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# Goniasmidae and Orthonemidae: two new families of the Palaeozoic Caenogastropoda (Mollusca, Gastropoda)

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With 3 figures

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**Abstract:** Two families of late Palaeozoic caenogastropods (Cerithimorpha) are newly introduced: Goniasmidae and Orthonemidae. They comprise high-spired gastropods with a protoconch morphology distinctly different from that of other Palaeozoic gastropods and similar to that of some modern Cerithioidea. The genera of the Palaeozoic Cerithimorpha were formerly included in the families Murchisoniidae, Acanthonematidae, and Turritellidae. However, *Murchisonia* is not a caenogastropod but an archaeogastropod as is indicated by its protoconch morphology. The family Acanthonematidae is based on the unsufficiently known, problematic Devonian genus *Acanthonema*. The Turritellidae represent a modern group which originates in the late Mesozoic.

**Zusammenfassung:** Die zwei neuen spätpaläozoischen Familien Goniasmidae und Orthonemidae werden benannt. Sie umfassen hochturmförmige Caenogastropoden, deren Protoconch sich von den Protoconchen anderer paläozoischer Caenogastropoden deutlich unterscheidet. Der Protoconch der Goniasmidae und Orthonemidae ist weitgehend glatt, umfasst bis zu drei gerundete Windungen und ist von heliciformer Gestalt. Dieser Protoconchtyp ähnelt dem mancher moderner Cerithioidea; daher werden die beiden neuen Familien in die Ordnung Cerithimorpha gestellt. Die Goniasmidae besitzen einen Sinus oder Schlitz in der Außenlippe des Teleoconchs, während die Außenlippe der Orthonemidae mehr oder weniger gerade verläuft. Die Gattungen der Goniasmidae, *Goniasma, Stegocoelia* und *Cerithioides*, wurden bisher den Murchisoniidae zugeordnet. *Murchisonia* besitzt jedoch einen Protoconch, der typisch für die Unterklasse Archaeogastropoda ist. Die Familie Orthonemidae enthält die Gattungen *Orthonema, Metorthonema Knightella, Palaeostylus* und *Spiromphalus*. *Orthonema* wurde bisher entweder der Familie Turritellidae oder der Familie Acanthonematidae zugeordnet. Die Turritellidae sind eine moderne,

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abgeleitete Gruppe, die erst seit dem späten Mesozoikum bekannt ist. Die Acanthonematidae basieren auf der unzureichend bekannten devonischen Gattung *Acanthonema*, deren Typusart sich von den Arten der Gattung *Orthonema* deutlich unterscheidet. *Acanthonema* gehört möglicherweise noch nicht einmal der Unterklasse Caenogastropoda an.

## Introduction

It is widely assumed that the subclass Caenogastropoda was already present in the Palaeozoic (e.g. KNIGHT et al. 1960). However, the composition of the Palaeozoic Caenogastropoda is poorly known. Caenogastropods can be recognized by their protoconch morphology which differs from the other gastropod subclasses, i.e. the Archaeogastropoda, the Neritimorpha, and the Heterostropha (BANDEL 1982, 1997). Planktonic larval shells of the Caenogastropoda are also highly informative for their subdivision, especially since the teleoconch morphology is often homeoplastic in this group.

NÜTZEL (1998, p. 199-205, pl. 32, 33) noticed a characteristic heliciform, poorly ornamented larval shell (Fig. 1) in the late Palaeozoic genera *Cerithioides, Orthonema, Knightella*, and *Palaeostylus*. NÜTZEL (1998) grouped these and some additional genera tentatively with the Acanthonematidae WENZ, 1938 and assigned them to the Cerithimorpha because their heliciform larval shell resembles that of many modern Cerithimorpha. But the Acanthonematidae are based on the poorly known Devonian genus *Acanthonema* SHERZER & GRABAU, 1908. The type species of *Acanthonema* is known from external molds only; it is a trochoid to moderately high-spired, minutely phaneromphalous gastropod with a nodose spiral ornament (KNIGHT 1941). FRÝDA & BANDEL (1997) and FRÝDA & MANDA (1997) have since demonstrated that presumed caenogastropods like the Palaeozygopleuridae and the Loxonematidae are actually archaeogastropods. Similarly, *Acanthonema* could belong to the Archaeogastropoda. In any case, the Acanthonematidae are not a good choice for a systematic placement of *Orthonema* and *Goniasma*. In contrast to *Acanthonema*, they are slender and distinctly high-spired, have no knobby ornament and they have an anomphalous base (among the genera assigned to the Orthonemidae only *Spiromphalus* has a phaneromphalous base). The protoconch of *Acanthonema* is unknown.

