATIC PALAEONTOLOGY

Class TERGOMYA Horný, 1965
(*nom. transl.* Peel 1991*a*, *ex* Subclass Tergomya Horný, 1965)
Order CYRTONELLIDA Horný, 1963
Genus TELAMOCORNU gen. nov.

Derivation of name. From *telamon* (Greek), belt or strap, combined with *cornu* (Latin), horn. For Thomas Belt, author of the type species.

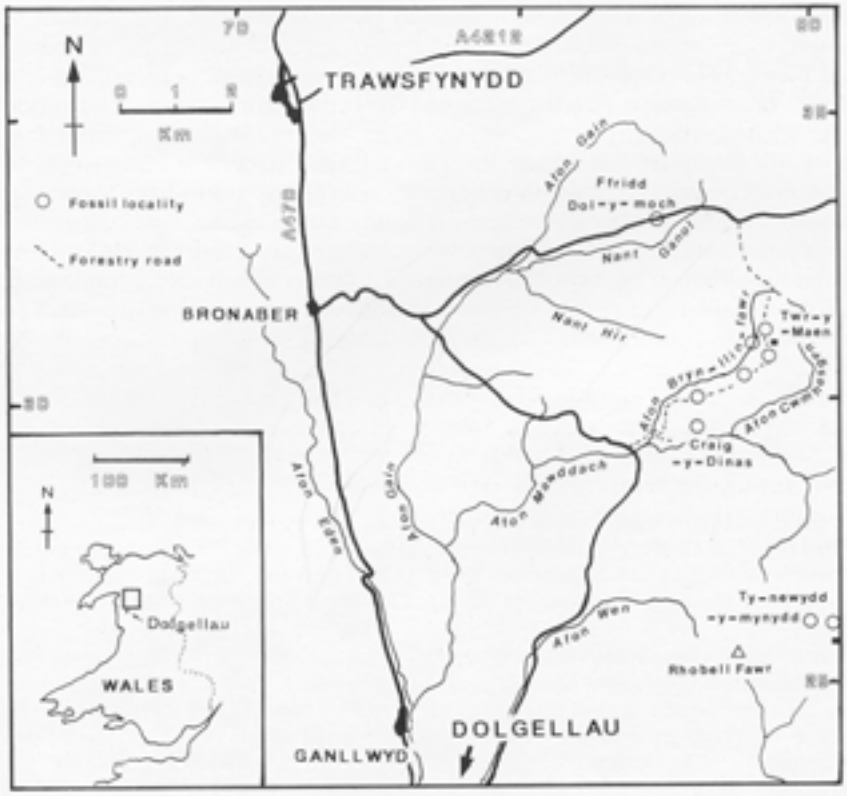
Type species. Bellerophon cambriensis Belt, 1868.

Diagnosis. Loosely coiled, in early stages open coiled, rapidly expanding but laterally compressed cyrtonellid tergomyan with about 1·5 whorls. Dorsum uniformly convex; aperture with broad and shallow median sinus and tendency to produce umbilical sinuses. Ornamentation of transverse rugae and fine growth lines, crossed by weak spiral lines.

