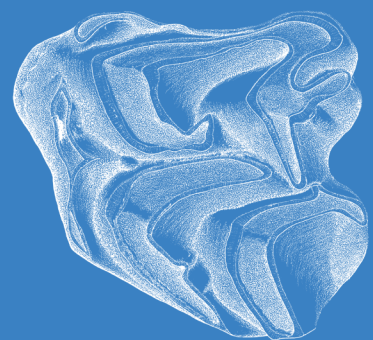
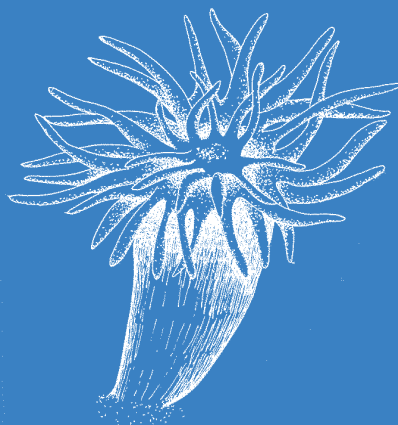


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of Palaeontology and Geobiology

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50
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Cover illustrations: (from left to right) Shell of the gastropod *Loxonema regium* DE KONINCK from the Carboniferous of Belgium (redrawn from DE KONINCK 1881); Solitary coral *Caninia* sp. from the Carboniferous of England (redrawn from RAMSBOTTOM in MCKERROW 1978); Tooth of the rare ruminant *Orygotherium escheri* VON MEYER from the Miocene of Germany (after RÖSSNER & MÖRS 2001). **Back cover:** Atrium of the Munich Palaeontological Museum, view from the main entrance.

Umschlagbilder: (von links nach rechts) Gehäuse der Schnecke *Loxonema regium* DE KONINCK aus dem Karbon von Belgien (neu gezeichnet nach DE KONINCK 1881); Solitärkoralle *Caninia* sp. aus dem Karbon von England (neu gezeichnet nach RAMSBOTTOM in MCKERROW 1978); Zahn des seltenen Wiederkäuers *Orygotherium escheri* VON MEYER aus dem Miozän von Deutschland (nach RÖSSNER & MÖRS 2001). **Rückseite:** Lichthof des Paläontologischen Museums München, Blick vom Haupteingang.

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A review of the Triassic gastropod genus *Kittliconcha* BONARELLI, 1927 – implications for the phylogeny of Caenogastropoda

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Abstract

Eight Triassic species and one variety have been included in the genus *Kittliconcha* BONARELLI, 1927. In this composition, *Kittliconcha* is polyphyletic. The holotypes of *Kittliconcha cassiana* BONARELLI, 1927 (type species of *Kittliconcha*) and *Settsassia obliquecostata* (MÜNSTER, 1841) (type species of *Settsassia*), as well as the type material of “*Loxonema*” *walmstedti* (KLIPSTEIN, 1843) are studied and illustrated (all are from the Cassian Formation). All three species are considered to be synonymous here. The former diagnosis of *Kittliconcha* encompassed the presence of a varix and reduction of axial ribs on the last whorl. However, these characters resulted from a repaired shell fracture in the holotype of *Kittliconcha cassiana*. This specimen represents actually *Melania obliquecostata* MÜNSTER, 1841, which is the type species of *Settsassia* BANDEL, 1992. Therefore, *Settsassia* BANDEL, 1992 is a synonym of *Kittliconcha* BONARELLI, 1927. *Kittliconcha* alias its junior synonym *Settsassia* is probably a representative of the cerithimorph stem line as is indicated by its small, smooth larval shell which resembles that of Campaniloidea. A relationship with Littorinimorpha or other basal caenogastropods is also possible. Only a single additional nominate Triassic species may actually represent *Kittliconcha*: *K. obesa* from the Middle Triassic of China. Two species from the Late Triassic of South America have been previously assigned to *Kittliconcha*. They are based on poorly preserved and insufficiently documented material so that any generic assignment is basically speculative. These species are *K. dissimilis* HAAS, 1953, and *K. peruviana* HAAS, 1953. *K. doelloi* BONARELLI, 1927 from Argentina is also based on poorly preserved material which is of unknown age. The material from the Late Triassic Cassian Formation which was assigned to *Kittliconcha* by ZARDINI (1978) does not belong here. It represents the new sinistral genus *Triadosinister* and two species (including one new species) which are tentatively assigned to the genus *Katosira*. These species are *Katosira? cortinensis* n. sp. and *Katosira? giauensis* ZARDINI, 1978. The holotype of the type species of the sinistral genus *Allostrophia* from the Cassian Formation is illustrated. Due to its poor pre-