The heliciform larval shell (Fig. 1) which is typical for the late Paleozoic cerithimorphs can clearly be distinguished from the larval shells of other diverse groups of caenogastropods that lived at the same time. Members of the family Pseudozygopleuridae KNIGHT, 1930 have more high-spired proto-

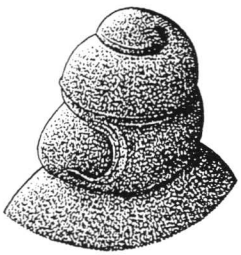

**Fig. 1.** Heliciform larval shell of *Cerithioides* sp. from the Pennsylvanian of the USA; the larval shell is largely smooth with a spiral thread and a distinct sinusigera; this typical caenogastropod larval shell is shared between species of the Goniasmidae and the Orthonemidae; it is basically similar to protoconchs of modern cerithimorphs; the protoconch is about 0.5 mm high; from NÜTZEL (1998, fig. 36).

conch with its larval portion ornamented with prominent collabral axial ribs (e.g. KNIGHT 1930, NÜTZEL 1998). The heliciform larval shell differs also from the larval shells of the late Palaeozoic Subulitoidea LINDSTRÖM, 1884 (peronal observation). In addition, the Subulitoidea differ markedly in teleoconch characters since most subulitoids have a smooth fusiform teleoconch commonly with more or less straight growth lines, and since many late Palaeozoic subulitoids have columellar folds and an anterior siphonal notch. Devonian subulitoid-like genera like *Cuchlina* and *Zenospira* have an openly coiled protoconch (FRÝDA & BANDEL 1997, FRÝDA & MANDA 1997). Therefore, they are not closely related to the late Palaeozoic cerithimorphs.

We found that all late Palaeozoic *Murchisonia*-like (Goniasmidae) and *Orthonema*-like (Orthonemidae) gastropods with known protoconchs are caenogastropods. Their protoconchs are orthostrophic and comprise more than one whorl. Commonly, the protoconchs comprise two to three whorls which are largely devoid of an ornament. These larval shells have a heliciform shape, i.e. they are trochispiral and nearly as high as wide with distinctly convex whorls. Clearly, the protoconchs of the Goniasmidae and Orthonemidae are not of the archaeogastropod type which typically consists of less than one whorl and is devoid of a larval shell built during the planktonic veliger stage (e.g. BANDEL 1982). In contrast, most of the Goniasmidae and Orthonemidae have typical planktonic larval shells with a well developed sinusigera.

*Goniasma, Cerithioides* and *Stegocoelia* (the Goniasmidae) were formerly included in the Murchisoniidae KOKEN, 1896 because they are high-spired and have a slit (e.g. KNIGHT et al. 1960). FRÝDA & MANDA (1997) reported a typical archaeogastropod protoconch comprising less than one whorl in Early and Middle Devonian species of the genus *Murchisonia* ARCHIAC & VERNEUIL, 1841. The protoconch of the Middle Devonian type species of *Murchisonia* is still unknown. Since the Goniasmidae have a caenogastropod larval shell, they are not confamiliar with or closely related to *Murchisonia*.