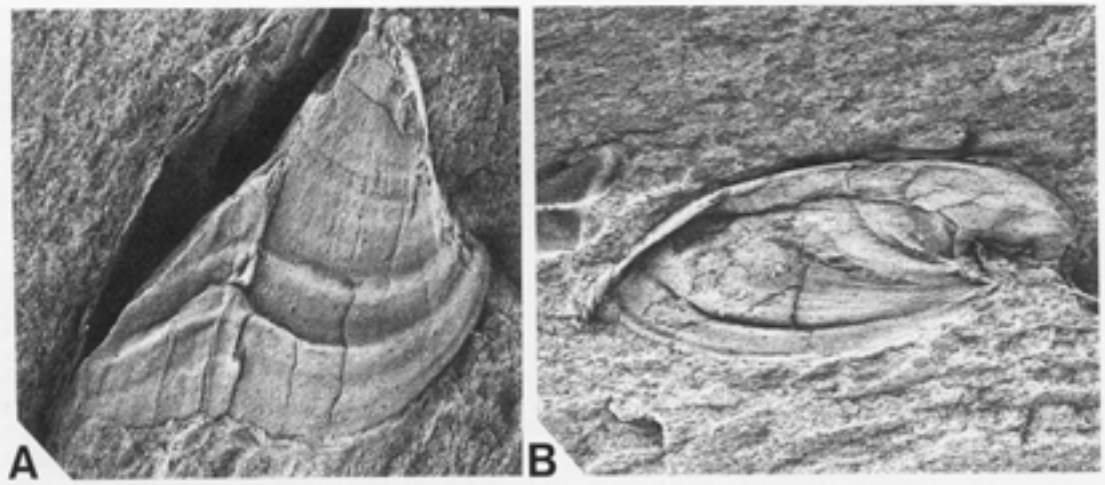
Discussion. Most of our knowledge of Late Cambrian bellerophontiform molluscs stems from two papers (Knight 1947, 1948) mainly based on North American material. In these papers, six new genera were described (*Anconochilus*, *Chalarostrepsis*, *Cloudia*, *Cycloholcus*, *Sinuella* and *Strepsodiscus*) and *Owenella* Ulrich and Scofield, 1897 redescribed. He also redescribed *Coreospira* Saito, 1936, from the Middle Cambrian of Korea and British Columbia but this genus, and possibly also *Cycloholcus*, is an unusual helcionelloid.

Of the genera listed above, only *Anconochilus* from the middle Upper Cambrian (Franconian) can be closely compared to *Telamocornu* of similar age; it is distinguished by being more involute and less rapidly expanding. Ornamentation is poorly known in *Anconochilus barnesi* Knight, 1947, the type and only described species, but Knight (1947) recorded a shallow median sinus in the apertural margin.

Telamocornu closely resembles *Sinuitella* Yochelson, 1962, from the Lower Ordovician (Tremadoc) of Norway. It is distinguished, however, by its much larger size (*c.* 22 mm compared with 5–8 mm for *Sinuitella norvegica* (Brøgger, 1882) and greater rate of whorl expansion, particularly antero-posteriorly. *Sinuitella norvegica* is open coiled, with the whorls not in contact,



TEXT-FIG. 1. Localities of Cambrian tergomyan molluscs described in the text (modified from Allen *et al.* 1981).



TEXT-FIG. 2. *Telamocornu cambriense* (Belt, 1868). Upper Ffestiniog Flags Formation; ×3; BM62087. A, lectotype; fragment of dorsal surface showing transverse rugae and median sinus. B, paralectotype; lateral view of specimen crushed in shale.

whereas *Telamocornu* is apparently loosely coiled in larger specimens, with shallow impression of the earlier whorl.

Pharetrolites Wenz, 1943 is similar in general form to *Telamocornu* but has a lower rate of whorl expansion. This Silurian genus is also distinguished by its deeper median dorsal sinus and crenulate ornamentation.

Latouchella aperta Orlowski, 1968 from the Upper Cambrian of the Holy Cross Mountains of Poland is more tightly coiled than *Telamocornu cambriense* and seems to have a more angular dorsal profile; Orlowski's original generic assignment is highly questionable.

Jago and Corbett (1990, fig. 2F–J) figured three bellerophontiform molluscs from a topmost Cambrian sandstone-siltstone sequence in western Tasmania. Their 'Bellerophontida gen. et sp. indet. 1' resembles *Telamocornu* in its rate of expansion and size, whereas two other indeterminate forms are more laterally compressed, with an arched dorsal profile.

Telamocornu cambriense (Belt, 1868)

Plate 1; Text-figure 2

1868 *Bellerophon Cambriensis* Belt, p. 11, pl. 2, figs 19–20.

