



## On Paleozoic platycerate gastropods

Alexander Nützel<sup>1,2,3</sup>, Jan Ove Ebbestad<sup>4</sup>, Barbara Seuss<sup>5</sup>, Axel Munnecke<sup>5</sup>, Royal H. Mapes<sup>6</sup>, Alex G. Cook<sup>7</sup>

<sup>1</sup> SNSB-Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Str. 10, 80333 München, Germany

<sup>2</sup> Department of Earth and Environmental Sciences, Paleontology and Geobiology, Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, 80333 München, Germany

<sup>3</sup> GeoBio-Center, Ludwig-Maximilians-Universität München, Richard-Wagner-Str. 10, 80333 München, Germany

<sup>4</sup> Museum of Evolution, Uppsala University, Norbyvägen 16, SE 75236 Uppsala, Sweden

<sup>5</sup> Friedrich-Alexander-Universität Erlangen-Nürnberg, GeoZentrum Nordbayern, Loewenichstraße 28, 91054 Erlangen, Germany

<sup>6</sup> Division of Paleontology, American Museum of Natural History, Central Park West at 79th Street, New York, NY, 10024, USA

<sup>7</sup> 21 Thompson Cres, Clontarf, 4019 Queensland, Australia

<https://zoobank.org/BA2DA079-4906-4AC8-AE11-05E21BBF12B9>

Corresponding author: Alexander Nützel ([nuetzel@snsb.de](mailto:nuetzel@snsb.de))

Academic editor: M. Krings ♦ Received 13 November 2023 ♦ Accepted 19 November 2023 ♦ Published 12 December 2023

## Abstract

The platycerate gastropods *Orthonychia yutaroi* Ebbestad, **sp. nov.** (Ordovician, Boda Limestone, Sweden), *O. enorme* (Silurian, Sweden, Gotland), *O. parva* (Pennsylvanian, Finis Shale Member, USA), and *Orthonychia* sp. (Mississippian, Imo Formation, USA) are studied including their protoconch morphology. *Orthonychia yutaroi* is the oldest known species in *Orthonychia*. Platycerates contain species with both, openly and tightly coiled protoconchs. This is the first report that tightly coiled protoconchs occur in *Orthonychia*. This and previously published observations blur the diagnostic difference between orders Cyrtoneritimorpha (openly coiled protoconch) and Cycloneritimorpha (tightly coiled protoconch). We suggest to treat Cyrtoneritimorpha and Cycloneritimorpha as synonyms of Neritimorpha. The monotypic Devonian genus *Pragoserpulina* is morphological so close to the *Orthonychia* species reported herein that synonymy of both genera seems to be possible (and thus of the families Pragoserpuliniidae and Orthonychiidae). Protoconch morphology and dimensions suggest that the studied platycerate species had planktotrophic larval development. By contrast, two studied Carboniferous euomphaloid species (one with an openly and the other with tightly coiled protoconch) have paucispiral, large protoconchs indicating non-planktotrophic larval development. We assume that openly and tightly coiled protoconchs were present in various Paleozoic gastropod clades and that selection acted against the openly coiled protoconch morphology. It has previously been proposed that increasing predation pressure in the plankton was the reason for the demise of openly coiled protoconchs (Paleozoic plankton revolution). The presence of larval planktotrophy in platycerates excludes the possibility that they belong to extant basal gastropod clades such as Patellogastropoda, Cocculiniformia, and Vetigastropoda. However, a previously proposed close relationship to Neritimorpha is corroborated.

## Keywords

Mollusca, Gastropoda, Neritimorpha, Ordovician, Silurian, Carboniferous, Sweden, USA, protoconchs, systematics, larval development

## Introduction

*Platyceras*, *Orthonychia* and other similar genera are more or less limpet-shaped Paleozoic gastropods that occur often abundantly from the Ordovician to the Permian. Such *Platyceras*- and *Orthonychia*-like gastropods are informally called platycerates herein. They are best known for their association with crinoids and there are numerous reports of them still being attached to their crinoid host (e. g., Baumiller and Gahn 2002) although by far most specimens are known isolated (unattached to crinoids). Simplified, *Platyceras* is more strongly bent and coiled, and becomes limpet-shaped with a widened aperture only late in ontogeny. By contrast, *Orthonychia* shows strong coiling of the teleoconch only in its early ontogeny whereas the late shell is almost straight conical and tube-like. These morphologies are unusual in Gastropoda and are interpreted as adaptations to their sedentary life on crinoids (e. g., Frýda et al. 2008b and references therein). Phylogeny and systematic placement of platycerates have been a matter of debate. Wenz (1938) placed Platyceratidae in Archaeogastropoda: Trochonematoida, Knight et al. (1960) in Archaeogastropoda: Trochina, and Bouchet et al. (2005, 2017), based on Bandel and Frýda (1999) in Neritimorpha. Close phylogenetic links to euomphalids (Wagner 2002; Kaim 2004) and patellids (Sutton et al. 2006, see Frýda et al. 2009 for a discussion) have been discussed.

Simplified current classification of *Platyceras* and *Orthonychia* based on Bouchet et al. (2005, 2017):

Subclass Neritimorpha Koken, 1896

Order uncertain

Superfamily Platyceratoidea Hall, 1879

Family Platyceratidae Hall, 1879

Order Cyrtoneritimorpha

Family Orthonychiidae Bandel & Frýda, 1999

Family Vltaviellidae Bandel & Frýda, 1999

*Orthonychia* was commonly used as a subgenus of *Platyceras* and even synonymy of both genera has been discussed. For instance, Rollins and Brezinski (1988: 209) stated: "Even the distinction between *Platyceras* (*Platyceras*) and *Platyceras* (*Orthonychia*) is most likely no more than a morphological convenience (Yochelson 1969; Keyes 1894). The differentiation of the two subgenera depends entirely upon the nature of the juvenile whorls; they are in contact in the subgenus *Platyceras* and disjunct in the subgenus *Orthonychia*" (it is unclear as to whether "juvenile whorls" includes the protoconch here). However, based on the presence of openly coiled protoconchs, *Orthonychia* was placed in the family Orthonychiidae and in the order Cyrtoneritimorpha (Bandel and Frýda 1999). Thus, these character states had been considered diagnostic at a high level in systematics i. e., for the order Cyrtoneritimorpha (including *Orthonychia*) (Bandel and Frýda 1999). But then, Frýda et al. (2009) reported that Platyceratoidea contain both, members with uncoiled and with tightly coiled larval shells. This could suggest, that

Cyrtoneritimorpha are not monophyletic or that this character is not (or at least not always) diagnostic at high systematic levels i. e., both character states may be present in a single superfamily, family or genus.

Well-preserved high-conical limpet-shaped gastropods of the *Orthonychia*-type from the Late Ordovician Boda Limestone, Sweden (Fig. 2), the Silurian of Gotland, Sweden (Figs 3–8), the Pennsylvanian Finis Shale, Texas, USA (Figs 9–12), and the Mississippian Imo Formation, Arkansas, USA (Fig. 13) are reported in the present contribution. They provide new morphological details about this gastropod group that may help to better understand its evolutionary history.

## Teleoconch morphology

Probably due to their sedentary, parasitic or commensal life style, shell plasticity and intraspecific variability are pervasive in platycerates including *Orthonychia* making alpha taxonomy and systematics particularly difficult (Knight 1934; Yochelson 1956; Frýda et al. 2008b and references therein). As outlined above, *Platyceras* species are more strongly coiled, cap-shaped with wide apertures. The teleoconch of *Orthonychia* is only initially coiled and later uncoiled, often forming an almost straight tube. Most of these cap-shaped gastropods lack shell ornaments but commonly have irregular co-marginal rugae and longitudinal folds towards the aperture probably reflecting the morphology of their substratum, namely their crinoid hosts. The Devonian *Crossoceras* Boucot & Yochelson, 1966 (originally placed in Platyceratidae) has the shape of *Platyceras* but is ornamented with co-marginal sharp ribs (frills, lamellae) and a fine spiral lineation. This type of teleoconch ornament is also present in *Orthonychia yutaroi* sp. nov. and *Orthonychia enorme* from the Silurian of Gotland as is reported in the following. A similar shell ornament is also present in the Devonian *Pragoserpulina* Frýda, 1998a which also has disjunct late teleoconch whorls (Frýda 1998a, b). Pronounced frills are also present in "*Platyceras* (*Platyceras*) *cornutum loricatum* Lindström, 1884" as reported by Rohr et al. (1981) from the Silurian of the Canadian Arctic. Some platycerate shells have pronounced hollow spines (e. g., Blodgett et al. 1988; Blodgett and Frýda 1999; Cook and Jell 2016). The taxonomic and systematic relevance of such ornaments in *Orthonychia* and similar forms is obscured by the fact that the Devonian type species of *Orthonychia* is known from steinkerns only (Knight 1941) and hence its ornament type is unknown.

## Shell mineralogy

*Platyceras* and *Orthonychia* have calcitic shells (Knight 1934; Yochelson and Kriz 1974; Batten 1984; Carter and Hall 1990). Carter and Hall (1990) reported chiefly crossed semi-foliated and complex crossed semi-foliated

shell microstructures. As to whether shells were bi-mineralic with an inner aragonitic layer (as is found in Recent Neritimorpha) is unclear. Thin sections of Silurian specimens from Gotland provided herein support that *Orthonychia* has a primarily calcitic, foliated shell micro-structure (Fig. 6). Thin calcitic outer shell layers are also present in Mesozoic and modern Neritimorpha and also in Paleozoic/Mesozoic Naticopsidae which would corroborate the assumption that these groups are closely related.

## Operculum

Opercula have not been reported for *Platyceras*- and *Orthonychia*-like gastropods which seems unsurprising considering their attached lifestyle. However, mineralized opercula are well-known in other Neritimorpha including Paleozoic Naticopsidae (e. g., Kaim and Sztajner 2005; Nützel and Nakazawa 2012).

## Protoconch morphology

Protoconch morphology may yield crucial information for gastropod taxonomy, systematics and larval ecology. Unfortunately, protoconchs are unknown for the majority of Paleozoic gastropods due to insufficient preservation (Nützel 2014). Protoconchs of a few platycerates have been reported (Knight 1934; Yochelson 1956; Bandel and Frýda 1999; Frýda et al. 2009). Knight (1934), Bandel and Frýda (1999), and Frýda et al. (2009) showed that the Pennsylvanian *Orthonychia parva* has an openly coiled protoconch, that is partly even straight and elongated. Yochelson (1956: 259) stated that “It may be that the vermiform protoconch represents a free living stage, and as soon as the specimen became attached to a crinoid calyx it expanded rapidly to increase the area of attachment.” However, he did not consider the possibility that the hook-like protoconch is a larval shell of the planktotrophic type. Yochelson (1969: 31) stated: “Species of *Platyceras* that have a curved horn shape to the body whorl may or may not have the protoconch coiled. The presumed distinction between *Platyceras* in a restricted sense, with half a whorl or more in contact, and the subgenus *Orthonychia*, without any of the juvenile shell in contact, may be artificial, especially in those forms where the area of contact is extremely small compared to the size of the mature shell.” Thus, Yochelson (1969) was aware of the fact that both, openly coiled and tightly coiled protoconchs are present in platycerates.

Many Ordovician and Silurian internal molds of gastropod protoconchs (many from micro-samples dissolved with acid for conodonts) display open coiling resulting in almost straight to fish-hook-like morphologies as was also reported for *Orthonychia parva* (Nützel and Frýda 2003; Nützel et al. 2006, 2007a). In some cases, such a morphology might represent a preservational artifact (Dattilo et al. 2016) but this is clearly not so in all cases. Rare-

ly the openly coiled morphology has also been found in Paleozoic protoconchs with preserved shells (and not as steinkerns) and more of such rare examples are reported herein. The openly coiled protoconch morphology gradually vanished until the Late Triassic (Nützel and Frýda 2003; Nützel et al. 2006, 2007a; Nützel 2014; Seuss et al. 2012; Dzik 2020). In the Late Paleozoic, such uncoiled protoconchs are present only in a small minority of species for which the protoconchs are known. However, the large majority of Late Paleozoic gastropods with preserved protoconchs have tightly coiled larval shells (Nützel and Frýda 2003; Nützel 2014) as is also usual for modern marine gastropods (only some modern holoplanktonic gastropods have elongated protoconchs). Here, we report openly coiled protoconchs for two Carboniferous taxa and we will discuss whether these protoconchs reflect planktotrophic larval development.

## Repository, institutional abbreviations

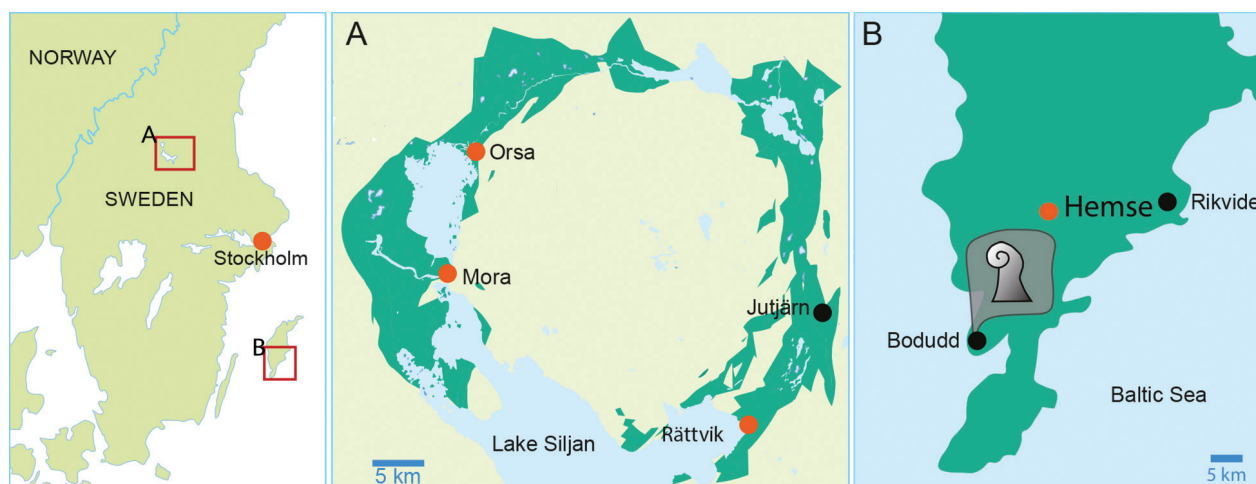
The studied material is deposited in the following institutions:

<b>NRM</b>	Department of Palaeobiology, Swedish Museum of Natural History, Stockholm, Sweden.
<b>PMU</b>	Palaeontological collections, Museum of Evolution, Uppsala University, Sweden.
<b>SNSB-BSPG</b>	Staatliche Naturwissenschaftliche Sammlungen Bayerns - Bayerische Staatssammlung für Paläontologie und Geologie, München, Germany

## Material and methods

As mentioned, well-preserved high-conical limpet-shaped gastropods of the *Orthonychia*-group from the Late Ordovician Boda Limestone, the Silurian of Gotland (both Sweden), the Mississippian Imo Formation, Arkansas, USA, and the Pennsylvanian Finis Shale, Texas, USA are reported in the present contribution. Details about the four localities from which the studied gastropods stem are provided in the material section for each of the taxa.

The **Boda Limestone** is represented by large carbonate mud mounds of Late Ordovician (Katian) age, exposed in several quarries in the Siljan district of central Sweden (Fig. 1A). The mound fauna is exceptionally diverse and well-preserved (Ebbestad and Höglström 2007). More than 50 species of gastropods are present but although several species are described the main gastropod fauna remains to be studied (e. g., Angelin and Lindström 1880; Koken 1897; Koken and Perner 1925; Wängberg-Eriksson 1964, 1979; Ebbestad 1999; Gubanov et al. 1999; Ebbestad and Peel 2001). Case studies of failed predatory attacks on Boda Limestone gastropods were given by Ebbestad and Peel (1997). A number of platycerate gastropod species occur in the Boda Limestone but no one shows obvious



**Figure 1.** Locations of the studied material of the Ordovician Boda Limestone (A) and the Silurian Eke Formation, Gotland (B).

morphological modifications of the shape of the aperture during growth, which would otherwise indicate obligatory attachment to a substrate or host (e. g., Baumiller and Gahn 2002). Furthermore, one cannot assume that this mode of life applied to all platycerates or cyrtoconic platycerates. Crinoidal packstone is common as flank deposits but nearly absent in the main mound facies, so any crinoidal hosts are not obvious. Fossils in the Boda Limestone are mainly preserved in shell accumulations in deep and often large and complex syndimentary fissures (Suzuki and Bergström 1999; Kröger et al. 2016). The main constituency of the accumulations consist of trilobite remains, typically made up of only one specific taxon where *Stenopareia linnarssoni* and *Eobronteus laticauda* are the two most common. Only one accumulation consisting of gastropods is known, represented by a block made up of *Subulites* specimens (Thorslund 1936, fig. 9). Gastropods are otherwise found as scattered remains within the trilobite accumulations and mostly only one or two specimens are known of the more uncommon species.