The genus *Orthonema* was placed in the Turritellidae LOVÉN, 1847 by KNIGHT (1934) and KNIGHT et al. (1960) and in the Acanthonematidae by WENZ (1938). *Orthonema* is certainly not confamiliar with Turritella which has a Tertiary type-species. *Turritella* comprises highly derived modern gastropods which live as infaunal filter feeders and therefore have reduced their radula. The oldest turritellid with known protoconch is *Haustator polonicus* SCHRÖDER, 1995 from the Middle Jurassic. It has an acute conical smooth larval shell with a gradual transition to the teleoconch (SCHRÖDER 1995). Even Recent species of the turritellids have an acute, high-spired larval shell (BANDEL et al. 1997, KOWALKE 1998). Previously, HOUBRICK (1988, p. 95) criticized the placement of Palaeozoic genera in the family Turritellidae. He noted that most Recent cerithioidean families appear to have arisen in the late Cretacous and early Tertiary. However, some late Triassic and Jurassic Procerithiidae are very close to modern Cerithioidea (e.g. BANDEL 1993, SCHRÖDER 1995, NÜTZEL & SENOWBARI-DARYAN 1999). BANDEL (1992, 1993, 1994) reported several Triassic caenogastropods with Cerithioidea-like protoconchs, i.e. the families Popenellidae, Settsassiidae, and Ladinulidae. Thus, the Cerithimorpha were diversfied in the early Mesozoic and it is resonable to assume that they were a distinct group in the late Palaeozoic. Among the Palaeozoic caenogastropods with known protoconch, the newly erected families Orthonemidae and Goniasmidae are closest to the post-Palaeozoic cerithimorphs.

*Orthonema* and *Goniasma* share the heliciform larval shell. Thus, the families Goniasmidae and Orthonemidae are probably closely related. Members of both families are high-spired and have a crossed lamellar shell structure (pers. observation). Moreover, *Goniasma* and *Orthonema* share a teleoconch ornament of spirals. In contrast to *Orthonema, Goniasma* has a slit - a very unusual feature for a caenogastropod. Therefore, *Orthonema* and *Goniasma* cannot be considered to belong to the same family. It is not clear whether the slit is a primitive or a derived character, but it is certainly a good character to distinguish the Goniasmidae and the Orthonemidae.

## Systematic Palaeontology

Subclass Caenogastropoda COX, 1959
Order Cerithimorpha GOLIKOV & STAROBOGATOV, 1975
Family Goniasmidae n. fam.
Genus *Goniasma* TOMLIN, 1930
Genus *Stegocoelia* DONALD, 1889
Genus *Cerithioides* HAUGHTON, 1859

Family Orthonemidae n. fam.
Genus *Orthonema* MEEK & WORTHEN, 1862
Genus *Metorthonema* ERWIN, 1988
Genus *Knightella* LONGSTAFF, 1933
Genus *Palaeostylus* MANSUY, 1914
Genus *Spiromphalus* HAYASAKA, 1939

### Goniasmidae new family

Typical genus: *Goniasma* TOMLIN, 1930
Diagnosis: High-spired gastropods with a slit or distinct sinus in the outer lip. The protoconch that comprises more than one whorl is typical for caenogastropods. Species with planktotrophic larval development have a heliciform larval shell with a well developed sinusigera. The larval shell is predominantly smooth but may have a spiral thread at the upper edge of the projection of the larval shell.

Differences: The genus *Murchisonia*, the typical genus for the family Murchisoniidae KOKEN, 1896, has a lecitotrophic protoconch of less than one whorl (FRÝDA & MANDA 1997), typical for the Archaeogastropoda (BANDEL 1982, HASZPRUNAR 1993). The Pseudozygopleuridae KNIGHT, 1930 have a larval shell with axial ribs (e.g. KNIGHT 1930, NÜTZEL 1998). The Jurassic Procerithiidae have an angulated larval shell with stronger lirae and with nodular rows (BANDEL 1992, SCHRÖDER 1995, GRÜNDEL & NÜTZEL 1998). The Soleniscidae have a conical larval shell which is devoid of major ornament (own observation).