Type material. Lectotype (here designated) is the specimen figured by Belt (1868, pl. 2, fig. 20); paralectotype, the original of Belt (1868, pl. 2, fig. 19). Both specimens (Text-fig. 2) carry the registration number BM 62087, and were collected at Craig-y-Dinas, Dolgellau district, North Wales, in strata containing *Parabolinoides bucephalus*, indicative of the uppermost part of the late Cambrian Ffestiniog Flags Formation.

Other material. A collection (BGS Zv9778, Zv9781, Zv9783–86, Zv9788, Zv9789) made by Stephen Jusypiw and presented to the British Geological Survey, comes from a fine-grained sandstone occurring at about the same horizon as the types on the Bryn-llin-fawr forestry road (National Grid Reference SH 7865 3035); the fauna (Pl. 1, figs 4–10) is assigned to the Zone of *Parabolina spinulosa*. Poorly preserved specimens (BGS RU9708A–B, collected by A. W. A. Rushton), possibly assigned to *Telamocornu* also occur in the underlying Maentwrog Formation (*cataractes* Subzone of the *Olenus* Zone) at Ffridd Dol-y-Moch on the Llanuwchllyn road, 7 km ESE of Traswfynydd (SH 7648 3298; Allen *et al.* 1981, p. 308), and in the Dolgellau Member (*Acerocare* Zone) of the Cwmhesgen Formation (BGS RU5281, collected by A. W. A. Rushton and S. P. Tunnicliff) which overlies the Ffestiniog Flags Formation (Ty-newydd-y-mynydd, 1·5 km E of Rhobell Fawr; Allen *et al.* 1981, p. 317 (SH 7996 2601), cf. Rushton, 1982, Text-fig. 1). In terms of the North American standard, these occurrences range from the upper Dresbachian (Upper Cambrian) upwards to the Cambrian–Ordovician boundary.

Description. (Based on two suites of specimens (see above), since the types are imperfectly preserved.) Type species of *Telamocornu* gen. nov. with about 1·5 whorls. Earliest growth stage apparently consisting of the rather blunt origin of the coil, not distinguished in terms of coiling or ornamentation from subsequent growth stages; the umbilici were probably perforate. In the latest preserved growth stage the whorls appear to be loosely in contact and the shell is laterally compressed, with width about half of the total length. The dorsum