servation this genus is considered here to represent a nomen dubium. The early Triassic species *Kittliconcha sciaphostera* (BATTEN & STOKES, 1986) also does not represent *Kittliconcha*. It is transferred to the genus *Pseudotrionium* which is assigned to the family Maturifusidae. A lectotype of the type species of *Pseudotrionium* (*P. venustum* from the Cassian Formation) is designated and illustrated. The cancellate ornament, shape, aperture, and the protoconch morphology of *Kittliconcha sciaphostera* suggest that this species is one of the earliest members of an evolutionary line leading to the Mesozoic family Maturifusidae, which could be the stem-group of Neogastropoda.

Key words: Triassic; Gastropoda; Systematics; New Taxa; Maturifusidae; Cassian Formation.

Zusammenfassung

Der Gattung *Kittliconcha* BONARELLI, 1927 wurden bislang acht triassische Gastropodenarten zugeordnet. In dieser bisherigen Zusammensetzung ist *Kittliconcha* polyphyletisch. Die Holotypen von *Kittliconcha cassiana* BONARELLI, 1927 (Typusart von *Kittliconcha*) und von *Settsassia obliquecostata* (MÜNSTER, 1841) (Typusart von *Settsassia*) sowie das Typusmaterial von “*Loxonema*” *walmstedti* (KLIPSTEIN, 1843) werden nachuntersucht und abgebildet (alle stammen aus der Cassian Formation). Sie drei Artnamen sind Synonyme. Die bisherige Diagnose von *Kittliconcha* beinhaltete das Vorhandensein einer Varix und die Reduktion von Axialrippen auf der letzten Windung. Diese Merkmale sind jedoch das Resultat einer reparierten Schalenfraktur beim Holotyp von *Kittliconcha cassiana*. Dieses Exemplar gehört der Art *Melania obliquecostata* MÜNSTER, 1841 an, die Typusart von *Settsassia* BANDEL, 1992 ist. Also ist *Settsassia* BANDEL, 1992 ein Synonym von *Kittliconcha* BONARELLI, 1927. *Kittliconcha* alias ihrem jüngeren Synonym *Settsassia* ist vermutlich ein Vertreter der Stammlinie der Cerithimorpha, worauf die kleine, glatte, heliciforme Larvalschale hinweist, die in ähnlicher Weise bei den Campaniloidea vorkommt. Eine engere verwandtschaftliche

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Beziehung ist auch zu den Littorinimorpha oder anderen basalen Caenogastropoden möglich. Nur eine weitere nominelle triassische Art steht vermutlich zu Recht in *Kittliconcha*: *K. obesa* aus der mittleren Trias von China. Drei Arten aus der oberen Trias von Südamerika wurden der Gattung *Kittliconcha* zugeordnet. Sie basieren auf schlecht erhaltenem und unzureichend dokumentiertem Material, so dass jegliche Gattungszuweisung spekulativ erscheint. Es handelt sich dabei um die Arten *K. dissimilis* HAAS, 1953 und *K. peruviana* HAAS, 1953. *K. doelloi* BONARELLI, 1927 aus Argentinien basiert ebenfalls auf ungenügend bekanntem Material und ist überdies unsicherer Alters. Das Material aus der obertriassischen Cassian Formation, das ZARDINI (1978) *Kittliconcha* zuordnete, gehört dieser Gattung nicht an. Es repräsentiert die neue sinistrale Gattung *Triadosinister* und zwei Arten (davon eine neue), die vorläufig der Gattung *Katosira* zugerechnet werden. Es sind dies die Arten *Katosira? cortinensis* n. sp. und *Katosira? giauensis* ZARDINI, 1978. Der Holotyp der Typusart der sinistralen Gattung *Allostrophia* aus der Cassian Formation wird abgebildet. Das Stück ist so schlecht erhalten, dass die Gattung als Nomen dubium anzusehen ist. Die untertriassische Art *Kittliconcha sciaphostera* gehört ebenfalls nicht der Gattung *Kittliconcha* an. Sie wird der Gattung *Pseudotrionium* zugeordnet und diese der Familie Maturifusidae. Für die Typusart von *Pseudotrionium* (*P. venustum* aus der Cassian Formation) wird ein Lectotyp festgelegt und abgebildet. Das gitterartige Ornament, die Gestalt, Mündung und die Protoconchmorphologie legen nahe, dass es sich bei *Kittliconcha sciaphostera* um einen der frühesten Vertreter der evolutionären Linie handelt, die zur mesozoischen Familie Maturifusidae führt, die ihrerseits die Stammgruppe der Neogastropoda sein könnte.