The gastropod fossils presented here from the **Silurian of Gotland** stem from the Eke Formation (Ludlow, South Gotland, localities Rikvide and Bodudd). The island of Gotland, Sweden, is situated in the Baltic Sea (Fig. 1B). The Silurian deposits of Gotland comprise a section of latest Llandovery- to Ludlow-aged deposits representing remnants of a former extended carbonate platform complex and the erosional leftovers create a succession that is up to 700 m thick (Calner et al. 2004). Late diagenetic alteration and tectonic disturbance of the rock sequences are rarely observed (Calner et al. 2004). The youngest strata occur in the southeast of the island and become older towards the northwest (compare Calner et al. 2004; Calner 2008). Deposits show a distinct difference in distribution: while the NE is dominated by sediments representative of shallow marine settings, the western part of Gotland is characterized by argillaceous limestones and marls of an open marine shelf (Samtleben et al. 1996; Hede 1960; Jeppsson 1994; Calner et al. 2004; Jeppsson et al. 2006).

Gastropods from the Silurian of Gotland are mainly known from the classic monograph of Lindström (1884)

who reported more than 160 species from this island. Since then, few taxonomic studies about this gastropod fauna have been conducted. A washed residue from marls of the Eke Formation (Ludlow, South Gotland) has yielded a fossil assemblage with numerous small vermiform, horn-shaped gastropods, here identified as *Orthonychia enorme*. This gastropod species is described and reported in detail herein. The samples also have yielded abundant oncoids, some of which are also cone-shaped and might have these gastropods as a substrate.

The Eke Formation contains deposits from the Lau event with its strong positive  $\delta^{13}\text{C}$  excursion, the highest in the entire Phanerozoic (Samtleben et al. 1996; Calner 2008). The Formation can be subdivided into three conodont zones, the Lower, Middle and the Upper Icriodontid Subzone (Jeppsson 2005). The Eke Fm. on western Gotland is characterized by a heterogeneous succession of oncooid-rich wacke-, pack-, and grainstones. Deposits studied derive from a section characterized by a micritic limestone-marl alternation from the Bodudd locality that is extremely rich in oncoids, microbial mats and crusts.

Samples were collected during a student field course in 2013 (Fig. 1C). The deposits containing oncoids and the studied mollusks derive from a topographically flat peninsula running from east to west. Along this into the Baltic Seas protruding headland the samples were collected at three localities (Eke A: 57°04'11.9"N, 18°11'19.2"E / Eke B: 57°04'10.9"N, 18°11'00.8"E / Eke C: 57°04'05.8"N, 18°11'34.7"E). At this locality, the Eke Formation is exposed as limestone-marl-alternations consisting of almost horizontal layers that fall in flat steps towards the Baltic Sea. Eke A and Eke B originate from the lower, Eke C from the upper part of the formation. The samples were dissolved in  $\text{H}_2\text{O}_2$ , sieved (>2 mm, >500  $\mu\text{m}$ , >250  $\mu\text{m}$ ) and the residues were picked.

Besides the common *Orthonychia enorme* reported herein, a large number of oncoids, brachiopods and echinoderm remains (especially crinoid remains) are present as well as rostroconchs and a few bivalves. Ostracods are rather common while remains of blastoids, tentaculites



and trilobite fragments are less abundant. To very rare elements belong fragments and teeth of tube worms and bryozoans. The sample also yielded the gastropod *Euomphalopterus* sp. Samtleben et al. (2000) reported the presence of orthoceratids and rugose corals from this locality. According Samtleben et al. (2000) crinoid remains are rare whereas they are abundant in the studied samples. The cauliflower-shaped oncoids contain biogenic components as core and including the here reported *Orthonychia enorme* as core (Fig. 6G–I).

Few well-preserved specimens of *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow) were recovered from of the **Finis Shale** Member of the Graham Formation (Pennsylvanian, Virgillian, North Central Texas, USA). The Finis Shale is a poorly lithified grey shale that has yielded an abundant and commonly well-preserved marine invertebrate fauna that is rich in brachiopods, bivalves, gastropods, and others. Several groups of gastropods from the Finis Shale have been studied (e.g., Nützel 1998; Nützel et al. 2000; Bandel 2002a, b; Nützel and Pan 2005; Karapınar et al. 2022a) although a comprehensive monograph on the entire gastropod fauna is pending. Case studies of failed predatory attacks on Finis Shale gastropods were given by Vermeij et al. (1981) and Lindström (2003).

Finally, two well-preserved specimens representing *Orthonychia* sp. are reported from the Mississippian (Ches-terian) **Imo Formation** of Arkansas, USA. The Imo Formation consist of dark shales that yielded a diverse bivalve (Hoare et al. 1989) and gastropod (Jeffery et al. 1994) fauna as well as other marine invertebrates.

## Results

### Systematic Paleontology

#### Class Gastropoda

#### Family Orthonychiidae Bandel & Frýda, 1999

**Remarks.** Bandel and Frýda (1999) erected this family for limpet-shaped Paleozoic gastropods formerly included in Platyceratidae. Based on the openly coiled fishhook-like protoconch of the Pennsylvanian limpet-shaped species *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), they placed Orthonychiidae in their new order Cyrtoneritimorpha. However, the protoconch of the Devonian type species of *Orthonychia* is yet unknown (see Knight 1941). The Ordovician family Pollicinidae resembles some members of Orthonychiidae but these shells are bilaterally symmetrical and their early ontogeny is largely unknown (see Peel 2020a, b).

#### Genus *Orthonychia* Hall, 1843

**Type species.** *Platyceras subrectum* Hall, 1859; by subsequent monotypy by Hall (1859).

**Remarks.** *Orthonychia* is a cap-shaped or elongate tube-like mollusk which has traditionally been placed in the in the Paleozoic gastropod family Platyceratidae and was also considered a subgenus of *Platyceras* (Knight et al. 1960). The Devonian type species of *Orthonychia*, *O. subrecta* (Hall, 1859), is known from steinkerns only (Knight 1941) and therefore, the status of shell ornamentation and protoconch morphology cannot be assessed. The general habitus (elongated slightly curved shell with only the early teleoconch being coiled) is close to that of *Orthonychia enorme* (Lindström, 1884) and *Orthonychia yutaroi* Ebbestad, sp. nov. as described below, especially regarding the tube-shaped, stretched late teleoconch. Based on an openly coiled fish-hook-like protoconch, present in the Pennsylvanian species *O. parva*, Bandel and Frýda (1999) erected the family Orthonychiidae and placed it in a new order Cyrtoneritimorpha, forming the fossil sister group of modern Neritimorpha (Cycloneritimorpha).

The tall shell morphology of some *Orthonychia* species including *O. yutaroi* and *O. enorme* as reported herein superficially resembles that of the Ordovician archaeogastropod *Pollicina*, described by Peel (2020a, b). This genus can reach a height of at least 3 cm, has a thick shell, with even co-marginal ribs, and an apex truncated by septa. The shell is bilaterally symmetrical, in contrast to that of *Orthonychia*.

#### *Orthonychia yutaroi* Ebbestad, sp. nov.

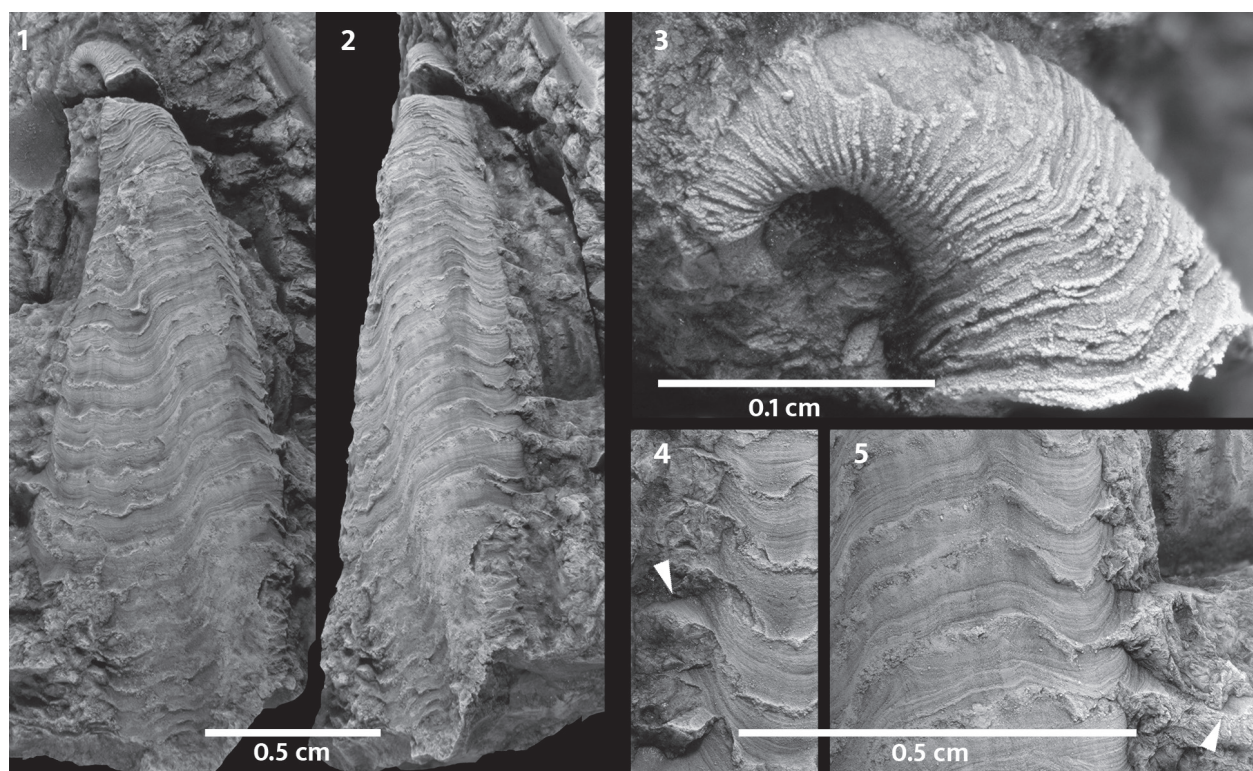
<https://zoobank.org/595BAF12-C8B3-4219-B528-657BAF5EEA0B>  
Fig. 2

**Material.** Only the holotype (PMU 37146) is known, from the Late Ordovician (Katian) Boda Limestone at Jutjärn quarry, Siljan district, Dalarna.

**Derivation of name.** After Dr Yutaro Suzuki, Shizuoka University, Japan, who found the specimen and who has made extensive studies of fossils and the mound ecology of the Boda Limestone.

**Diagnosis.** Shell tall, teleoconch forming a weakly cyrtconic tube, open coiled with apex coiled through half a whorl; supra-apical surface formed by raised and convex median section; teleoconch ornamentation consist of densely spaced, slightly undulating, strong co-marginal ribs on initial parts, widening later in ontogeny to distinct growth increments that end in a flared lamellae; growth lines corrugated, laterally forming two or three spaced flutes, across the median part only weakly undulating; last part of protoconch without visible ornament and abrupt transition to teleoconch; early protoconch whorls poorly preserved as imprint, possibly tightly coiled consisting of ca. two whorls.

**Description.** Shell tall, weakly cyrtconic, open coiled with apex coiled through at least half a whorl before shell coiling ends and a straight tube forms, widening gradually with length at base about 45% of total height (= 20 mm). Shell nearly planispiral but with weak translation down the axis if viewed with aperture in normal right-handed



**Figure 2.** *Orthonychia yutaroi* Ebbestad, sp. nov., holotype PMU 37146. (1, 2) Right lateral and anterior views. (3) Detail of initial whorls. (4) Detail of left periphery with arrow pointing to lamella. (5) Detail of left periphery with arrow pointing to lamella.

position. Apex overhang sub-apical margin. Supra-apical surface of shell forms a raised and convex median section, with concave transition to lateral surfaces. Ornamentation on initial conch consist of densely spaced, slightly undulating, strong co-marginal ribs. A couple of millimeters from the apex, the space between the ribs widens gradually and distinct growth increments (here taken as the growth accumulated in the space between subsequent lamellae) become apparent. Increments are spaced no more than 1 mm apart, consist of fine co-marginal growth lines and end with a lamella that extends prominently and nearly horizontal from the shell (arrows in Fig. 2A4, A5). Near the aperture the space between the increments again becomes narrower. The growth lines are corrugated, laterally forming two or three spaced flutes that have a pointed bell-shaped, whereas the growth lines across the median part only are weakly undulating. Ornamentation on inner margin obscured by matrix. Medially the growth-lines form a broad low-relief U-shape.

Last part of protoconch without visible ornament and abrupt transition to teleoconch; width of last protoconch whorl at termination about 200  $\mu\text{m}$ ; early protoconch whorls poorly preserved as imprint, possibly tightly coiled consisting of ca. two whorls.

**Remarks.** The conch of *Orthonychia yutaroi* resembles an orthonychian shell morphology in the tall elongated tube-like shell and has a similar crenulated teleoconch ornamentation as the Silurian *O. enorme* (see below). Compared with *O. enorme* it differs markedly in attaining an open coiled shell earlier, as the initial shell of *O. enorme*

coils more tightly. However, the teleoconch in *O. yutaroi* expands more slowly in late ontogeny than that of *O. enorme* and the shell of the Dalarna species is proportionally taller and straighter (less pronounced supra-apical curvature). The periodic flaring lamellae in *Orthonychia yutaroi* are much more extensive and more pronounced, and ribbing is much denser, especially in the early teleoconch, than in *O. enorme*. Furthermore, *O. yutaroi* has stronger crenulations forming flutes laterally, whereas the longitudinal flutes are weak or absent in *O. enorme*. But both species share the development of periodic growth increments that end with a crenulated lamella.

The protoconch of *Orthonychia yutaroi* is incompletely preserved but it is clear that it lacks visible ornament and has an abrupt transition to the teleoconch. It seems to be possible that the protoconch is tightly coiled and consists of ca. 2.5 whorls, similar to what we have found in *O. enorme* (see below).