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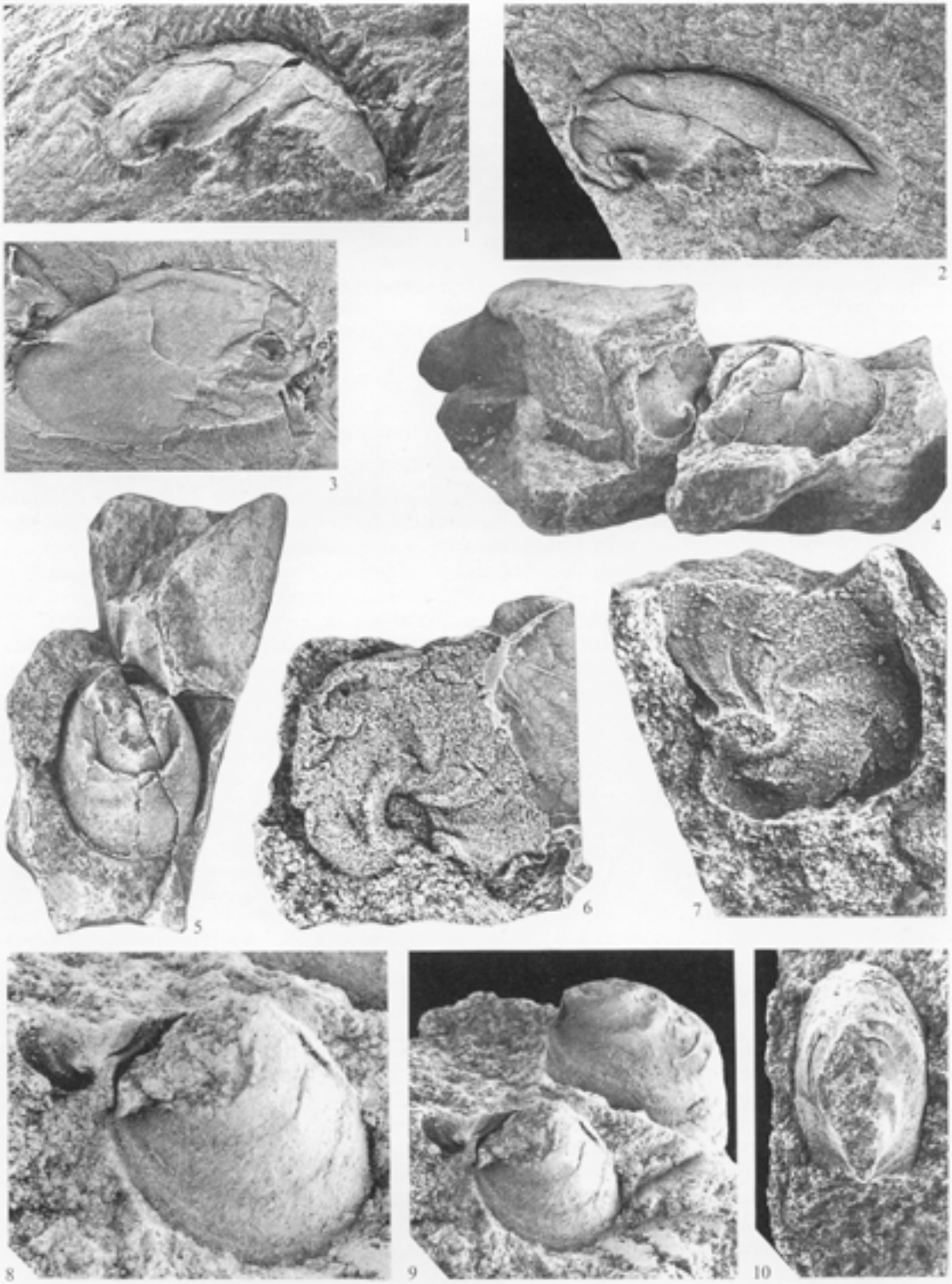
EXPLANATION OF PLATE 1

Figs 1–3. *Telamocornu cambriense* (Belt, 1868)? Poorly preserved specimens in lateral view. 1, BGS RU9708A; Maentwrog Formation; ×3. 2, BGS RU9708B; Maentwrog Formation; ×3. 3, BGS RU5281; Cwmhesgen Formation; showing fine transverse and spiral ornamentation; ×2.

Figs 4–10. *Telamocornu cambriense* (Belt, 1868). Ffestiniog Flags Formation. 4, BGS Zv9788; lateral view to show the external mould of the early growth stages; ×1·5. 5, same specimen in oblique dorsal view to show the convex dorsum; ×1·5. 6–7, BGS Zv9789; latex mould and corresponding external mould showing the umbilico-lateral sinus interpreted as inhalant in function; ×8. 8–10, BGS Zv9785; two specimens preserved as internal moulds with early growth stages broken away. 8, lowermost of two specimens figured in 9 (×4) showing external mould of earliest growth stages and internal mould of apertural region with transverse rugae; ×8; 10, dorsal view of upper specimen showing rounded dorsum; ×4.

PLATE 1



BERG-MADSEN and PEEL, *Telamocornu*

is convex, uniformly rounded, without median angulation or a keel. In plan view, the length:width ratio of the aperture is about 3:2. The aperture is sinuate having a broad, shallow, emargination in the mid-dorsal margin; apertural margins appear to be essentially co-planar but in laterally crushed specimens the lateral areas are adaperturally convex. A tendency for small sinuses to develop on the umbilico-lateral surface, near the suture with the previous whorl, is observed in a few specimens.