Schlüsselwörter: Trias; Gastropoda; Systematik; Neue Taxa; Maturifusidae; Cassian Formation.

1. Introduction

The subclass Caenogastropoda is richly diversified in the Triassic and the famous fauna from the Cassian Formation greatly contributes to this diversity. There are probably as many

as 200 described Triassic caenogastropod genera. Many of them are well characterized whereas others are obscure because they are based on poorly preserved or insufficiently documented material and many of them have never been revised since their original publication. One of the more obscure genera is *Kittliconcha* BONARELLI, 1927 which has a type species from the Cassian Formation. It was originally erected as a subgenus of *Zygopleura* KOKEN, 1892 but later promoted to genus level (KNIGHT et al. 1960; NÜTZEL 1998). The restudy of the type specimen in question shows that at least two diagnostic features, a special type of varix-like axial rib and the reduction of the ornament on the last part of the last whorl, are results of a healed shell fracture. The type species is here re-studied and a new diagnosis is given. Based on this, the species which have been placed in *Kittliconcha* are re-evaluated.

Seven Triassic species and one variety as well as one species of uncertain age have to date been assigned to the genus *Kittliconcha*:

K. cassiana BONARELLI, 1927, Cassian Formation, Carnian
K. contraria ZARDINI, 1978, Cassian Formation, Carnian
K. dissimilis HAAS, 1953, Pucara Formation, Peru, Late Triassic
K. doelloi BONARELLI, 1927 (age unclear, Argentina)
Zygopleura (*K.*) *cassiana* n. f. *fascicostata* ZARDINI, 1978, Cassian Formation, Carnian
K. giauensis ZARDINI, 1978, Cassian Formation, Carnian,
K. ? obesa YU, PAN & WANG, 1974, Qingyan Fm., S China
K. peruviana HAAS, 1953, Pucara Formation, Peru, Late Triassic
K. sciaphostera BATTEN & STOKES, 1986, Moenkopi Formation, Utah

These species are discussed below, showing that *Kittliconcha* in this composition is clearly polyphyletic.

2. Repositories

Geologische Bundesanstalt Wien; BSPG: Bayerische Staatssammlung für Geologie und Paläontologie München; MPRZ: Museo Paleontologico Rinaldo Zardini, Cortina d'Ampezzo; NHMW: Naturhistorisches Museum Wien; NHM: Natural History Museum London.; AMNH: American Museum of Natural History, New York.

Plate 1:

Kittliconcha obliquecostata (BRONN in MÜNSTER, 1841), Late Triassic Cassian Formation.

Fig. 1: Holotype of *Kittliconcha cassiana* BONARELLI, 1927 (synonym of *Kittliconcha obliquecostata*), KITTL's (1894: pl. 8, fig. 5) original; Geologische Bundesanstalt, Wien.

Fig. 1a–d: Lateral views at different angles, height of specimen 18.4 mm; repaired shell fracture on last whorl; axial ribs reduced on repaired shell after fracture.

Fig. 1e: Oblique lateral view to show varix-like, irregular rib on last whorl; height 10 mm.