Included genera: *Goniasma, Stegocoelia, Cerithioides.*

Remarks: The heliciform larval shell of *Goniasma* as illustrated in Figure 1 resembles that described by YOO (1994) from *Stegocoelia* DONALD, 1889 from the Tournaisian of Australia. The type species of *Stegocoelia* is from the Lower Carboniferous of Scotland and the genus comprises high-spired gastropods with prominent spiral threads or carinae. According to KNIGHT et al. (1960), *Stegocoelia* has a short slit and a selenizone above the periphery. The genus is subdivided into three intergrading subgenera: *S.* (*Stegocoelia*) DONALD, 1889, *S.* (*Taosia*) GIRTY, 1939, and *S.* (*Hypergonia*) DONALD, 1892;

all have Carboniferous type-species. *Stegocoelia* occurs at least until the middle Permian and might be related to the Late Triassic genus *Cheilotomona* STRAND, 1928 (BANDEL 1994). The *Stegocoelia* subgenera probably belong to the Goniasmidae but the protoconchs of *Hypergonia* and *Taosia* are unknown or imperfectly known. LONGSTAFF (1926) reported smooth orthostrophic protoconchs for several Carboniferous *Hypergonia* species but she did not report the teleoconch/protoconch transition which is crucial for the identification of a larval shell. In many species which have been assigned to *Stegocoelia* including the type species, a slit is barely visible. Therefore, the taxonomic importance of this character in the diagnosis of *Stegocoelia* is unclear. In the Triassic *Cheilotomona*, a slit appears only after several teleoconch whorls. YOO (1994) transferred *Stegocoelia* from the Murchisonioidea to the Loxonematoidea since he realized that the protoconch morphology of Lower Carboniferous species of *Stegocoelia* from Australia is typical for the Caenogastropoda. The placement of *Stegocoelia* in the Caenogastropoda is correct while the assignment to the Loxonematoidea is incorrect. The Loxonematoidea as previously understood represent a polyphyletic assemblage (BANDEL 1991, NÜTZEL 1998). Its Devonian families Loxonematidae and Palaeozygopleuridae are archaeogastropods (order Stylogastropoda FRÝDA & BANDEL, 1997). However, the Triassic genus *Polygyrina* KOKEN, 1892 (family Polygyrinidae BANDEL, 1991) which was formerly included in the Loxonematidae is a caenogastropod with a very characteristic larval shell (BANDEL 1991) which does not resemble the larval shell of the Goniasmidae. The protoconchs which were reported for *Stegocoelia* by YOO (1994) closely resemble the heliciform protoconch of *Goniasma* and therefore, we place *Stegocoelia* in the Goniasmidae. The heliciform larval shell of *Cerithioides* was reported by NÜTZEL (1998, see also fig. 1). Thus, *Cerithioides* with a smooth teleoconch and a distinct labral sinus does also belong here.

Genus *Goniasma* TOMLIN, 1930

Type species: *Murchisonia lasallensis* WORTHEN, 1890, Upper Carboniferous, Illinois, USA.

Diagnosis: The turriform shell has teleoconch whorls with a smooth slope above an angular periphery that bears a short slit which generates a selenizone. The teleoconch ornament consists of spiral lirae. The protoconch has a heliciform shape.

Remarks: *Goniasma* is known from several species, most of which have been reported from the Carboniferous and Permian of the USA. The oldest known species which have been assigned to the genus are from the Eifelian