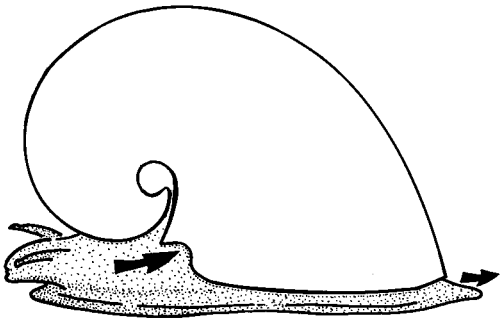
Ornamentation consists of transverse growth rugae, apparently produced by periodic slight expansion of the dorsal apertural margin, and fine growth lines, crossed by weakly developed, fine spiral lines. Shell thickness and structure are unknown.

Only a portion of the dorsal surface is preserved in the lectotype but this clearly shows the median dorsal sinus; the apparent median band is a result of crushing. The paralectotype is crushed in lateral view and also shows an apparent keel due to fracture along the periphery; the adaperturally convex curvature of the lateral margins is exaggerated by crushing.

The largest of the specimens from Bryn-llin-fawr (Zv9788; Pl. 1, figs 4–5) shows the early growth stages as an external mould of the lateral surface, while the partially embedded aperture is preserved as an internal mould. Notable among specimens from this locality is one (Zv9789) preserved as an external mould of the lateral surface, showing a sinus on the umbilico-lateral margin (Pl. 1, figs 6–7) which is interpreted below as having served an inhalant function.

FUNCTIONAL MORPHOLOGY OF *TELAMOCORNU*

Few of the genera and species of bellerophontiform molluscs currently known from the Upper Cambrian and Lower Ordovician preserve morphological features of the shell which facilitate interpretation of their systematic affinities either with the Gastropoda or with the Tergomya (the presence of some helcionelloid taxa within this plexus also cannot be excluded). An important feature in such interpretations is the presence and distribution of emarginations in the apertural margin. *Sinuitella*, as illustrated by Yochelson (1962, pl. 1, fig. 7), preserves a shallow sinus at the umbilico-lateral shoulder reminiscent of those noted above in *Telamocornu cambriense* (Pl. 1, figs 6–7; Text-fig. 3). Horný (1991*b*) described similar structures in *Sinuitopsis neglecta* Perner, 1903 from the Ordovician of Bohemia. Such sinuses are also described in specimens of younger age, such as *Pharetrolites bambachi* Peel, 1975 from the Silurian Arisaig Group of Nova Scotia (Peel 1975).



TEXT-FIG. 3. Reconstruction of *Telamocornu cambriense* (Belt, 1868) as a tergomyan mollusc, with the anterior to the left. Water currents (arrows) enter the mantle cavity anteriorly, by way of the umbilico-lateral sinus (cf. Pl. 1, figs 6–7) located on each side of the shell, prior to exhalation via the posterior median dorsal sinus.

The umbilico-lateral sinuses can be interpreted as the locus of inhalant currents entering the mantle cavity, with the median dorsal sinus marking the position of the posterior exhalant stream (Text-fig. 3). If the exhalant stream is posterior, the shell is coiled exogastrically, with the initial whorls located anteriorly, overhanging the anterior margin of the aperture (Peel 1991*b*, p. 19, fig. 12). Following this reconstruction, *Telamocornu* (together with *Sinuitella*, *Sinuitopsis* and *Pharetrolites*) is interpreted as an untorted, exogastric, bilaterally symmetrical mollusc, a cyrtonellid tergomyan in the sense of Peel (1991*b*). If *Telamocornu* is interpreted as torted, and assigned to the Gastropoda, the shell would be endogastric with the earlier coiled portion located posteriorly. This interpretation, however, is not supported by the presence of the supposed inhalant umbilico-lateral sinuses.

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V. BERG-MADSEN
Palaeontological Museum
Uppsala University
Norbyvägen 22
S-752 36 Uppsala, Sweden

J. S. PEEL
Institute of Earth Sciences
Department of Historical Geology and Palaeontology
Uppsala University
Norbyvägen 22
S-752 36 Uppsala, Sweden

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