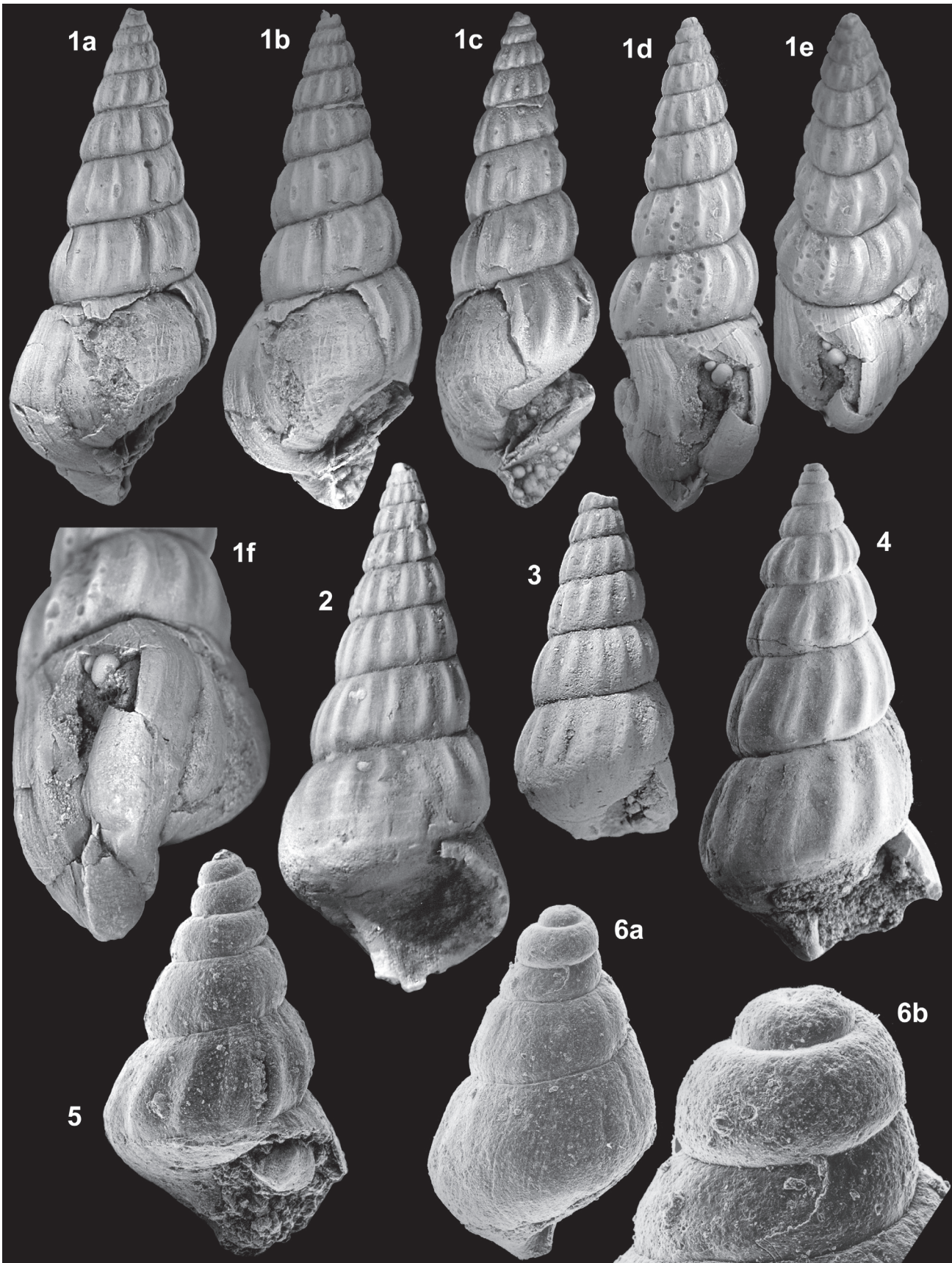
Fig. 2: Lectotype of *Melania obliquecostata* selected from MÜNSTER's type collection, type species of *Kittliconcha* and its junior synonym *Settsassia*; 17 mm high, BSPG AS VII 506.

Fig. 3: *Turritella walmstedti* Klipstein from the type series of Klipstein, Natural History Museum, London (NHM 35692C); this taxon represents a junior synonym of *Kittliconcha obliquecostata*; height 13.4 mm.

Fig. 4: *Kittliconcha obliquecostata*; height 6 mm; from NÜTZEL (1998: pl. 27N), NHMW 1997/0040/0087.

Fig. 5: *Kittliconcha obliquecostata*; juvenile specimen showing smooth protoconch, smooth early teleoconch, and transition to teleoconch with axial ribs; height 4.4 mm; from NÜTZEL (1998, pl. 27P), NHMW 1997/0040/0088.

Fig. 6: *Kittliconcha obliquecostata*; juvenile specimen showing smooth protoconch and smooth early teleoconch; NHMW 1997/0040/0089; 6a: height 0.9 mm; from NÜTZEL (1998: pl. 27Q); 6b: small, smooth protoconch of about 2.5 whorls; larval shell terminating at sinusigera; height 0.34 mm; from NÜTZEL (1998: pl. 27R).