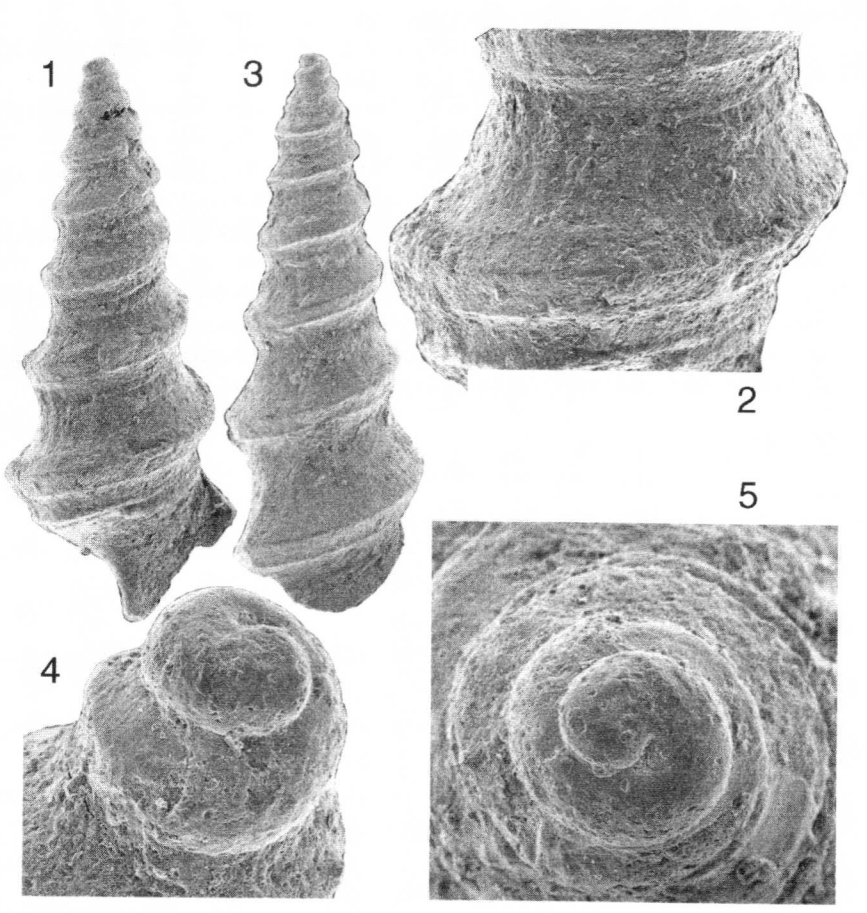


**Fig. 2.** *Goniasma lasallensis* (WORTHEN); from the Brush Creek (At-9, see HOARE & STURGEON, 1978), Pennsylvanian, Ohio, USA.
**1**: side view, apertural, height 1.3 mm. **2**: same specimen, detail of teleoconch whorl, height 1 mm. **3**: side view, abapertural, height 3.9 mm. **4**: same specimen, protoconch side view, protoconch heliciform nearly as high as wide, largely smooth with a sinusigera at about one and a half whorls, height 0.3 mm. **5**: same specimen, protoconch apical view, width 0.4 mm.

(BLODGETT 1992a, b). These are known only from their teleoconch which is close to that of the Carboniferous representatives. The protoconch of *Goniasma* as here illustrated for the first time belongs to two late Carboniferous species from the USA including the type species *Goniasma lasallensis* (Fig. 2). *Goniasma lasallensis* is a slender gastropod with two prominent spiral lirae well below the midwhorl of the teleoconch so that there is a wide adapical ramp. The teleoconch whorls are distinctly angulated. The protoconch comprises only about 1.4 whorls and was probably formed during a lecitotrophic ontogeny with short larval life. *Goniasma* sp. (Fig. 3) has two prominent spiral lirae on the mid-whorl with a selenizone in between. The protoconch comprises about two whorls. In both species the abrupt protoconch/teleoconch transition and the presence of a sinusigera suggest that pelagic and perhaps even planktonic larvae were present.

### Orthonemidae new family

Typical genus: *Orthonema* MEEK & WORTHEN, 1862.
Diagnosis: High-spired Cerithimorpha with a moderately arched to more or less straight outer lip. The protoconch has a heliciform shape.

Differences: The Goniasmidae have a slit or a distinct sinus in the outer lip. The protoconch of the Pseudozygopleuridae has an axially ribbed larval portion.

Included genera: *Orthonema, Metorthonema, Knightella, Palaeostylus* and *Spiromphalus*.

Remarks: NÜTZEL (1998) reported and figured the heliciform larval shells for the genera *Orthonema, Knightella*, and *Palaeostylus*. The protoconch of *Metorthonema* ERWIN, 1998 is still unknown, but the genus is so similar to *Orthonema* that it is probably closely related. ANDERSON et al. (1985) studied several Pennsylvanian species of the genus *Orthonema* from the Appalachian Basin. Even though they described the protoconch as smooth and simple, they did not figure such a type of protoconch and also based no taxonomic systematic conclusions on protoconch characters.
*Spiromphalus* closely resembles *Palaeostylus* in the high-spired cyrtoconoid shape and the teleoconch ornament of axial ribs. HOARE (1980) reported a probably (badly preserved) heliciform protoconch for *Spiromphalus*. But in contrast to *Palaeostylus, Spiromphalus* has an open umbilicus. Superficially, both genera resemble the Pseudozygopleuridae. But HOARE (1980) showed that *Spiromphalus* has a smooth protoconch while the Pseudozygopleuridae have a protoconch with axial ribs. Therefore, HOARE (1980) transferred *Spiromphalus* from the Pseudozygopleuridae to the Palaeozygopleuridae