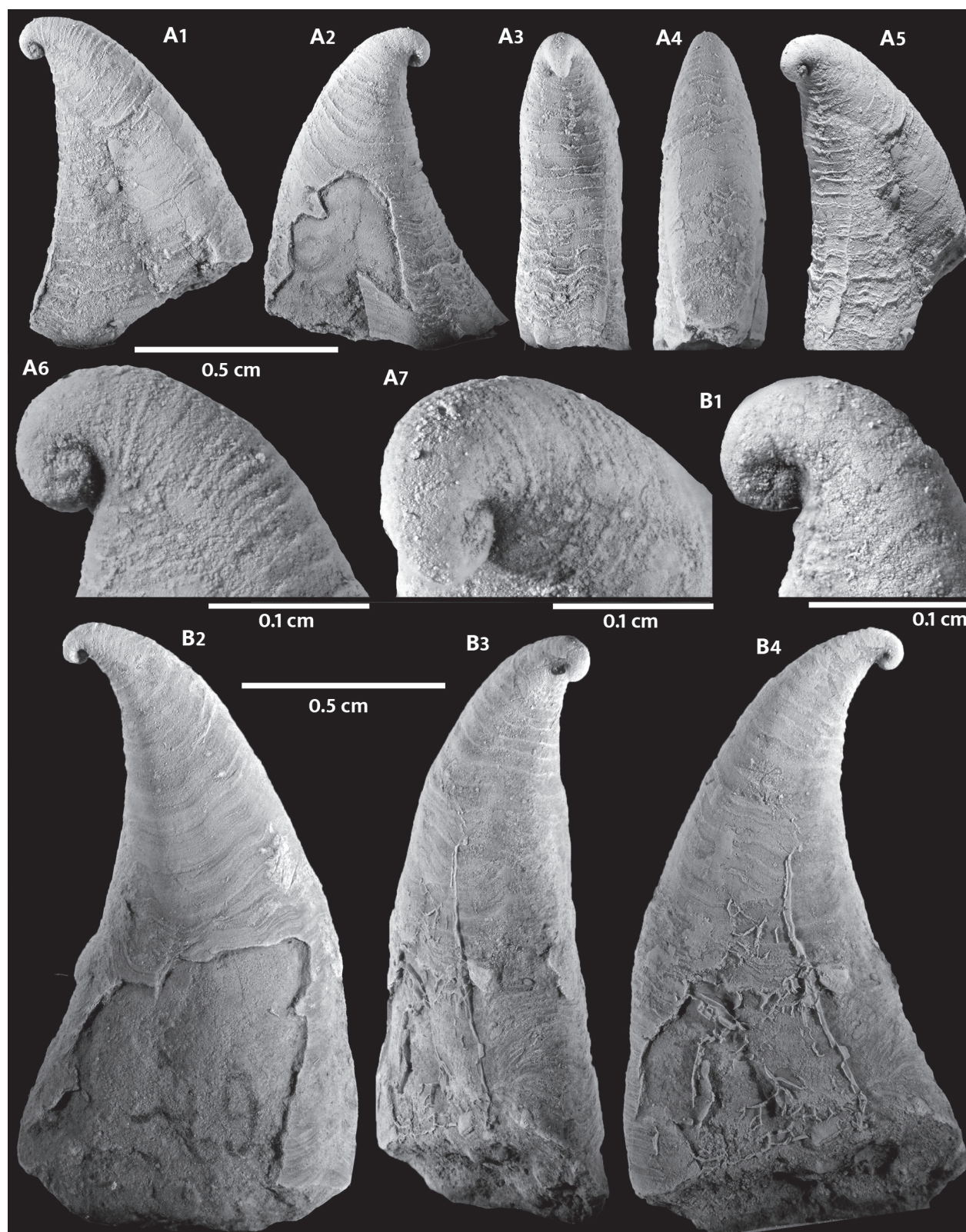
### *Orthonychia enorme* (Lindström, 1884)

Figs 3–8

1884 *Platyceras enorme* sp. nov. – Lindström: 69, pl. 2, figs 59–72.  
cf. 1976 *Platyceras* (*Orthonychia*) cf. *P. (Orthonychia) enorme*  
Lindström, 1884 – Peel and Yochelson: 17.

**Lectotype.** Selected here, NRM Mo 38219 from the Eke Formation at Rikvide, Gotland, illustrated by Lindström (1884, pl. 2, figs 60, 61, re-illustrated here in Fig. 3A. The





**Figure 3.** *Orthonychia enorme* (Lindström, 1884) **(A)** Lectotype NRM 38219. **(A1–A5)** Right lateral, left lateral, posterior, anterior, and posterior oblique views. **(A6, A7)** Details of apex; illustrated by Lindström (1884 pl. 2, figs 60, 61). **(B)** Paralectotype NRM 38220. **(B1)** Detail of apex. **(B2–B3)** Left lateral, posterior oblique and right lateral views; illustrated by Lindström (1884, pl. 2, figs 62, 63). Scale bar: 0.5 mm (**A1–A5, B2–B4**).

specimen is laterally compressed and incomplete when it comes to height but shows the early ontogeny, the tube-like expansion of the shell and the distinct ornamentation.

**Other type material.** Lindström (1884) illustrated an additional six specimens from the same locality as the lectotype, and these are here considered paralectotypes

(NRM Mo 38218, Mo 38220–Mo 38324); see Figs 3B–5B. The identity of specimens listed by Lindström (1884) from other localities cannot be established, with the exception of the specimen from Slite which is not conspecific with *O. enorme* (see below). The other localities mentioned by Lindström (1884) span older strata (Djupvik and Klinteberget = Slite beds of Sheinwoodian/Homerian age; Havdhem and Hammar in Kräklingbo = Hemse beds of Gorstian/Ludfordian age) and younger strata (Burgsvik = the Burgsvik Sandstone just overlying the Eke Formation).

**Additional material.** Ca. 240 juvenile shells (illustrated material SNSB-BSPG 2023 X 1–15). from the Eke Formation at Bodudd (S Gotland, Sweden, 57°04'05.8"N, 18°11'34.7"E, compare Calner et al. 2004, fig. 2) which is Ludfordian (Ludlow, upper Silurian) in age.

**Description of type material (Figs 3–5, Table 1).** Largest shell 16.5 mm tall and 7.5 mm in apertural length (in lateral view). On average the shell is twice as tall as long (in lateral view). NRM Mo 38219 (Fig. 3A) deviates by length of aperture being 75% of height, but the shell is laterally compressed. NRM Mo 38222 (Fig. 5B) has an aperture length that is only about 40% of shell height. Rate of expansion high when viewed in a lateral perspective, but less when viewed anteriorly/posteriorly, making aperture sub-oval. Growth lines irregularly crenulated, but overall attitude is straight across posterior section of shell (Figs 3A3, 4A4), gently arched on lateral surfaces and curved into broad median sinus anteriorly. Here the growth lines are sinusoid with two asymmetrical crenulations of which the left has greater amplitude (Figs 3A4, 4A3). Although the intensity and irregularity of the crenulations vary, there are no major deviations from the overall co-marginal alignment. The co-marginal ribs or frills seen in early ontogeny widens into distinct growth increments, spaced less than 1 mm apart and ending in seemingly short lamellae. Fine radial striae may be present within each growth increment. Specimen NRM 38220 appears to have a mostly smooth shell with fine growth lines only, but increments with lamellae are visible on the initial part of the shell (Figs 3B3, B4). Space between increments get narrower in late ontogeny (Fig. 4A, B). Radial ornamentation is absent.

**Description of additional material from sieved bulk samples (juvenile and encrusted shells, Figs 6–8).** Shell with tightly coiled ca. 1.5–2.5 initial whorls including protoconch and early teleoconch; largest shell studied with SEM 4.1 mm long, 1.9 mm wide; encrusted specimens (forming cores of oncoids) probably belonging to the present species up to 20 mm long; protoconch with round, convex whorls and slightly elevated spire, lacking ornament (but re-crystallized); encrusted (oncoid) specimens possibly belong to this species up to 20 mm long; diameter of first whorl 0.17–0.25 mm, diameter of protoconch 0.37–0.68 mm (two measurements); protoconch/teleoconch-transition indistinct due to preservation (re-crystallization) but apparent by sudden onset of co-marginal ribs (may also appear as frills or lamellae) and rapid increase of expansion rate of whorl diameter;

later teleoconch detaches and becomes uncoiled, bent to slightly elongated, slowly increasing in diameter, forming a cap-shaped tube; teleoconch ornamented by sharp, narrow co-marginal ribs separated by wide interspaces; strength of ribs and density of ribbing variable; ribs can also form lamellae; ribs appear much longer (lamellae) in specimens studied in thin sections than ribs in specimens from bulk samples suggesting that such lamellar ribs broke off during processing of sample; teleoconch also ornamented by thin spiral lirae, much weaker than co-marginal ribs; shell having a calcitic layer as suggested by thin sections.

**Remarks.** Lindström (1884, p. 69) mentioned several specimens from various localities on Gotland, but figured only specimens from Rikvide. In the NRM collection only specimens from Rikvide and Burgsvik are registered, but specimens from the latter locality were not available for study. The specimen from Slite in the PMU collections, mentioned by Lindström (1884), is illustrated here in Fig. 5B. It comes from the much older Slite Group sediments and is here treated as *Orthonychia* sp. The species was also listed from the Slite Beds by Manten (1971, table 11). However, it differs markedly from *O. enorme* in the initial shell having higher rate of coiling, possibly more coiled whorls before extending into the tubular shell, the shell is proportionally broader at the aperture, the W/H ratio is higher (0.65), it lacks clear growth increments and lamellae, and have a distinct radial ornamentation crossing the fine co-marginal growth lines thus creating a fine reticulate pattern. Furthermore, the shell reverses curvature during growth.

Lindström (1884, p. 69, pl. 2, fig. 71) described and illustrated a fine radial ornamentation. Some faint striations may be discerned in NRM 38218 (Fig. 4B2) but similar ornamentation is not seen in other macro-specimens. Fine and widely spaced lirae are present in early ontogeny (Gotland Ortho 1, C2). The two-element illustration in Lindström (1884) cannot readily be linked to any of the available specimens.

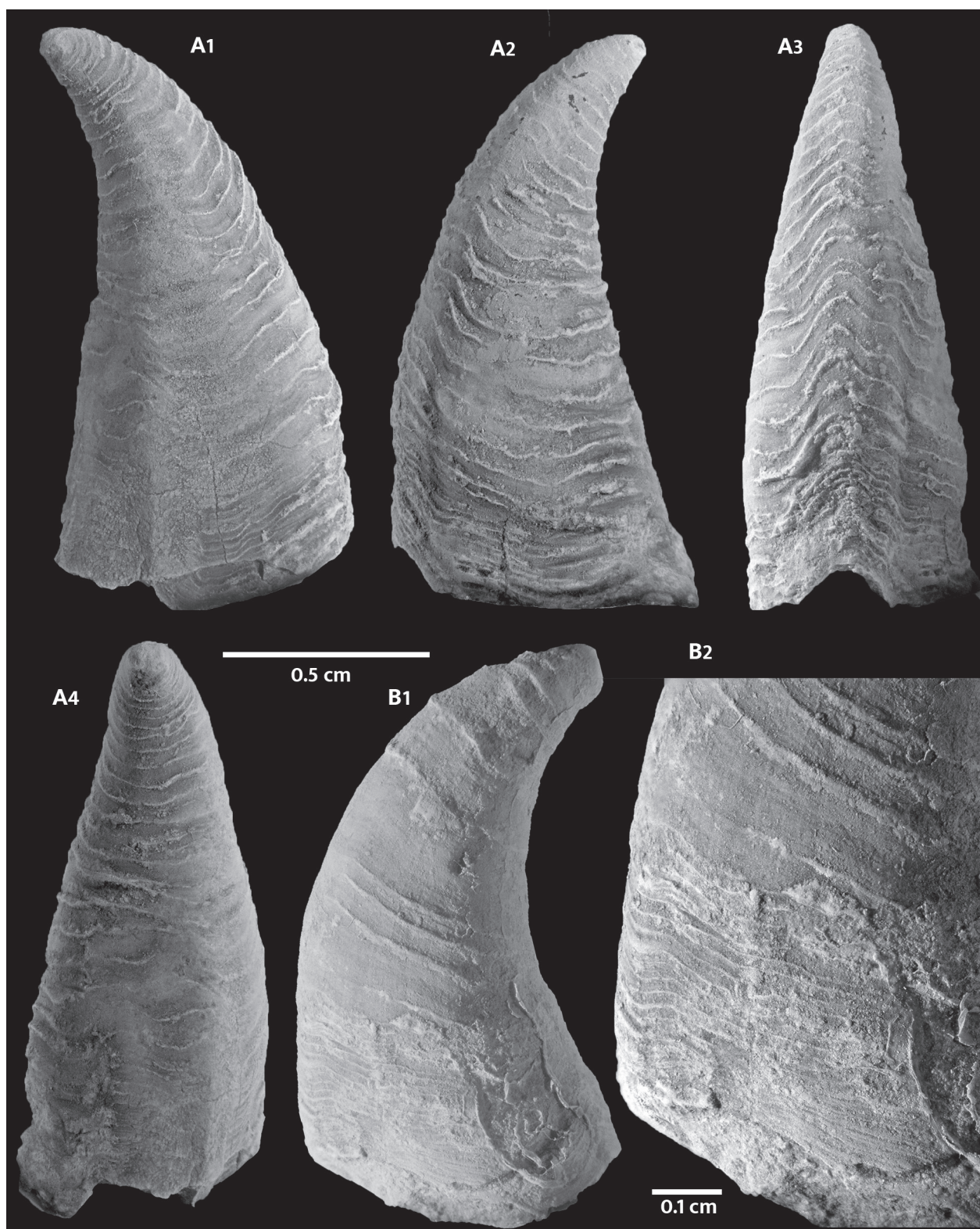
Peel and Yochelson (1976, p. 17) listed *Platyceras* (*Orthonychia*) cf. *P. (Orthonychia) enorme* Lindström, 1884 from the Telychian of Norway.

**Table 1.** Measurements of type specimens of *Platyceras enorme* Lindström, 1884.

	Height [cm]	Width at aperture [cm]	W/H
NRM Mo 38219	0.82	0.6	0.73
NRM Mo 38220	1.5	0.83	0.55
NRM Mo 38221	1.4	0.73	0.52
NRM Mo 38222	1	0.42	0.42
NRM Mo 38223	1.65	0.75	0.45

The present material from the bulk samples closely resembles the type material of *Platyceras enorme* Lindström, 1884 as described and illustrated above. The type specimens are much larger (more than 16 mm long)



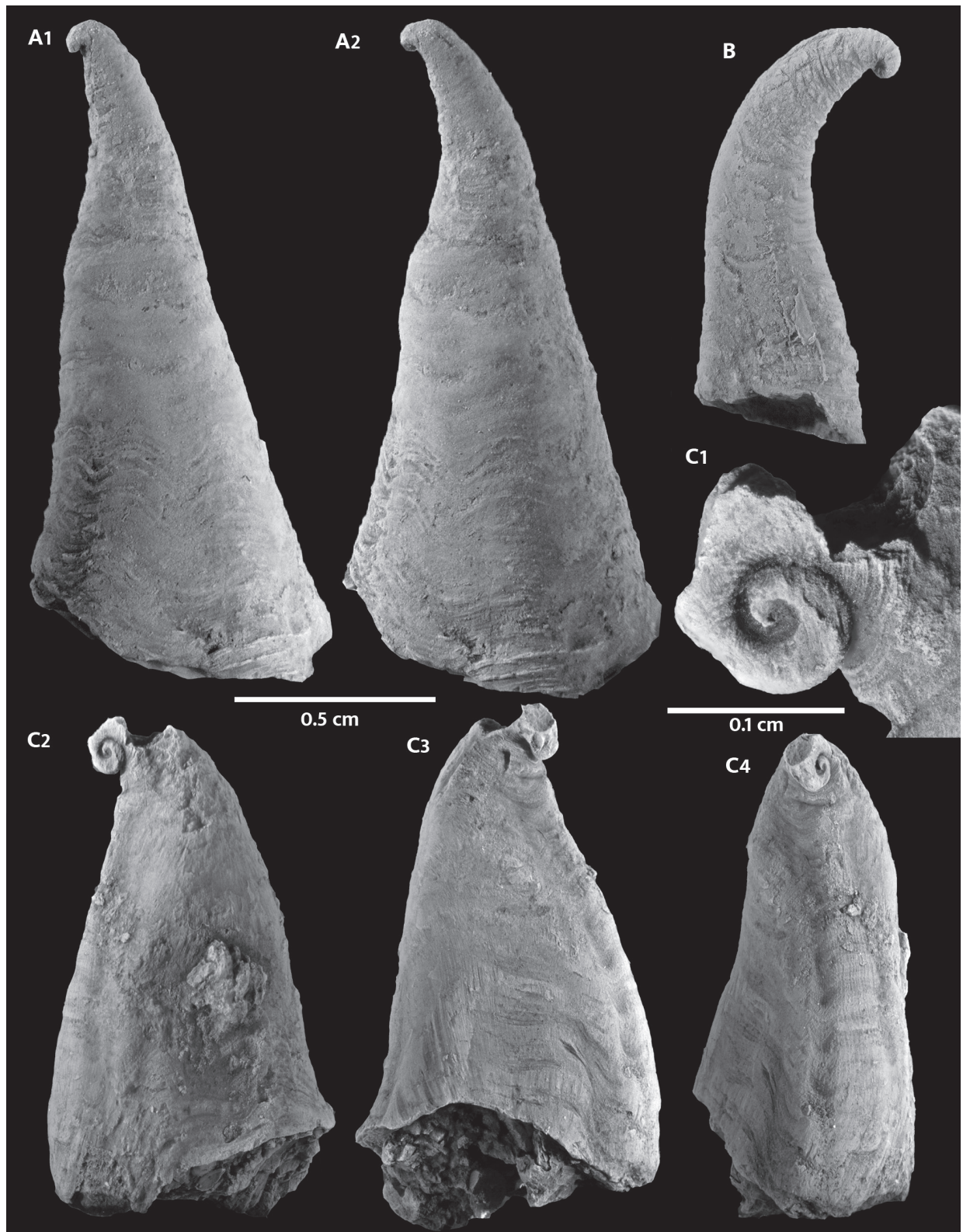


**Figure 4.** (A, B) *Orthonychia enorme* Lindström (1884). (A) Paralectotype NRM 38221. (A1–A4) Right lateral, left lateral, anterior, and posterior views; illustrated by Lindström (1884, pl. 2, figs 64–66). (B) Paralectotype NRM 38218. (B1) Left lateral view. (B2) Detail of ornamentation near the aperture. The museum label indicates that this is the specimen illustrated by Lindström (1884, pl. 2, fig. 59), but the specimen does not match the illustration particularly well. Scale bar: 0.5 cm (A, B1).