3. The genus *Kittliconcha*

Genus *Kittliconcha* BONARELLI, 1927

Type species: *Zygopleura (Kittliconcha) cassiana* BONARELLI, 1927 pro *Loxonema walmstedti* (KLIPSTEIN, 1843) sensu KITTL (1894: pl. 8, fig. 5) = “Gehäuse mit abnormer (?) Schlußwindung” (“Shell with abnormal (?) final whorl”); early Carnian, Cassian Formation.

Other species originally included: *Kittliconcha doelloi* BONARELLI, 1927, Argentina (age unknown).

Remarks: BONARELLI (1927) designated *Zygopleura (Kittliconcha) cassiana* BONARELLI, 1927 as the type species. He based this species on a specimen which was illustrated by KITTL (1894: pl. 8, fig. 5) under the name *Loxonema walmstedti* (KLIPSTEIN, 1843). KITTL noted that this specimen has an “abnormal (?) final whorl”. When BONARELLI (1927) erected the type species *Zygopleura (Kittliconcha) cassiana*, he just referred to this specimen which therefore is the holotype. This type specimen is housed in the collection of the Geologische Bundesanstalt in Vienna (Austria). Obviously, BONARELLI never studied this specimen or topotypical material from the Cassian Formation. The holotype is re-described and illustrated below. BONARELLI (1927) gave no formal diagnosis for *Kittliconcha* but his description and comparisons to other taxa warrants the validity of the new subgenus. However, BONARELLI (1927) had no material from the Cassian Formation at hand and his interpretation of KITTL’s (1894) illustration is obviously flawed, therefore, his taxonomical considerations are largely irrelevant. A short diagnosis for *Kittliconcha* was given by KNIGHT et al. (1960): “Broader and less acute than in most genera of the family [Zygopleuridae]; whorls strongly convex; collabral riblets strong on spire whorls, where only their opisthocyrt upper part is exposed, obsolete on last whorl except for a varix; no spiral ornament.” In the following the holotypes of the type species of *Kittliconcha* and *Settsassia* are re-described and illustrated. It becomes clear that both taxa are synonyms and consequently *Settsassia* Bandel, 1992 is a junior synonym of *Kittliconcha* BONARELLI, 1927.

3.1 Re-description of the holotype of *Kittliconcha cassiana*

Kittliconcha cassiana BONARELLI, 1927

Pl. 1, Fig. 1

1894 *Loxonema walmstedti* (KLIPSTEIN, 1843) – KITTL: 169, pl. 8, fig. 5.

Material: The holotype of *Zygopleura (Kittliconcha) cassiana*, KITTL’s original specimen (1894, pl. 8, fig. 5) from the Stuores Meadows, Cassian Formation, N Italy, Early Carnian; housed in the Geologische Bundesanstalt Wien.

Description: Shell high-spined; about 8.5 whorls, 18.4 mm high, 7.4 mm wide; apical angle 26°; whorls convex,

ornamented with 12 to 14 axial ribs per whorl; ribs round, orthocline to slightly opisthocyrt, little narrower than space between ribs; ribs do not continue onto base; base smooth, convex, without ledge when joining whorl face; suture incised; last whorl with pronounced deep, healed shell fracture; shell after fracture without regular ribs, but with one irregular varix and a varix-like aperture.

Remarks: It is clear that the presence of a varix and the reduction of the ribs on the last whorl which have been considered diagnostic for *Kittliconcha* by KNIGHT et al. (1960) resulted from a healed shell fracture. The animal survived a rather deep shell fracture but was unable to build a shell with regular axial ribs afterwards. Shell fractures are common in the Cassian gastropods as can be seen in ZARDINI’s (1978) monograph and as was discussed by VERMEIJ et al. (1982). KITTL (1894) interpreted this varix as a not resorbed apertural varix but this is obviously not the case.