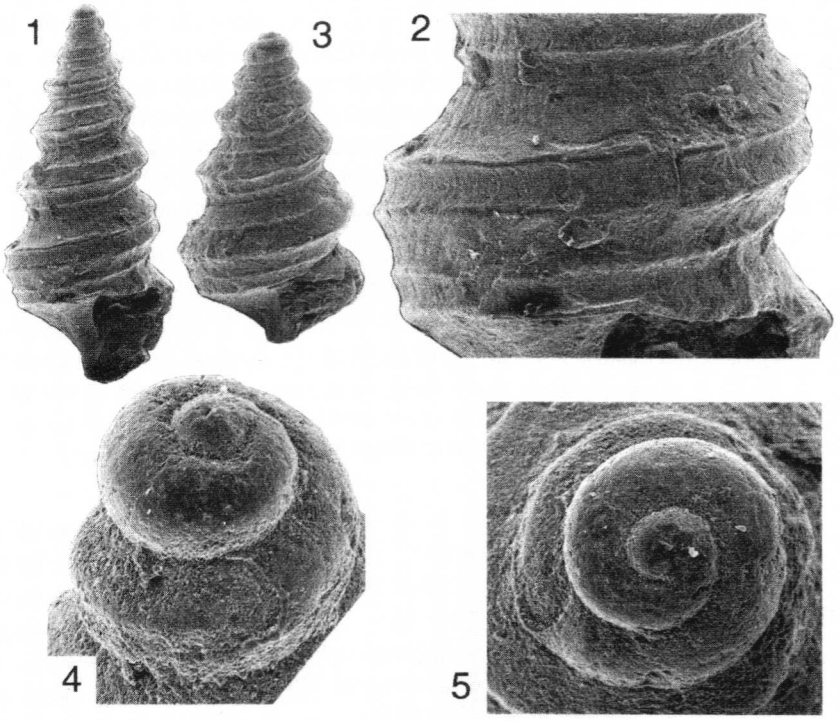


**Fig. 3.** *Goniasma* sp. from the Cambridge Shale (Gwe-1, see HOARE & STURGEON, 1978), Pennsylvanian, Ohio, USA.
**1**: side view, apertural, height 3 mm. **2**: same specimen, detail of teleoconch whorl, growth lines sinuous between the spiral lirae forming a selenizone, height 1 mm. **3**: side view, apertural, height 1.9 mm **4**: same specimen, protoconch side view, protoconch heliciform nearly as high as wide, largely smooth with a distinct sinusigera, height 0.3 mm. **5**: same specimen, protoconch apical view, sinusigera distinctly visible at about two whorls, width 0.34 mm.

HORNÝ, 1955. However, NÜTZEL (1998) suggested that the protoconch of *Spiromphalus* is a heliciform larval shell which is fundamentally different from the large direct protoconch of *Palaeozygopleura* HORNÝ, 1955. *Palaeozygopleura* was placed in the *Archaeogastropoda* by FRÝDA & BANDEL (1997) because of its protoconch morphology. NÜTZEL (1998) reported also

a heliciform larval shell for *Palaeostylus* and placed the genus preliminary in the Acanthonematidae (Cerithimorpha). Previously, BATTEN (1985) had placed *Palaeostylus* in the cerithimorph family Procerithiidae because of features of the aperture. But it is more appropriate to place the genus in the Orthonemidae because the Mesozoic Procerithiidae differ in the ornament of the larval shell, i.e. most have a bicarinate larval shell (BANDEL 1993, SCHRÖDER 1995, GRÜNDEL & NÜTZEL 1998, KOWALKE 1998). In addition, most of the Mesozoic procerithiids have a reticulate teleoconch ornament.

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