than the specimens from the washed residue reported here. However, strongly encrusted specimens studied by Schugmann (2015) and herein (Fig. 6) are also in this

larger size range suggesting that the specimens from the residues are juveniles. *Platyceras cornutum* from the upper Silurian of Gotland as illustrated by Lindström (1884)



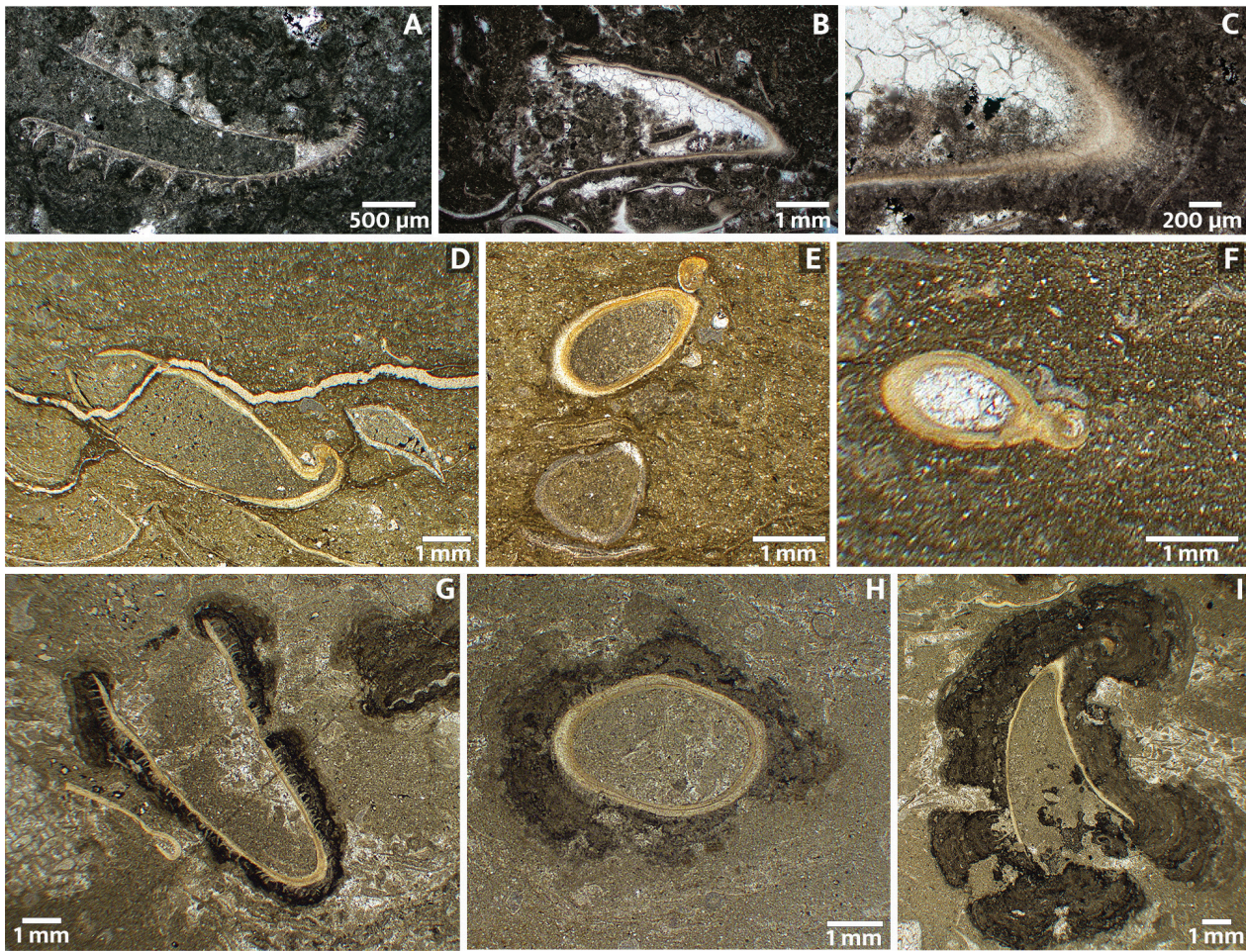


**Figure 5.** (A, B) *Orthonychia enorme* Lindström (1884). (A) Paralectotype NRM 38223. (A1, A2) Right lateral and anterior oblique views; illustrated by Lindström (1884, pl. 2, figs 69, 70). (B) Paralectotype NRM 38222. Left lateral view; illustrated by Lindström (1884, pl. 2, fig. 68). (C) *Orthonychia* sp., PMU 21576. (C1) Detail of apex. (C2–C4) Right lateral, left lateral and posterior views. Specimen collected by Cleve and mentioned by Lindström (1884, p. 69). Scale bar: 0.5 cm (A, B, C2–C4).

is similar but lacks ornamentation of axial ribs/frills and spiral lirae; instead it has co-marginal irregular bulges. Moreover, the teleoconch of *Platyceras cornutum* is generally more curved.

The Devonian *Crossoceras* Boucot & Yochelson, 1966 (Platyceratidae) is ornamented with co-marginal sharp ribs (frills) and a fine spiral lineation similar to the ornament of *Platyceras enorme*. However, *Crossoceras* has a





**Figure 6.** *Orthonychia enorme* (Lindström, 1884) in thin sections, Silurian Eke Formation, Gotland; the type of preservation of the shells suggests that they were primarily calcitic with foliated micro-structures; some of the shells have very long frills; these frills are much longer than those on specimens from the type series (Figs 3–5) and washed samples (Figs 7–8) suggesting they broke off during weathering and the processing of the samples. Thin sections repositied Friedrich-Alexander-Universität Erlangen-Nürnberg, GeoZentrum Nordbayern, Erlangen, Germany. (A) Shell in longitudinal section, specimen with pronounced frills. (B, C) Shell in longitudinal section, specimen with pronounced frills in apical portion (C). (D) Shell in longitudinal section, specimen shows coiling in its apical portion. (E) Upper portion of image, shell in transverse section of one whorl (large oval) and tangential to earlier whorl (round). (F) Middle left portion of image, shell in transverse section of one whorl (left large oval) and earlier whorl (right circular). (G) Shell in longitudinal section, specimen shows pronounced frills covered by a thick microbial crust. (H) Shell in transverse section, covered by a thick microbial crust. (I) Shell in longitudinal section, covered by a thick microbial crust.

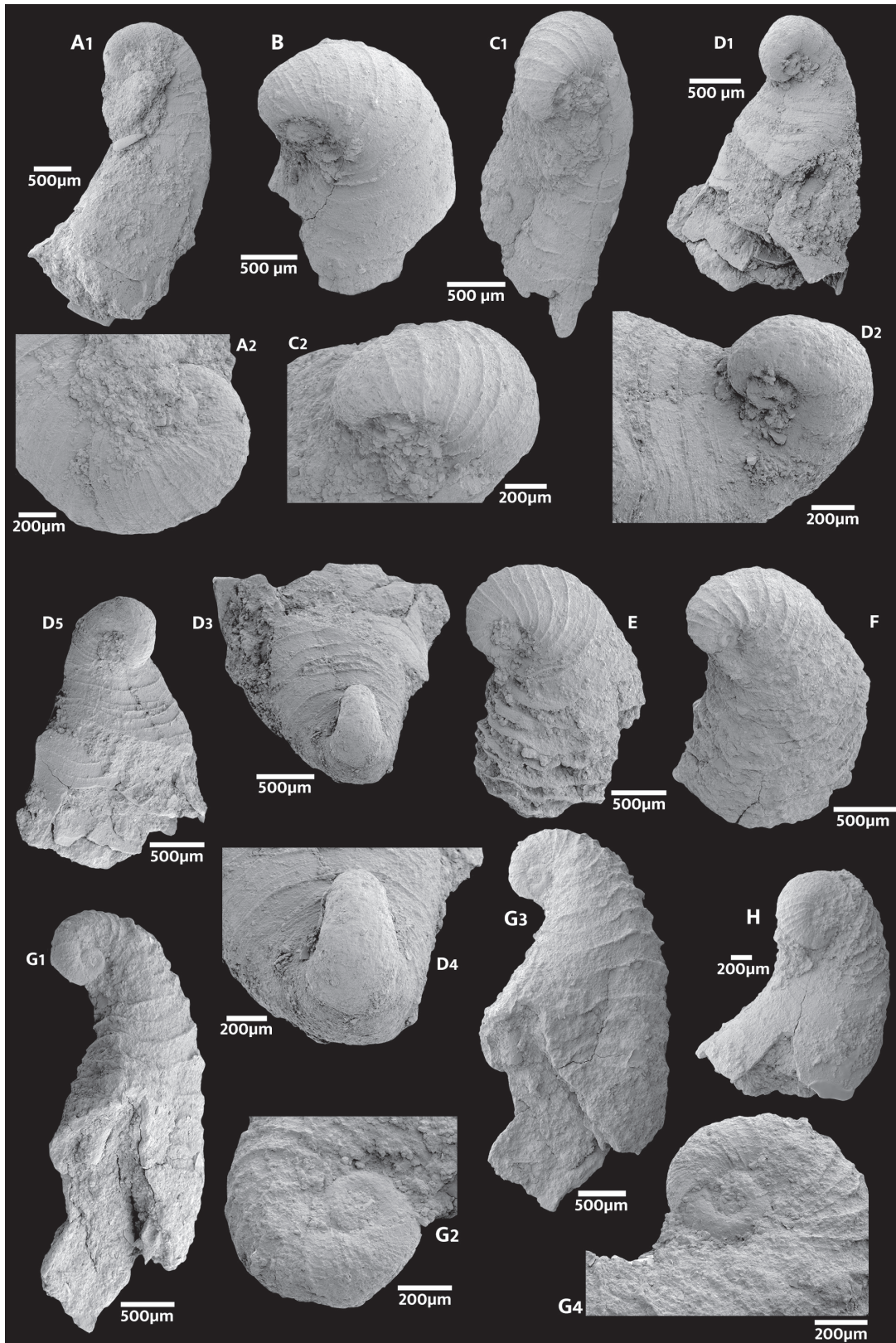
stronger curvature of the teleoconch and is thus close to *Platyceras* in this respect. A close phylogenetic relationship of *Crossoceras* and *Orthonychia enorme* seems to be likely. The protoconch of *Crossoceras* is unknown; judging from the illustration given by Boucot and Yochelson (1966, pl. 3, fig. 11) it could be tightly coiled as in *Orthonychia enorme* but the preservation is insufficient to be sure.

*Pragoserpulina tomasi* Frýda, 1998a, type species of *Pragoserpulina* Frýda, 1998a, family Pragoserpulidae Frýda, 1998a, from the Early Devonian of the Czech Republic (Dvorce-Prokop Limestone, Praha Formation, Pragian, Czech Republic) closely resembles *O. enorme* in teleoconch morphology and in having the same type of tightly coiled protoconch. However, the uncoiled teleoconch of *P. tomasi* is more bent, its ribbing is denser, the co-marginal ribs are stronger; the ribs are rounded and not as sharp (no frills). Bouchet et al. (2005, 2017) classi-

fied Pragoserpulidae as a Paleozoic taxon that certainly belongs to gastropods, unassigned to superfamily – it is possible that *Pragoserpulina* is platycerate.

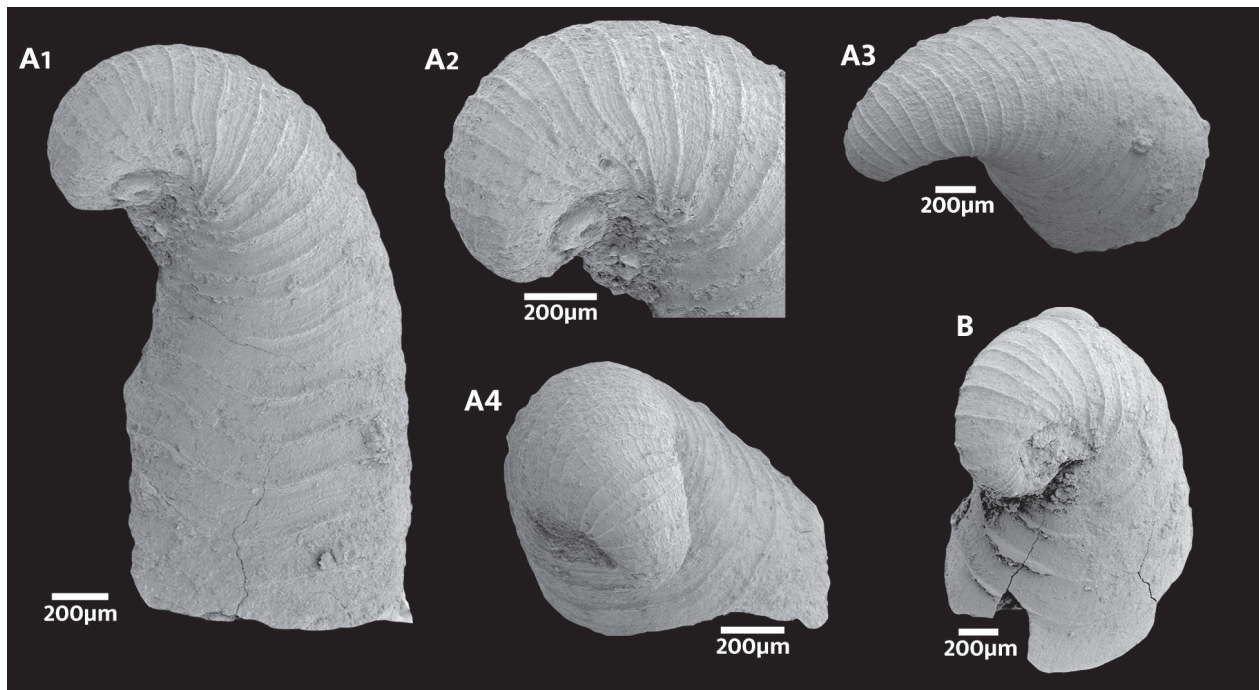
The tightly coiled protoconchs shown here for *Orthonychia enorme* and that illustrated by Frýda (1998a) for *Pragoserpulina tomasi* are clearly not of the vetigastropod type (see e. g., Bandel 1982; Haszprunar et al. 1995; Nützel 2014). They probably were produced by larvae with a short-termed planktotrophic phase. Similar protoconchs were reported for the Paleozoic neritimorph *Naticopsis* (Nützel and Mapes 2001; Nützel et al. 2007b) and *Platyceras* (Frýda et al. 2009). The same type of protoconch was found in Devonian and early Carboniferous gastropods with a cap-shaped teleoconch placed in the family Pragoscutulidae Frýda, 1998a (Cook et al. 2008). They were classified as Caenogastropoda but a neritimorph relation seems also possible. Pragoscutulidae are much stouter i.e., they have a much wider apical angle.