3.2 Re-description of *Kittliconcha obliquecostata* including designation of lectotype

Kittliconcha obliquecostata (BRONN in MÜNSTER, 1841)

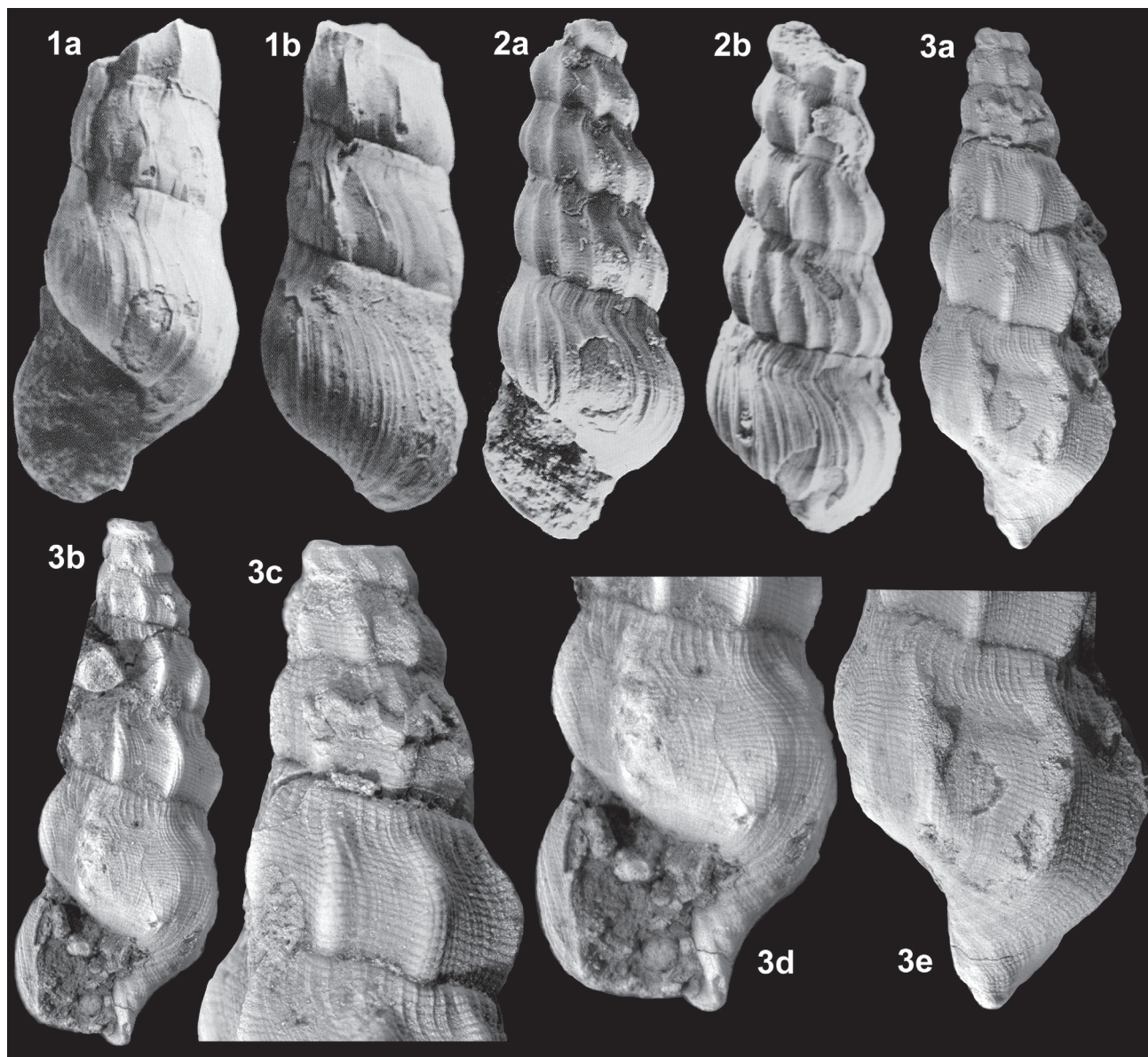
Pl. 1, Figs 2–6

- * 1841 *Melania obliquecostata* n. sp. – BRONN in MÜNSTER: 97, pl. 9, fig. 43.
- 1843 *Turritella walmstedti* n. sp. – KLIPSTEIN: 179, pl. 11, figs 28, 29.
- 1843 *Melania haueri* – n. sp. KLIPSTEIN: 190, pl. 12, fig. 30.
- 1978 *Zygopleura walmstedti* (KLIPSTEIN, 1843) – ZARDINI: 40, pl. 24, figs 13–16.
- 1978 *Zygopleura obliquecostata* (BRONN in MÜNSTER, 1841) – ZARDINI: 40, pl. 24, figs 17–22.
- 1978 *Zygopleura haueri* (KLIPSTEIN, 1843) – ZARDINI: 40, pl. 25, figs 8, 9.
- 1992 *Settsassia obliquecostata* (BRONN in MÜNSTER, 1841) – BANDEL: 64, pl. 11, figs 3, 4, non fig. 7, pl. 12, figs 1, 2.
- 1993 *Settsassia obliquecostata* (BRONN in Münster, 1841) – BANDEL: 13, pl. 4, fig. 2.
- 1994 *Settsassia obliquecostata* (Bronn in Münster, 1841) – BANDEL: 145, pl. 3, fig. 1.
- 1998 *Settsassia obliquecostata* (Bronn in Münster, 1841) – NÜTZEL: 167, pl. 27 figs L–R.

For additional synonyms, refer to DIENER (1926) and KUTASSY (1940).

Lectotype: BSPG AS VII 506, from the type series, specimen illustrated by BRONN in MÜNSTER (1841: pl. 9, fig. 43).

Description: Shell high-spined, conical, straight-sided; lectotype comprising 10 teleoconch whorls (apical whorls missing), 17 mm high, 7.1 mm wide; whorls regularly expanding, evenly convex; suture distinct; first two to three teleoconch whorls smooth; later whorl with 12 to 15 axial ribs per whorl; ribs wave-like, round, approximately as wide as interspaces between them; ribs almost straight, orthocline, slightly opisthocyrt or somewhat prosocline; ribs of about equal strength over the whorl but submedian somewhat stronger in some



Textfigure 1: *Triadosinister contrarius* (Zardini, 1978), Late Triassic Cassian Formation. (1.1) Paralectotype, height 17.5 mm; from the location Rumerlo, from ZARDINI (1978: pl. 26, fig. 5), MPRZ 1492. (1.2) lectotype height 21 mm; from the location Alpe di Specie, from ZARDINI (1978: pl. 26, fig. 6), MPRZ 1493. (1.3) height 21 mm; from the location Misurina Skilift, BSPG 2010 III 1; 1.3a, b: height 6 mm; 1.3c: apex detail, height 2.3 mm; 1.3d, e: last whorl detail, height 3 mm.