**Figure 7.** *Orthonychia enorme* (Lindström 1884), Silurian Eke Formation, Gotland. **(A)** SNSB-BSPG 2023 X 1. **(A1)** Lateral view. **(A2)** Initial whorls in oblique apical view. **(B)** SNSB-BSPG 2023 X 2, juvenile specimen in lateral view. **(C)** SNSB-BSPG 2023 X 3. **(C1)** Lateral view. **(C2)** Early teleoconch with distinct axial ribs/frill and faint spiral lirae. **(D)** SNSB-BSPG 2023 X 4. **(D1)** Juvenile specimen in lateral view. **(D2)** Initial whorls in oblique apical view including tightly coiled protoconch without visible ornament. **(D3, D4)** Dorsal views including last smooth whorl of protoconch. **(E)** SNSB-BSPG 2023 X 10, juvenile specimen with strong frills in lateral view. **(F)** SNSB-BSPG 2023 X 6, juvenile specimen with strong frills in lateral view. **(G)** SNSB-BSPG 2023 X 11. **(G1)** Lateral view. **(G2)** Initial whorls including tightly coiled protoconch without visible ornament in oblique apical view. **(G3)** Lateral view. **(G4)** Initial whorls including tightly coiled protoconch without visible ornament in apical view. **(H)** SNSB-BSPG 2023 X 12, juvenile specimen in lateral view.





**Figure 8.** *Orthonychia enorme* (Lindström, 1884), Silurian Eke Formation, Gotland. (A) SNSB-BSPG 2023 X 13, specimen with distinct co-marginal ribs and longitudinal lirae. (A1) Lateral view. (A2) Initial whorls in oblique apical view. (A3) Dorsal lateral view. (A4) Dorsal view. (B) SNSB-BSPG 2023 X 15, lateral view.

### ***Orthonychia parva* (Swallow, 1858 in Shumard and Swallow)**

Figs 9–12

\*1858 *Capulus parvus* sp. nov. - Swallow (in Shumard and Swallow): 205.

1967 *Platyceras (Orthonychia) parvum* (Swallow, 1858) - Yochelson and Saunders: 173 [additional synonymy and chresonymy therein].

1999 *Orthonychia parva* (Swallow, 1858) - Bandel and Frýda: text-fig. 1, pl. 2, figs 5–8, pl. 3 figs 1–2.

2005 *Orthonychia parva* - Frýda: 382, fig. 3D.

2008a *Orthonychia parva* - Frýda et al.: 254, fig. 10.8E, G.

2009 *Orthonychia parva* (Shumard & Swallow, 1858) - Frýda et al.: 112, 116, fig. 5C–D.

2012 *Orthonychia parva* - Frýda et al.: 417, fig. 14E, M.

2014 *Pseudorthonychia* - Nützel: 491, fig. 14E, H.

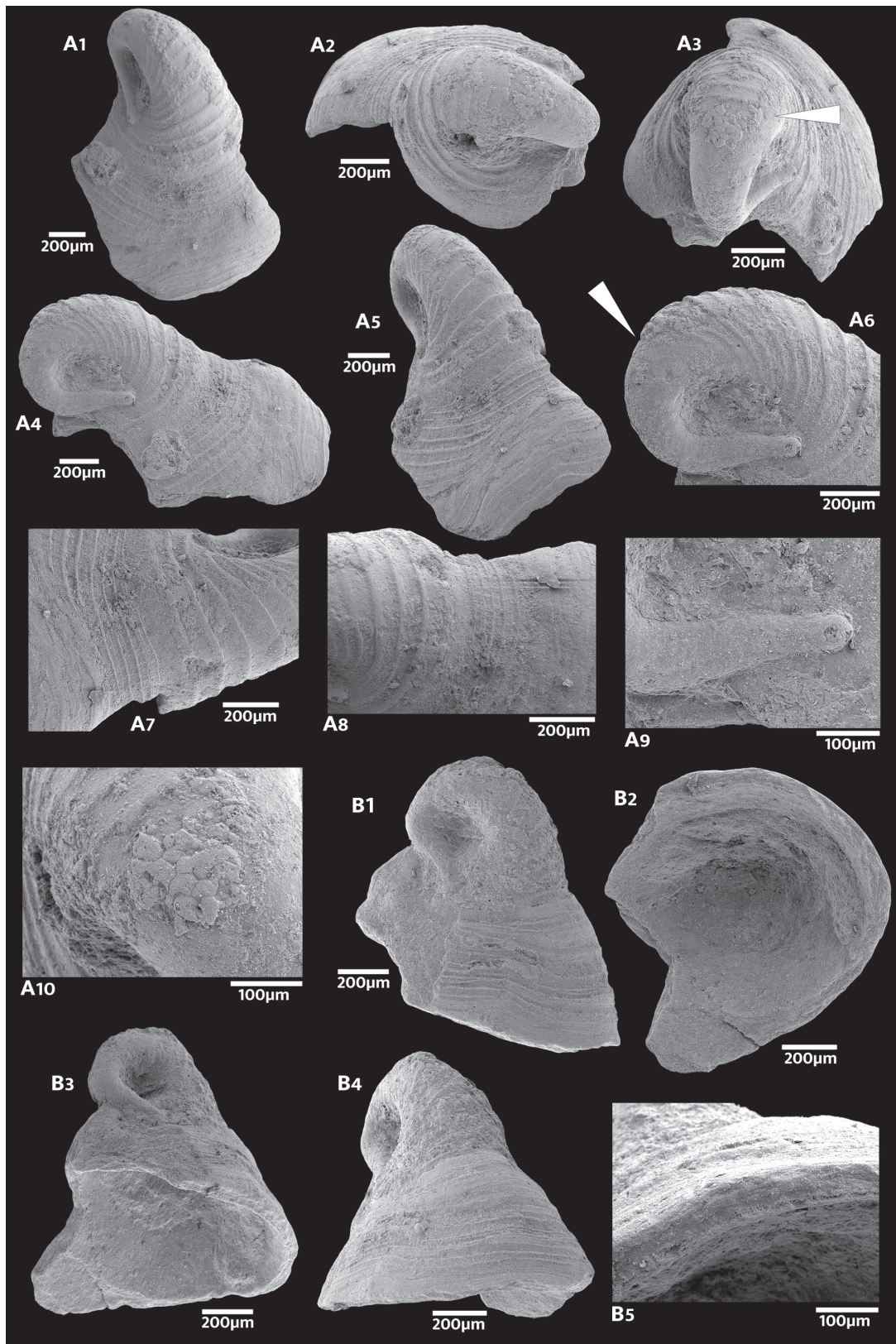
**Material.** 6 specimens (SNSB-BSPG 2020 XCI 117–122) from the Finis Shale Member of the Graham Formation (late Pennsylvanian, Virgillian, North Central Texas, USA) at the locality TXV–200: Lost Creek Lake emergency spillway at dam, approximately 4 km northeast of Jacksboro, Jack County, Texas on Texas Highway 59. AMNH Locality 5562, 33°14'11.17"N, 98°07'11.33"W, 33.230, -98.136.

**Description.** Shell limpet-shaped; protoconch (description largely based on SNSB-BSPG 2020 XCI 117, Figs 9A, 12) with an initial bulb (Fig. 12 I) slightly elongated, 100–120 µm long, 70–75 µm wide, terminating in a slight constriction; width of initial bulb at 100 µm shell length 70–80 µm; shell after initial bulb forming a straight tube slowly increasing in width (Fig. 12 II); dextral coiling

starts at 270–360 µm shell length and coiling comprises 100–180° (Fig. 12 III) until strong co-marginal ribs develop on the shell; the smooth initial shell has the form of a hook that encloses a central gap i. e., it is openly coiled; terminal width of whorl of initial smooth shell 0.5–0.6 mm; smooth initial whorl followed by rapidly expanding shell portion with strong collabral ribs (Fig. 12 IV); ribs separated by wider interspaces, prosoclyt in apical view and prosocline in lateral view; initial smooth shell part resting on axially ribbed shell; shell part with strong axial ribs has width of 0.8–1 mm at termination; shell distinctly and abruptly widening after initial shell with axial ribs resulting in a cap-shaped morphology (Fig. 12 V), transition at an angle; following shell cap-shaped with variable co-marginal ornament; one specimens shows fine longitudinal lirae on the teleoconch (Fig. 10B6).

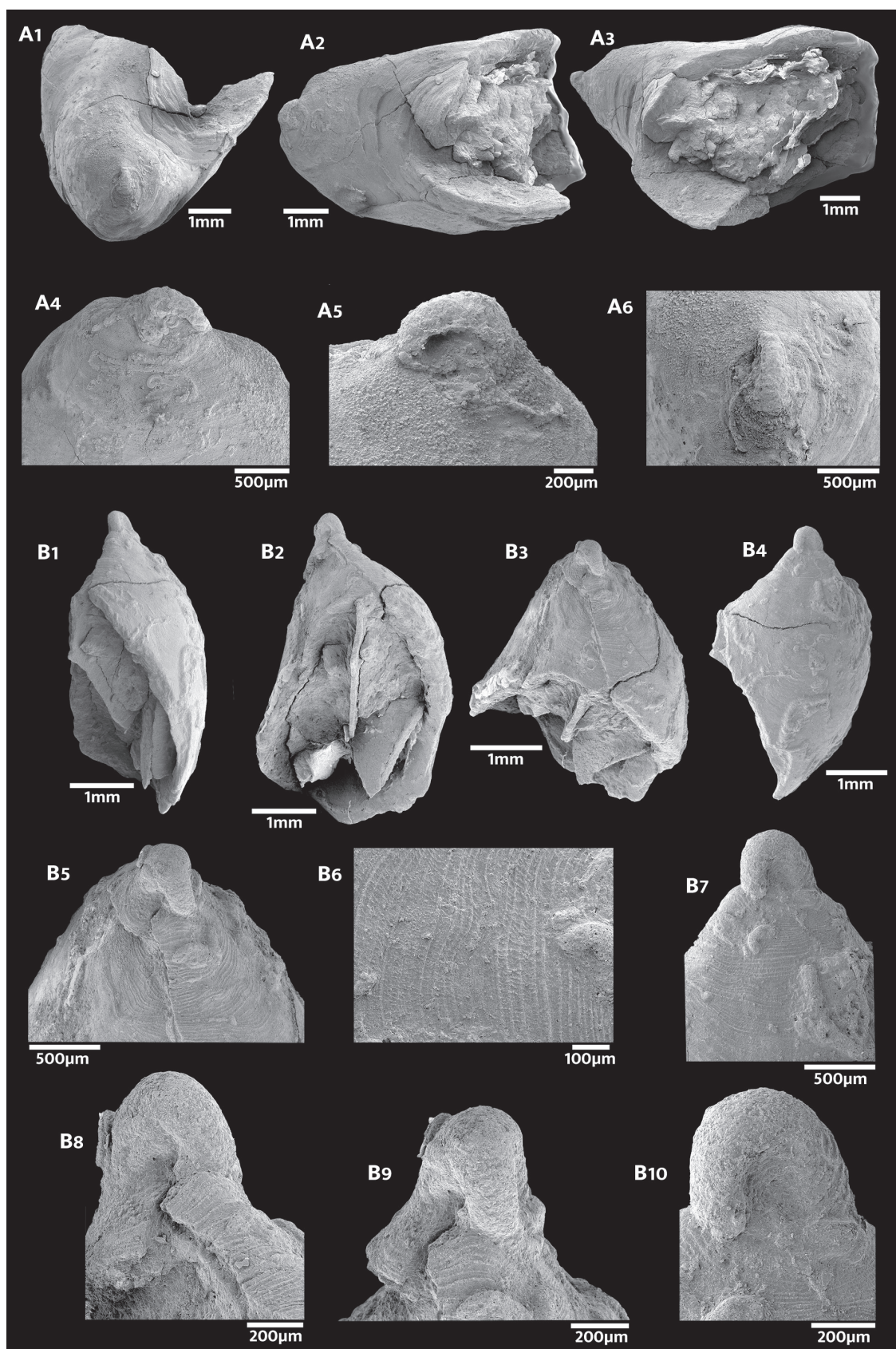
**Discussion.** *Orthonychia parva* is widely distributed throughout the Carboniferous of the US (Yochelson and Saunders 1967). It has also been reported from the Pennsylvanian of North Central Texas (Mineral Wells Fm.) (Plummer and Moore 1921) although not from the Finis Shale. To our knowledge, Knight (1934, figs 1d–g) reported the only specimens (four) with preserved protoconchs. Two of these specimens were also illustrated in detail (SEM) by Bandel and Frýda (1999, pl. 2 figs 5–8): (reproduced by Frýda 2005, fig. 3D; Frýda et al. 2008a, fig. 10.8 E, G; Frýda 2012, fig. 14E,M; Nützel 2014, fig. 14E, H, erroneously as *Pseudorthonychia*). The same type of protoconch with stretched initial part and open coiling has been reported for the Devonian *Praenatica cheloti* by Frýda et al. (2009).

The present shell displays considerable ontogenetic change. There can be little doubt that the initial bulb rep-



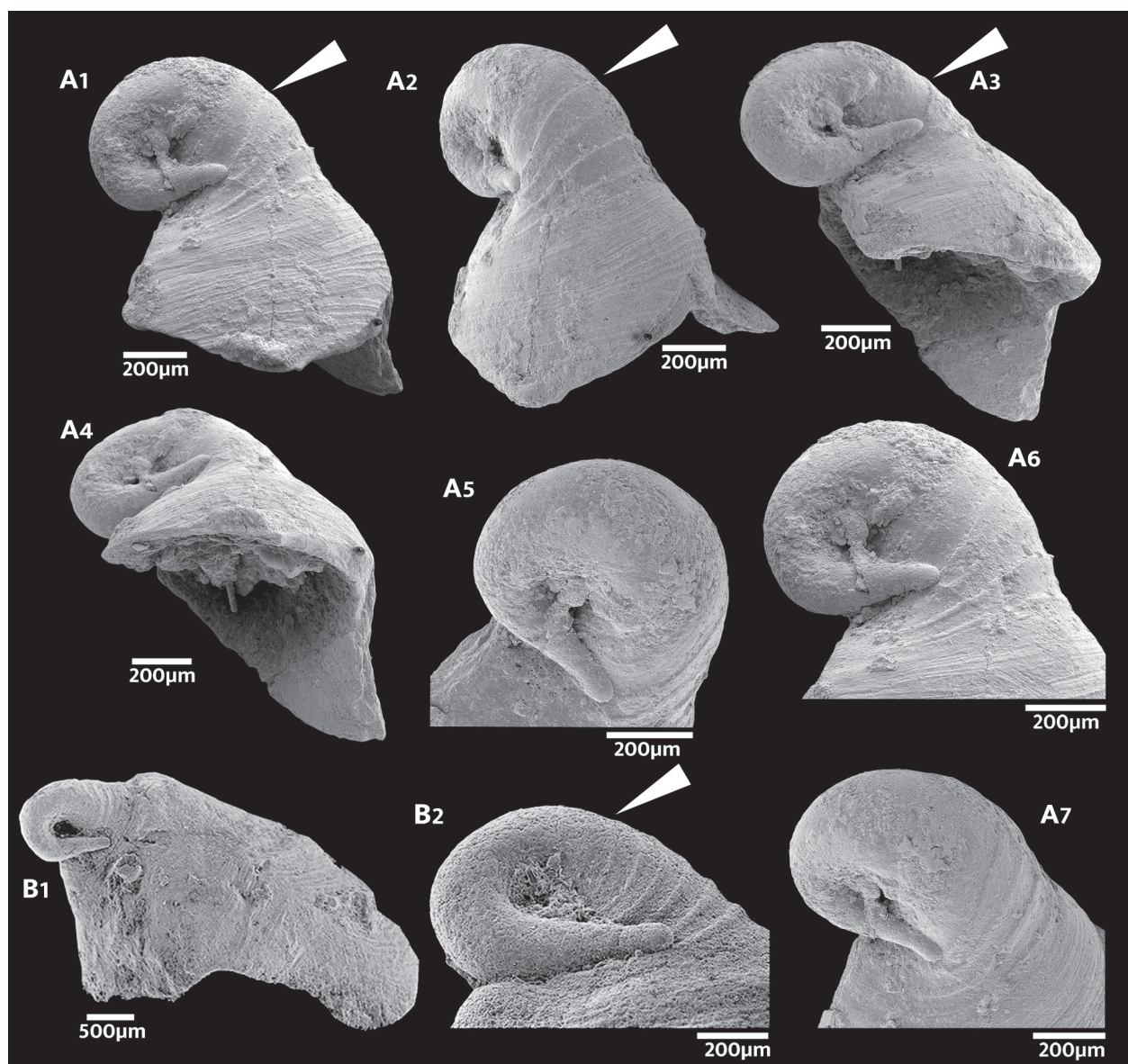
**Figure 9.** *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), two juvenile specimens with uncoiled, hook-like protoconchs in various views; Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. **(A)** SNSB-BSPG 2020 XCI 117. **(A1)** Oblique anterior view. **(A2)** Oblique dorsal view. **(A3)** Dorsal view. **(A4)** Lateral view, openly coiled protoconch well visible. **(A5)** Oblique lateral view. **(A6)** Detail initial whorl including openly coiled protoconch. **(A7, A8)** Detail early teleoconch at rapid widening of shell, openly coiled protoconch well visible. **(A9)** Detail of straight part of openly coiled protoconch including initial bulb. **(A10)** Detail encrustation at transition from smooth protoconch to ribbed early teleoconch. **(B)** SNSB-BSPG 2020 XCI 118. **(B1)** Lateral view, openly coiled protoconch well visible. **(B2)** Apertural view. **(B3)** Oblique lateral view, openly coiled protoconch well visible. **(B4)** Oblique anterior view. **(B5)** Detail of shell to show foliated micro-structure.