specimens; ribs terminate somewhat above the suture; they do not continue onto base; base flatly convex, smooth; last whorl of lectotype with very faint, obscure spiral lineation which is absent in earlier whorls; protoconch smooth, heliciform, consisting of 2.5 to 3 whorls, up to 0.34 mm high and 0.25 mm wide; diameter of initial whorl 0.10 to 0.13 mm; protoconch whorls convex, terminating at a distinct sinusigera.

Remarks: As outlined above, *Kittliconcha cassiana* represents a synonym of “*Melania*” *obliquecostata*. Exhaustive descriptions of *Kittliconcha obliquecostata* are available from KITTL (1894) and BANDEL (1992). The small smooth heliciform larval shell of the planktotrophic type and the smooth early teleoconch separate it from similar, convergent species of the Zygopleuridae (BANDEL 1992; NÜTZEL 1998). BANDEL (1992) reported that the last whorl is detached and becomes phane-

romphalous. This could not be observed in the present material. KITTL (1994) noted that a faint spiral striation can be present as is the case in the lectotype figured here (Pl. 1, Fig. 2). KITTL (1894) and BANDEL (1992) found that there are morphological transitions to *Turritella walmstedti* KLIPSTEIN, 1843 and *Melania haueri* KLIPSTEIN, 1843 from the Cassian Formation. The three taxa differ in minor details of the axial ornament and in the spiral angle. These differences can be interpreted as intraspecific variation. Thus, NÜTZEL (1998) treated both KLIPSTEIN taxa as synonyms of *Kittliconcha obliquecostata*. For instance, in Plate 1, Fig. 3, a specimen of *Turritella walmstedti* from KLIPSTEIN’s type collection (Natural History Museum London) is illustrated. This teleoconch fragment shows no differences to *M. obliquecostata* and its synonym *K. cassiana*.

Kittliconcha obliquecostata is abundant at the Stuores Meadows localities (Prati di Stuores). ZARDINI (1978) reported this

species also from the area near Cortina d'Ampezzo, especially at the locations Costalaresc and Alpe di Specie.