**Figure 10.** *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. **(A)** SNSB-BSPG 2020 XCI 121. **(A1)** Apical view. **(A2, A3)** Apertural views at different angles. **(A4, A5)** Protoconch remains in lateral view. **(A6)** Protoconch remains in apical view. **(B)** SNSB-BSPG 2020 XCI 122. **(B1, B2)** Apertural views at different angles. **(B3, B4)** Lateral views at different angles. **(B5, B7)** Protoconch remains and early teleoconch with strengthened growth lines. **(B6)** Detail of early teleoconch ornament consisting of strengthened growth lines and very delicate longitudinal lirae. **(B8–B10)** Protoconch remains in lateral views.





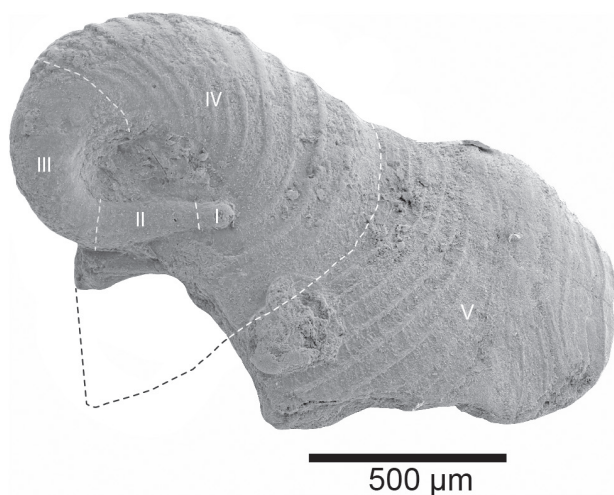
**Figure 11.** *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow). **(A)** SNSB-BSPG 2020 XCI 119, juvenile shell portion, Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. **(A1)** Lateral view, openly coiled protoconch well visible. **(A2)** Oblique anterior view. **(A3)** Oblique lateral view. **(A4)** Oblique apertural view. **(A5)** Openly coiled, smooth protoconch. **(A6)** Openly coiled, smooth protoconch in apical view and early teleoconch in lateral view. **(A7)** Openly coiled, smooth protoconch and early teleoconch. **(B)** From Bandel and Frýda 1999, pl. 2, figs 6, 8, Pennsylvanian Labette Shale, Saint Louis, Missouri, USA. **(B1)** lateral view, openly coiled protoconch well visible. **(B2)** Openly coiled protoconch well visible including initial bulb, straight and coiled parts followed by early teleoconch with so-marginal ribbing.

resents the embryonic shell as was also concluded by Bandel and Frýda (1999), Frýda et al. (2008b), and Frýda (2012). Its small size of 100–120 µm × 70 µm suggests indirect, planktotrophic larval development. The question is at which stage the larval shell terminates and the teleoconch starts. Knight (1934) for the first time reported and described this type of protoconch and noticed its morphology which is unusual for gastropods ('curious vermiform nuclei'). He described the 'nucleus' as a narrow vermiform hook of one smooth revolution. The abrupt expansion of the shell which then bears co-marginal ribs was called by him 'neanic' i. e., as representing the early juvenile teleoconch. By contrast, based on

the restudy of Knight's (1934) material from the Labette Shale, Bandel and Frýda (1999) and Frýda (2012) assumed that the axially ribbed part following the smooth hook-like shells belongs to the larval shell. Here, we follow Knight's (1934) interpretation because the smooth shell terminates abruptly and the size of the following axially ribbed portion of the shell (here Fig. 12 IV) has a width of ca. 2 mm at its termination which is too large for a larval shell. Hence the larval shell of *O. parva* comprises portions I–III as given in Fig. 12.

The change from a straight narrow tube to a coiled tube (Fig. 12 II to III) is readily explained: it would be highly disadvantageous for the pediveliger to settle with an entirely





**Figure 12.** *Orthonychia parva* (Swallow, 1858 in Shumard and Swallow), SNSB-BSPG 2020 XCI 117, juvenile specimen with uncoiled, hook-like protoconch (same as Fig. 9A4); Late Pennsylvanian Finis Shale Member, Graham Formation, North-central Texas. I–III smooth protoconch consisting of initial bulb formed within the egg (I), straight part of larval shell (II) coiled part of larval shell (III) first portion of teleoconch with strong ribbing (IV) second portion of teleoconch with rapidly widening (V).

straight narrow tube (stretched, uncoiled shell tube would probably be vulnerable and hinder locomotion) and therefore coiling in the last period of larval life does make sense as a preparation for benthic life. The early axially ribbed teleoconch was probably formed by the crawling juvenile and the sudden widening of the shell could indicate the start of the sedentary life on crinoids.

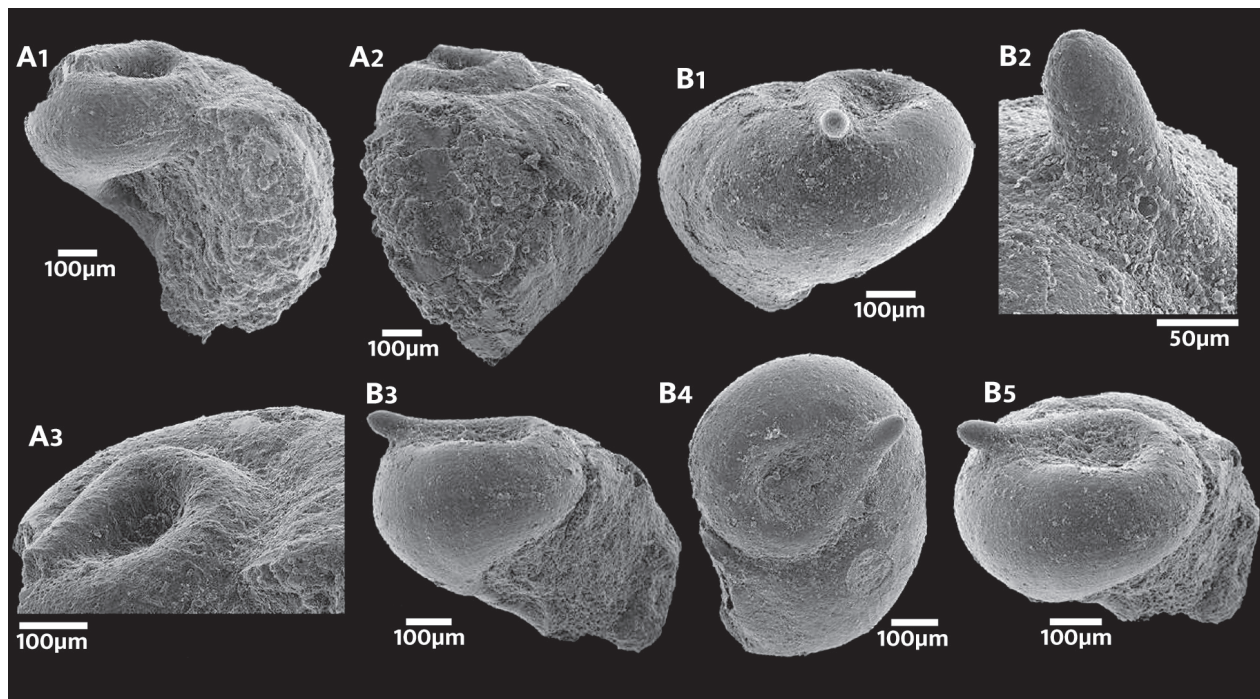
### *Orthonychia* sp.

Fig. 13A, B

**Material.** Two specimens from the Upper Mississippian (Chesterian) Imo Formation, Arkansas (SNSB-BSPG 2023 I 89, SNSB-BSPG 2023 I 90). The material was sampled by R. H. Mapes (ARC-02, samples Imo-6 and Imo-8.) at the Location #1 as given by Jeffery et al. (1994), figs 1 and 2). This location, the Peyton Creek Roadcut, was also described in detail by Manger (1977) who measured a section in the outcrop (Manger 1977, fig. 1). The sample Imo-6 sample came from position 20 in this section, approximately 110 feet above the base of his measured section and the Imo-8 sample came from position 24, which is about 135 feet above the base of his measured section. NE1/4 sec. 11 and NW1/4 sec. 12, T. 13 N., R. 15 W. Van Buren County, Arkansas

**Description.** Juvenile shell 0.66 mm wide, 0.52 mm high; shell starts with a slightly elongated initial bulb with a length of 87 μm and a width of 63 μm; width of shell at shell length 100 μm is 66–68 μm; initial bulb is bent slightly apically in relation to the following straight shell-tube; following shell is an entirely straight, smooth tube that increases slowly in diameter. At a total shell length of 320 μm the tube starts a sharp coiling in a dextral direction and at the same time, it is strongly expanding in diameter; shell is smooth except of a faint micro-striation visible on the coiled part of the first whorl.

**Remarks.** We suppose that approximately the first openly coiled whorl represents the larval shell and that the faint micro-striation is the larval shell ornament. The protoconch of this species resembles the above described



**Figure 13.** *Orthonychia* sp., with openly coiled larval shell; Mississippian (Chesterian) Imo Formation, Arkansas, USA. (A) SNSB-BSPG 2023 I 89. (A1) Apertural view. (A2) Lateral view. (A3) Oblique lateral view on openly coiled protoconch. (B) SNSB-BSPG 2023 I 90. (B1) Lateral view. (B2) Detail initial bulb of protoconch. (B3) Apertural view. (B4) Apical view. (B5) Oblique lateral view.

*Orthonychia parva* by having an initial bulb, representing most likely the embryonic shell (protoconch 1) and a following straight tube. However, the early shell of *Orthonychia* sp. lacks any strong co-marginal ribs or frills. Among the gastropod species described from the Imo Formation by Jeffery et al. (1994), *Platyceras* (*Orthonychia*?) sp. is the most likely candidate to be conspecific with the two juvenile specimens studied herein. They reported a single specimen from their rich collections and thus the species is very rare in this fauna.

## Discussion

With this contribution, more evidence has been provided that openly coiled and tightly coiled protoconchs occur in platycerate gastropods as was already illustrated by Yochelson (1956), noted by Yochelson (1969), and shown by Frýda et al. (2009). If openly coiled protoconchs are diagnostic on family (Platyceratidae and Orthonychiidae) or higher (order Cyrtoneritimorpha) systematic levels, then these taxa would be probably polyphyletic in their current composition (i. e., species with tightly coiled protoconch would have to be removed). Previously, Karapınar et al. (2022b) argued against placing *Orthonychia* and *Platyceras* in distinct families or orders, because the protoconch of *Platyceras* has not been documented yet. Openly coiled and tightly coiled protoconchs are also present in other clades such as Paleozoic Caenogastropoda (Nützel et al. 2000; Nützel and Cook 2005), and Euomphaloidea (Bandel and Frýda 1998; Nützel 2002). The gradual decline of gastropods with openly coiled protoconchs during the Paleozoic and the absence of openly coiled protoconchs in extant gastropods (except of some holoplanktonic species) was described and quantified by Nützel and Frýda (2003) who interpreted this decline as a trend driven by increasing predation pressure in the plankton that selected against this probably vulnerable larval shell morphology. According to the meaning of the openly coiled protoconch morphology for phylogeny and systematics, these authors formulated two hypotheses:

- 1) Paleozoic gastropod clades with openly coiled protoconchs became extinct selectively during the Paleozoic and all modern gastropods are exclusively descendants of Paleozoic gastropods that had tightly coiled protoconchs.
- 2) Openly coiled protoconchs were present in the stem lines of most extant gastropod clades, but were differentially lost across major clades.

Given our new data and the current state of knowledge, we favor the second hypothesis: the trend against the openly coiled protoconch morphology persisted within various gastropod clades including platycerates. If true, Cyrtoneritimorpha and Cycloneritimorpha are synonyms of Neritimorpha.

Regarding the systematic placement of platycerate gastropods it is crucial to infer whether they contained species with planktotrophic larval development or not because extant members of basal gastropod clades such as Patellogastropoda, Neomphaliones, and Vetigastropoda obligatorily lack planktotrophic larval development (Bandel 1982; Haszprunar et al. 1995; Nützel 2014). As mentioned, the tightly coiled protoconch with up to more than two whorls and a small initial whorl reported for *Orthonychia enorme* herein is clearly unlike those in the mentioned basal gastropod clades and reflect larval planktotrophy. In gastropods with tightly coiled protoconchs, small initial whorls and a high number of protoconch whorl are diagnostic for larval planktotrophy (Nützel 2014). However, this does not work for openly coiled protoconchs and for protoconch steinkerns from micro-samples. Nützel et al. (2006, 2007a) introduced a method to overcome this problem: the measurement of the width of the shell at a length of 100  $\mu\text{m}$  (measured from the zenith of the initial cap). This measurement serves as a proxy for the size of the embryonic shell, thus also for egg size and thus the amount of yolk. The smaller this value is, the higher is the likelihood that the measured shell was produced by a planktotrophic larva. Conversely, if the shell is very wide at a shell length of 100  $\mu\text{m}$ , non-planktotrophy is likely. Table 2 shows values for eight platycerate species from the Silurian and Carboniferous and six values for Carboniferous Euomphaloidea - in both groups tightly and openly coiled protoconchs were measured (see Fig. 14 for two examples of Carboniferous euomphaloid species with well well-preserved protoconchs). The results show that the measured platycerates have much smaller values than Euomphaloidea (Tables 2, 3). The protoconchs of well-preserved Euomphaloidea consist of slightly less than one whorl (in species with tightly coiled protoconchs) and the shell is much wider at a shell length of 100  $\mu\text{m}$ ; this suggests non-planktotrophic early ontogeny like that of extant members of basal gastropod clades (see also Nützel 2002).

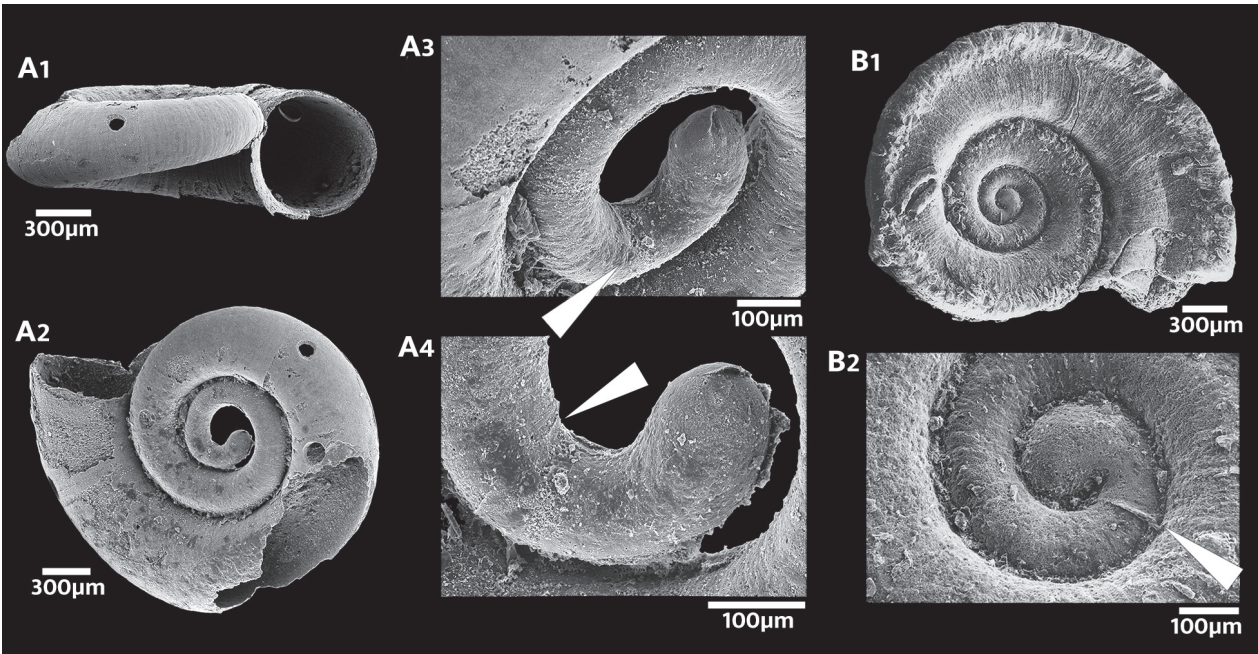
The shell width at 100  $\mu\text{m}$  shell length of the investigated platycerate specimens are relatively small and are in the range of Ordovician/Silurian protoconch steinkerns from conodont samples measured by Nützel et al. (2006) that were interpreted as larval fall out communities of planktotrophic larvae. Besides these measurements, the protoconch morphology, as discussed in the systematic section, also supports the assumption of larval planktotrophy for the studied platycerate species.

The presence of larval planktotrophy shows that platycerates do not belong to Patellogastropoda and Vetigastropoda (extant members lack planktotrophic larval development), or Euomphaloidea as was previously assumed (e. g., Wenz 1938; Knight et al. 1960; Ponder and Lindberg 1997; Wagner 2002). The assumption that platycerates are Neritimorpha (Knight 1934; Bandel 1992; Bandel and Frýda 1999; Frýda et al. 2009) is corroborated herein by our new protoconch data. The Neritimorpha-hypothesis is also supported by the pres-



**Table 2.** Shell width at 100 µm shell length of the investigated platycerate and euomphaloid specimens, measured from SEM-images. The values for platycerates are much smaller indicating larval planktotrophy.

	Width at 100 µm shell length	Protoconch coiling	Age	Country	Specimen
<b>Platyceratoids</b>					
<i>Orthonychia enorme</i>	82 µm	tight	Silurian	Sweden	SNSB-BSPG 2023 X 6
<i>Orthonychia enorme</i>	80 µm	tight	Silurian	Sweden	SNSB-BSPG 2023 X 13
<i>Orthonychia parva</i>	71 µm	open	Pennsylvanian	USA	SNSB-BSPG 2020 XCI 117
<i>Orthonychia parva</i>	74 µm	open	Pennsylvanian	USA	SNSB-BSPG 2020 XCI 119
<i>Orthonychia parva</i>	82 µm	open	Pennsylvanian	USA	Bandel and Frýda (1999)
<i>Orthonychia parva</i>	76 µm	open	Pennsylvanian	USA	Bandel and Frýda (1999)
<i>Orthonychia</i> sp.	68 µm	open	Mississippian	USA	SNSB-BSPG 2023 I 89
<i>Orthonychia</i> sp.	66 µm	open	Mississippian	USA	SNSB-BSPG 2023 I 90
<b>Euomphaloids</b>					
<i>Euomphalus</i> sp.	136 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 91
<i>Euomphalus</i> sp.	117 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 92
<i>Euomphalus</i> sp.	150 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 93
<i>Amphiscapha catilloides</i>	160 µm	tight	Pennsylvanian	USA	SNSB-BSPG 2023 I 88
<i>Amphiscapha</i> sp.	147 µm	tight	Mississippian	USA	SNSB-BSPG 2023 I 94
<i>Euomphalus</i> sp.	127 µm	open	Mississippian	Australia	SNSB-BSPG 2023 I 87



**Figure 14.** Carboniferous euomphaloids with preserved protoconch (one openly coiled (A), one tightly coiled (B)) reflecting non-planktotrophic early ontogeny. (A) *Euomphalus* sp. SNSB-BSPG 2023 I 87, Locality 28 (Marohn) of Yoo (1994): Scone 1:25,000, GR 084544. Bioclastic limestone in the upper part of the Dangarfield Formation, 150 m west of ‘Marohn’ homestead, 4 km south-west of Gundy, Early Carboniferous, Tournaisian. (A1) Apertural view. (A2) Umbilical view. (A3, A4) Detail of openly coiled initial whorl; arrows mark end of protoconch. (B) *Amphiscapha catilloides* (Conrad, 1842), SNSB-BSPG 2023 I 88, Graham Formation, Finis Shale Member, Pennsylvanian, Texas, USA. (B1) Umbilical view. (B2) Protoconch of less than one whorl, demarcated by a ledge (arrow).

ence of a calcitic teleoconch and by the neritoid shape of many platycerates. Modern marine Neritimorpha have a characteristic highly convolute larval shell (e. g., Robertson 1971; Bandel 1982; Nützel et al. 2007b). However, Paleozoic forms have a larval shell that is similar to those present in Caenogastropoda (Nützel and Mapes 2001; Nützel et al. 2007b). In limpets with a tightly coiled larval shell, such as the Devonian *Pragoscutula* Frýda, 1998a and the Mississippian *Australoscutula* Cook, Nützel & Frýda, 2008, a decision as to whether they belong to Neritimorpha or Caenogastropoda re-

mains difficult. It is possible that these taxa also belong to platycerate gastropods.

**Table 3.** Average and range of shell width at 100 µm shell length of the investigated platycerate and euomphaloid specimens. The values for platycerates are much smaller indicating larval planktotrophy.

	Average	Range	Stdv.	n
Platyceratoids	75 µm	66–82 µm	6.2	8
Euomphaloids	140 µm	117–160 µm	15.9	6

## Conclusions

Based on the data presented here and previous publications (mainly Bandel and Frýda 1999; Frýda et al. 2009) we conclude the following:

- We are reporting the oldest well-preserved *Orthonychia* species from the Late Ordovician.
- In each, *Platyceras*- and *Orthonychia*-like gastropods, openly coiled and tightly coiled protoconchs occur.
- Thus, either both groups or genera are polyphyletic or openly coiled and tightly coiled protoconchs occur in closely related taxa; in the latter case, the order Cyrtoneritimorpha that was based on the presence of an openly coiled protoconch cannot be maintained. We suggest to treat Cyrtoneritimorpha and Cycloneritimorpha as synonyms of Neritimorpha as was previously suspected by Karapınar et al. (2022b).
- The monotypic Devonian genus *Pragoserpulina* and family Pragoserpulidae are morphological so close to the *Orthonychia* species reported herein that synonymy of both genera seems to be possible.
- Morphology and dimensions of the known protoconchs of *Platyceras*- and *Orthonychia*-like gastropods suggest that they had planktotrophic veliger larvae. These protoconchs are unlike those of Vetigastropoda, Patellogastropoda, and Euomphalina which all have obligatory non-planktotrophic early ontogeny with a protoconch consisting of ca. one whorl.
- By contrast, the protoconch of *Orthonychia enorme* has distinctly more than one whorl (up to ca. 2) and that of *Orthonychia parva* has a small initial bulb (hatchling) followed by a much longer, elongated larval shell; both protoconchs reflect larval planktotrophy.
- The protoconch of *Orthonychia enorme* resembles that of Naticopsidae and those of some caenogastropods.
- The morphology of tightly coiled protoconchs, the teleoconch morphology of genera like *Platyceras* and the presence of a calcitic shell suggest that *Platyceras*- and *Orthonychia*-like gastropods belong to Neritimorpha and are probably closely related to Naticopsidae.

## Acknowledgements

We thank Andrzej Kaim and Baran Karapınar for their helpful reviews. AN acknowledges financial support from the Deutsche Forschungsgemeinschaft (DFG, project-number NU 96/10–1, 2). Yutaro Suzuki kindly made material from the Boda Limestone available for study. BS thanks the Dallas Paleontological Society as they were massively helping during field work to collect Finis Shale

material. BS acknowledges financial support from the Deutsche Forschungsgemeinschaft (DFG, project-number SE2283/2-1).

## References

- Angelin NP, Lindström G (1880) *Fragmenta Silurica e dono Caroli Henrici Wegelin*. Samson & Wallin, Stockholm, 60 pp.
- Bandel K (1982) Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken. *Facies* 7: 1–198. <https://doi.org/10.1007/BF02537225>
- Bandel K (1992) Platyceratidae from the Triassic St. Cassian Formation and the evolutionary history of the Neritimorpha (Gastropoda). *Paläontologische Zeitschrift* 66: 231–240. <https://doi.org/10.1007/BF02985816>
- Bandel K (2002a) About Heterostropha (Gastropoda) from the Carboniferous and Permian. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 86: 45–80.
- Bandel K (2002b) Reevaluation and classification of Carboniferous and Permian Gastropoda belonging to the Caenogastropoda and their relation. *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 86: 81–188.
- Bandel K, Frýda J (1998) The systematic position of the Euomphalidae. *Senckenbergiana lethaea* 78: 103–131. <https://doi.org/10.1007/BF03042762>
- Bandel K, Frýda J (1999) Notes on the evolution and higher classification of the subclass Neritimorpha (Gastropoda) with the description of some new taxa. *Geologica et Palaeontologica* 33: 219–235.
- Batten RL (1984) The calcitic wall in the Paleozoic families Euomphalidae and Platyceratidae (Archaeogastropoda). *Journal of Paleontology* 58: 1186–1192.
- Baumiller TK, Gahn FJ (2002) Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid–crinoid interaction. In: Kowalewski M, Kelley PH (Eds) *The Fossil Record of Predation*. The Paleontological Society Papers 8: 195–209. <https://doi.org/10.1017/S1089332600001091>
- Blodgett RB, Frýda J (1999) New Devonian gastropod genera important for paleogeographic reconstructions. *Journal of the Czech Geological Society* 44: 293–308.
- Blodgett RB, Rohr DM, Boucot AJ (1988) Lower Devonian gastropod biogeography of the western hemisphere. In: McMillan NJ, Embry AF, Glass DJ (Eds) *Devonian of the world. Proceedings of the second international symposium on the Devonian system*, Calgary, Canada. Canadian Society of Petroleum Geologists, Calgary, Alberta, Canada, 281–294.
- Bouchet P, Frýda J, Hausdorf B, Ponder WF, Valdés Á, Warén A (2005) Working classification of the Gastropoda. In: Bouchet P, Rocroi J–P (Eds) *Classification and nomenclator of gastropod families*. *Malacologia* 47: 1–397.
- Bouchet P, Rocroi J–P, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61: 1–526. <https://doi.org/10.4002/040.061.0201>
- Boucot AW, Yochelson EL (1966) Paleozoic Gastropoda from the Moose River Synclinorium, Northern Maine. *Geological Survey Professional Paper* 503-A: 1–20. <https://doi.org/10.3133/pp503A>



- Calner M, Jeppsson L, Munneke A (2004) The Silurian of Gotland – Part 1: Review of the stratigraphic framework, event stratigraphy, and stable carbon and oxygen isotope development. *Erlanger Geologische Abhandlungen – Sonderband 5, Field Guide*, 113–131.
- Calner M (2008) Silurian global events – at the tipping point of climate change. In: Elewa AMT (Ed.) *Mass extinctions*. Springer, Berlin and Heidelberg, 21–58. [https://doi.org/10.1007/978-3-540-75916-4\\_4](https://doi.org/10.1007/978-3-540-75916-4_4)
- Carter JG, Hall RM (1990) Part 3. Polyplacophora, Scaphopoda, Archaeogastropoda and Paragastropoda (Mollusca). In: Carter JG (Ed.) *Skeletal biomineralization: patterns, processes and evolutionary trends*. Volume II. Atlas and index. Van Nostrand Reinhold, New York, 29–51, pls 122–134. [https://doi.org/10.1007/978-1-4899-5391-9\\_3](https://doi.org/10.1007/978-1-4899-5391-9_3)
- Conrad TA (1842) Observations on the Silurian and Devonian systems of the United States, with descriptions of new organic remains. *Journal of the Academy of Natural Sciences of Philadelphia* 8: 228–280.
- Cook A, Jell PA (2016) Carboniferous platyceratid gastropods from Western Australia and a possible alternative lifestyle adaptation. *Alcheringa* 40: 34–44. <https://doi.org/10.1080/03115518.2015.1079693>
- Cook A, Nützel A, Frýda J (2008) Two Carboniferous caenogastropod limpets from Australia and their meaning for the ancestry of the Caenogastropoda. *Journal of Paleontology* 82: 183–187. <https://doi.org/10.1666/06-028.1>
- Dattilo BF, Freeman RL, Peters WS, Heimbrock WP, Deline B, Martin AJ, Kallmeyer JW, Reeder J, Argast A (2016) Giants among micromorphs: were Cincinnati (Ordovician, Katian) small shelly phosphatic faunas dwarfed? *Palaios* 31: 55–70. <https://doi.org/10.2110/palo.2015.040>
- Dzik J (2020) Decline in diversity of early Palaeozoic loosely coiled gastropod protoconchs. *Lethaia* 53: 32–46. <https://doi.org/10.1111/let.12334>
- Ebbestad JOR (1999) Bucaniid gastropods from the Upper Ordovician of Baltica, with a discussion of the Bucaniinae. *Palaeontology* 42: 149–169. <https://doi.org/10.1111/1475-4983.00066>
- Ebbestad JOR, Höglström AES (2007) Ordovician of the Siljan district, Sweden. In: Ebbestad JOR, Wickström LM, Höglström AES (Eds) *WOGOGOB 2007. 9th meeting of the Working Group on Ordovician Geology of Baltoscandia. Field guide and Abstracts*. Sveriges geologiska undersökning Rapporter och meddelanden 128: 7–26.
- Ebbestad JOR, Peel JS (1997) Attempted predation and shell repair in middle and upper Ordovician gastropods from Sweden. *Journal of Paleontology* 71: 1007–1019. <https://doi.org/10.1017/S002233600003599X>
- Ebbestad JOR, Peel JS (2001) An unusual trochiform gastropod from the upper Ordovician of Sweden. *Palaeontology* 44: 375–387. <https://doi.org/10.1111/1475-4983.00184>
- Fletcher HO (1958) The Permian gastropods of New South Wales. *Records of the Australian Museum* 24: 115–164. <https://doi.org/10.3853/j.0067-1975.24.1958.648>
- Frýda J (1998a) Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia). *Bulletin of the Czech Geological Survey* 73: 41–49.
- Frýda J (1998b) Some new and better recognized Devonian gastropods from the Prague Basin (Bohemia): part II. *Bulletin of the Czech Geological Survey* 73: 355–363.
- Frýda J (2005) Gastropods. In: Taylor PD, Lewis DN (Eds) *Fossil invertebrates*. Harvard University Press, Cambridge, Massachusetts, 378–388. <https://doi.org/10.1016/B0-12-369396-9/00040-X>
- Frýda J (2012) Phylogeny of Palaeozoic gastropods inferred from their ontogeny. In: Talent JA (Ed.) *Earth and Life – Global biodiversity, extinction intervals and biogeographic perturbations through time*. Series: International Year of Planet Earth. Springer, New York, 395–435. [https://doi.org/10.1007/978-90-481-3428-1\\_12](https://doi.org/10.1007/978-90-481-3428-1_12)
- Frýda J, Nützel A, Wagner PJ (2008a) Paleozoic Gastropoda. In: Ponder WF, Lindberg DR (Eds) *Phylogeny and evolution of the Mollusca*. University of California Press, Berkeley, Los Angeles, London, 239–270. <https://doi.org/10.1525/california/9780520250925.003.0010>
- Frýda J, Racheboeuf PR, Frýdová B (2008b) Mode of life of early Devonian *Orthonychia protei* (Neritimorpha, Gastropoda) inferred from its post-larval shell ontogeny and muscle scars. *Bulletin of Geosciences* 83: 491–502. <https://doi.org/10.3140/bull.geosci.2008.04.491>
- Frýda J, Racheboeuf PR, Frýdová B, Ferrova L, Mergl M, Berkýová S (2009) Platyceratid gastropods - stem group of patellogastropods, neritimorphs or something else? *Bulletin of Geosciences* 84: 107–120. <https://doi.org/10.3140/bull.geosci.1125>
- Gubanov AP, Ebbestad JOR, Bogolepova OK (1999) Microfossil assemblage of the Boda Limestone (Upper Ordovician, Sweden). *Acta Universitatis Carolinae Geologica* 43: 421–423.
- Hall J (1843) *Geology of New York, Part 4. Comprising the survey of the fourth geological district*. Carroll and Cook, Albany, 683 pp.
- Hall J (1859) Contributions to the palaeontology of New-York; being some results of investigations made during the years 1855, '56, '57, & '58: Twelfth Annual Report of the Regents of the University of the State of New-York, on the Condition of the State Cabinet of Natural History, and the Historical and Antiquarian Collection Connected therewith, State of New York in Assembly Document 186, C. van Benthuyssen, Albany, 8–110.
- Hall J (1879) *Natural history of New York. Geological Survey of New York. Palaeontology. vol. 5, part 2*. Van Benthuyssen, Albany, [xv +] 492 pp., [113 pls.]
- Haszprunar G, Salvini-Plawen L von, Rieger RM (1995) Larval planktotrophy - a primitive trait in the Bilateria? *Acta Zoologica* 76: 141–154. <https://doi.org/10.1111/j.1463-6395.1995.tb00988.x>
- Hede JE (1960) The Silurian of Gotland. In: Regnéll G, Hede JE (Eds) *The Lower Palaeozoic of Scania. The Silurian of Gotland, Guide to excursions A22 and C17, 21st International Geological Congress Norden*, 44–89.
- Hoare RD, Heaney MJ, Mapes RH (1989) Bivalves (Mollusca) from the Imo Formation (Mississippian, Chesterian) of North-Central Arkansas. *Journal of Paleontology* 63: 582–603. <https://doi.org/10.1017/S0022336000041226>
- Jeffery DL, Hoare RD, Mapes RH, Brown CJ (1994) Gastropods (Mollusca) from the Imo Formation (Mississippian, Chesterian) of North-Central Arkansas. *Journal of Paleontology* 68: 58–79. <https://doi.org/10.1017/S0022336000025609>
- Jeppsson L (1994) A new standard Wenlock conodont zonation. *Berichte der Geologischen Bundesanstalt* 30: 133.
- Jeppsson L (2005) Conodont-based revisions of the Late Ludfordian on Conodont-based revisions of the late Ludfordian on Gotland, Sweden. *GFF* 127: 273–282. <https://doi.org/10.1080/11035890501274273>

- Jeppsson L, Eriksson ME, Calner M (2006) A latest Llandovery to latest Ludlow high-resolution biostratigraphy based on the Silurian of Gotland – a summary. *GFF* 128: 109–114. <https://doi.org/10.1080/11035890601282109>
- Kaim A (2004) The evolution of conch ontogeny in Mesozoic open sea gastropods. *Palaeontologia Polonica* 62: 1–182.
- Kaim A, Sztajner P (2005) The opercula of neritopsid gastropods and their phylogenetic importance. *Journal of Molluscan Studies* 71: 211–219. <https://doi.org/10.1093/mollus/eyi029>
- Karapınar B, Nützel A, Seuss B, Mapes RH (2022a) Taxonomy and diversity of slit-band gastropods (order Pleurotomariida) from the Pennsylvanian of the U.S.A. *Papers in Palaeontology* e1417: 1–95. <https://doi.org/10.1002/spp2.1417>
- Karapınar B, Nützel A, Ketwetsuriya C (2022b) A low-diversity *Peruvispira*-dominated gastropod assemblage from the Permian Ratburi Group of Central Thailand. *Alcheringa* 46: 147–155. <https://doi.org/10.1080/03115518.2022.2050814>
- Keyes CR (1894) Paleontology of Missouri. *Missouri Geological Survey* 5: 1–266. <https://doi.org/10.5962/bhl.title.30736>
- Knight JB (1934) The gastropods of the St. Louis, Missouri, Pennsylvanian outlier: The Euomphalidae and Platyceratidae. *Journal of Paleontology* 8: 139–166.
- Knight JB (1941) Palaeozoic gastropod genotypes. *Geological Society of America Special Papers* 32: 1–510. <https://doi.org/10.1130/SPE32-p1>
- Knight JB, Cox LR, Keen AM, Batten RL, Yochelson EL, Robertson R (1960) Systematic descriptions. In: Moore RC (Ed.) *Treatise on invertebrate paleontology, Part 1, Mollusca 1*. Geological Society of America and University of Kansas Press, Kansas, 1169–1310.
- Koken E (1896) Die Gastropoden der Trias um Hallstadt. *Jahrbuch der kaiserlich-königlichen geologischen Reichsanstalt* 46: 37–126.
- Koken E (1897) Die Gastropoden des baltischen Untersilurs. *Bulletin de l'Académie Impériale des Sciences de St Petersburg* 7: 97–214.
- Koken E, Perner J (1925) Die Gastropoden des Baltischen Untersilurs. *Mémoires de l'Académie des Sciences de Russie* 37: 1–326.
- Kröger B, Ebbestad JOR, Lehnert O (2016) Accretionary mechanisms and temporal sequence of formation of the Boda Limestone mud-mounds (Upper Ordovician), Siljan District, Sweden. *Journal of Sedimentary Research* 86: 363–379. <https://doi.org/10.2110/jsr.2016.12>
- Lindström A (2003) Shell breakage in two pleurotomarioid gastropods from the Upper Carboniferous of Texas, and its relation to shell morphology. *GFF* 125: 39–46. <https://doi.org/10.1080/11035890301251039>
- Lindström G (1884) On the Silurian Gastropoda and Pteropoda of Gotland. *Kongliga Svenska Vetenskaps-Akademiens Handlingar* 19: 1–250. <https://doi.org/10.5962/bhl.title.11879>
- Manger WL (1977) Stop descriptions - first day. In: Sutherland PK, Manger WL (Eds) *Upper Chesterian-Morrowan stratigraphy and the Mississippian-Pennsylvanian boundary in northeastern Oklahoma and northwestern Arkansas. Guidebook for Field Trip No. 5, August 5–7, 1977, preceding North American Paleontological Convention II- Oklahoma*; 11–17. *Geologica/Survey Guidebook* 18. The University of Oklahoma Norman, Norman.
- Manten AA (1971) Silurian Reefs of Gotland. *Developments in Sedimentology* 13: 1–539.
- Nützel A (1998) Über die Stammesgeschichte der Ptenoglossa (Gastropoda). *Berliner Geowissenschaftliche Abhandlungen, Reihe E* 26: 1–229.
- Nützel A (2002) An evaluation of the recently proposed Palaeozoic gastropod subclass Euomphalomorpha. *Palaeontology* 45: 259–266. <https://doi.org/10.1111/1475-4983.00236>
- Nützel A (2014) Larval ecology and morphology in fossil gastropods. *Palaeontology* 57: 479–503. <https://doi.org/10.1111/pala.12104>
- Nützel A, Cook AG (2002) *Chlorozyga*, a new caenogastropod genus from the Early Carboniferous of Australia. *Alcheringa* 26: 151–157. <https://doi.org/10.1080/03115510208619249>
- Nützel A, Frýda J (2003) Paleozoic plankton revolution: Evidence from early gastropod ontogeny. *Geology*: 829–831. <https://doi.org/10.1130/G19616.1>
- Nützel A, Mapes RH (2001) Larval and juvenile gastropods from a Mississippian black shale: Paleoeology, and implications for the evolution of the Gastropoda. *Lethaia* 34: 143–162. <https://doi.org/10.1080/00241160152418447>
- Nützel A, Nakazawa (2012) Permian (Capitanian) gastropods from the Akasaka Limestone (Gifu Prefecture, Japan). *Journal of Systematic Palaeontology* 10: 103–169. <https://doi.org/10.1080/14772019.2010.549659>
- Nützel A, Pan H-z (2005) Late Paleozoic evolution of the Caenogastropoda: larval shell morphology and implications for the Permian/Triassic mass extinction event. *Journal of Paleontology* 79: 1175–1188. [https://doi.org/10.1666/0022-3360\(2005\)079\[1175:LPEOTC\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2005)079[1175:LPEOTC]2.0.CO;2)
- Nützel A, Mapes RH (2001) Larval and juvenile gastropods from a Mississippian black shale: Paleoeology, and implications for the evolution of the Gastropoda. *Lethaia* 34: 143–162. <https://doi.org/10.1080/00241160152418447>
- Nützel A, Erwin DH, Mapes RH (2000) Identity and phylogeny of the late Paleozoic Subulitoidea (Gastropoda). *Journal of Paleontology* 74: 575–598. [https://doi.org/10.1666/0022-3360\(2000\)074%3C0575:IAPOTL%3E2.0.CO;2](https://doi.org/10.1666/0022-3360(2000)074%3C0575:IAPOTL%3E2.0.CO;2)
- Nützel A, Lehnert O, Frýda J (2006) Origin of planktotrophy - evidence from early molluscs. *Evolution and Development* 8: 325–330. <https://doi.org/10.1111/j.1525-142X.2006.00105.x>
- Nützel A, Lehnert O, Frýda J (2007a) Origin of planktotrophy - evidence from early molluscs: a response to Freeman and Lundelius. *Evolution and Development* 9: 313–318. <https://doi.org/10.1111/j.1525-142X.2007.00166.x>
- Nützel A, Frýda J, Yancey TE, Anderson JR (2007b) Larval shells of Late Palaeozoic naticopsid gastropods (Neritopsoidea: Neritimorpha) with a discussion of the early neritimorph evolution. *Paläontologische Zeitschrift* 81: 213–228. <https://doi.org/10.1007/BF02990173>
- Peel JS (2020a) Muscle scars, mode of life and systematics of *Pollicina* (Mollusca) from the Ordovician of Baltica. *Estonian Journal of Earth Sciences* 69: 20–36. <https://doi.org/10.3176/earth.2020.02>
- Peel JS (2020b) The Dala thumb: shell morphology and failed predation in *Pollicina cyathina* (Gastropoda) from the Ordovician of Dalarna, Sweden. *GFF* 142: 139–146. <https://doi.org/10.1080/11035897.2020.1728374>
- Peel JS, Yochelson EL (1976) Two new gastropod genera from the Lower Silurian of the Oslo Region, Norway. *Norsk Geologisk Tidsskrift* 56: 15–27.



- Plummer FB, Moore RC (1921) Stratigraphy of the Pennsylvanian formations of north-central Texas. Texas University Bulletin 2132: 1–237.
- Ponder WF, Lindberg DR (1997) Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zoological Journal of the Linnean Society 119: 83–265. <https://doi.org/10.1111/j.1096-3642.1997.tb00137.x>
- Robertson R (1971) Scanning electron microscopy of planktonic larval marine gastropod shells. The Veliger 14: 1–12.
- Rohr DM, Boucot AJ, Perry DG (1981) Silurian (Wenlockian) gastropods from Baillie-Hamilton Island, Canadian Arctic. Journal of Paleontology 55: 331–339.
- Rollins HB, Brezinski DK (1988) Reinterpretation of crinoid-platyceratid interaction. Lethaia 21: 207–217. <https://doi.org/10.1111/j.1502-3931.1988.tb02072.x>
- Samtleben C, Munnecke A, Bickert T, Pätzold J (1996) The Silurian of Gotland (Sweden): facies interpretation based on stable isotopes in brachiopod shells. Geologische Rundschau 85: 278–292. <https://doi.org/10.1007/BF02422234>
- Samtleben C, Munnecke A, Bickert T (2000) Development of facies and C/O isotopes in transects through the Ludlow of Gotland: Evidence for global and local influences on a shallow-marine environment. Facies 43: 1–38. <https://doi.org/10.1007/BF02536983>
- Schugmann G (2015) Bildung onkoidischer Kalke in der Eke-Formation von Bodudd. Master thesis, Friedrich-Alexander Universität Erlangen-Nürnberg, 146 pp.
- Seuss B, Nützel A, Scholz H, Frýda J (2012) The Paleozoic evolution of the gastropod larval shell: larval armor and tight coiling as a result of predation-driven heterochronic character displacement. Evolution and Development 14: 212–228. <https://doi.org/10.1111/j.1525-142X.2012.00536.x>
- Shumard BF, Swallow GC (1858) Descriptions of new fossils from the Coal Measures of Missouri and Kansas. Transactions of the Academy of Science of St. Louis 1: 198–227.
- Sutton MD, Briggs DEG, Siveter DJ, Siveter DJ (2006) Fossilized soft tissues in a Silurian platyceratid gastropod. Proceedings of the Royal Society B 273: 1039–1044. <https://doi.org/10.1098/rspb.2005.3403>
- Suzuki Y, Bergström J (1999) Trilobite taphonomy and ecology in Upper Ordovician carbonate buildups in Dalarna, Sweden. Lethaia 32: 195–172. <https://doi.org/10.1111/j.1502-3931.1999.tb00536.x>
- Thorslund P (1936) Siljansområdet brännkalkstenar och kalkindustri. Sveriges geologiska undersökning C 398: 1–64.
- Vermeij GJ, Schindel DE, Zipser E (1981) Predation through geological time: Evidence from gastropod shell repair. Science 214: 1024–1026. <https://doi.org/10.1126/science.214.4524.1024>
- Wängberg-Eriksson K (1964) *Isospira reticulata* n. sp. from the Upper Ordovician Boda Limestone, Sweden. Geologiska Föreningens i Stockholm Förhandlingar 86: 229–237. <https://doi.org/10.1080/11035897.1964.9626376>
- Wängberg-Eriksson K (1979) Macluritacean gastropods from the Ordovician and Silurian of Sweden. Sveriges Geologiska Undersökning, Serie C 758: 1–33.
- Wagner PJ (2002) Phylogenetic relationships of the earliest anisotrophically coiled gastropods. Smithsonian Contributions to Paleobiology 88: 1–152. <https://doi.org/10.5479/si.00810266.88.1>
- Wenz W (1938–1944) Gastropoda. Teil I: Allgemeiner Teil und Prosobranchia. In: Schindewolf OH (Ed.) Handbuch der Paläozoologie, Band 6, Bornträger, Berlin, [xii +] 1639 pp.
- Yochelson EL (1956) Permian Gastropoda of the southwestern United States. 1. Euomphalacea, Trochonematacea, Anomphalacea, Craspedostomatacea, and Platyceratacea. Bulletin of the American Museum of Natural History 110: 179–275.
- Yochelson EL (1969) Revision of some of Girty's invertebrate fossils from the Fayetteville Shale (Mississippian) of Arkansas and Oklahoma. Gastropods. United States Geological Survey Professional Paper 606-0: 25–33.
- Yochelson EL, Kriz J (1974) Platyceratid gastropods from the Oriskany Sandstone (Lower Devonian) near Cumberland, Maryland: synonymies preservation and color markings. Journal of Paleontology 48: 474–483.
- Yochelson EL, Saunders BW (1967) A bibliographic index of North American Late Paleozoic Hyolitha, Amphineura, Scaphopoda, and Gastropoda. Geological Survey Bulletin 1210: 1–271.
- Yoo EK (1994) Early Carboniferous Gastropoda from the Tamworth Belt, New South Wales, Australia. Records of the Australian Museum 46: 63–110. <https://doi.org/10.3853/j.0067-1975.46.1994.18>