3.3 Emended diagnosis for *Kittliconcha*, largely based on the diagnoses of *Settsassia* as given by BANDEL (1992) and NÜTZEL (1998)

Shell high-spined, conical, straight-sided, up to about 2 cm high; apical angle 25° to somewhat more than 30°; whorls regularly expanding, evenly convex; first two to three teleoconch whorls smooth; later whorl with axial ribs; ribs broad, round; almost straight, orthocline to slightly opisthocyrt or somewhat prosocline; base flatly convex, smooth; spiral ornament basically absent but an obscure spiral lineation may be present; protoconch small, smooth, heliciform, terminating at a distinct sinusigera.

3.4 Discussion of the systematic placement of *Kittliconcha*

It is now clear that the main diagnostic features of *Kittliconcha* as indicated by KNIGHT et al. (1960), rib reduction and varix on the last whorl, are results of a repaired shell fracture. This raises the question about the validity of the genus *Kittliconcha* and *K. cassiana*. A comparison of the holotypes of *K. cassiana* and *Melania obliquecostata* BRONN in MÜNSTER, 1841 from the Cassian Formation (see Pl. 1, Figs 1 and 2) shows that both specimens are very similar and are probably conspecific. Therefore, *K. cassiana* is a junior subjective synonym of *Melania obliquecostata*. *Melania obliquecostata* and its synonyms have long been attributed to the genus *Zygopleura* KOKEN, 1892. However, BANDEL (1992, 1993) reported a small smooth, heliciform larval shell which is untypical for *Zygopleura* (see also NÜTZEL 1998). Therefore, BANDEL (1992) introduced the genus *Settsassia* with the type species *Melania obliquecostata*. Thus, *Kittliconcha* and *Settsassia* have the same type species and therefore, *Settsassia* BANDEL, 1992 is a junior synonym of *Kittliconcha* BONARELLI, 1927. BANDEL (1992) also introduced the family Settsassiidae and this name remains valid according to the ICZN. Therefore, the following arrangement is suggested:

Family Settsassiidae BANDEL, 1992

Type genus: *Settsassia* BANDEL, 1992, a junior synonym of *Kittliconcha* BONARELLI, 1927.

Genus: *Kittliconcha* BONARELLI, 1927

Type species: *Melania obliquecostata* BRONN in MÜNSTER, 1841 (synonyms *Turritella walmstedti* KLIPSTEIN, 1843, *Melania haueri* KLIPSTEIN, 1843, and *Zygopleura (Kittliconcha) cassiana* BONARELLI, 1927).

Kittliconcha obliquecostata is certainly a caenogastropod and is probably related to the Cerithioidea (BANDEL 1992, 1993) or to the Campaniloidea. A close relationship to Littorinimorpha is also possible. The small, smooth heliciform larval shell of *Kittliconcha* strongly resembles that of the Mesozoic basal cerithimorph genera *Campanile*, *Metacerithium*, and *Dzikella*

(the latter is probably a synonym of *Metacerithium*) (see KIEL et al. 2000; KAIM 2004; KIEL 2006). The larval shells of the mentioned campanilids have a sinusigera which is heavily strengthened by a varix. However, this is not the case in *Kittliconcha*. Nevertheless, it seems to be possible that Campanilidae and Settsassiidae are closely related to each other. NÜTZEL (1998) supposed that Settsassiidae are descendants of the Palaeozoic Palaeostyloidea which encompass high-spined, axially ribbed gastropods with smooth or poorly ornamented larval shells.

4. Re-assignment and discussion of other species that have been included in *Kittliconcha*

As mentioned above, besides *Kittliconcha obliquecostata* alias *K. cassiana*, seven other species and one variety have been assigned to the genus *Kittliconcha*: two species and one variety from the Early Carnian Cassian Formation (*K. contraria* ZARDINI, 1978, *K. giauensis* ZARDINI, 1978, and *K. cassiana* n. f. *fascicostata* ZARDINI, 1978), two species from the Late Triassic of the Pucara Formation, Peru (*K. dissimilis* HAAS, 1953 and *K. peruviana* HAAS, 1953), *K. doelloi* BONARELLI, 1927 from Argentina (age uncertain), *K. ? obesa* YU, PAN & WANG, 1974 from the Middle Triassic of South China, and *K. sciaphostera* BATTEN & STOKES, 1986 from the Early Triassic Moenkopi Formation of Utah, USA. The new information on the type species of *Kittliconcha* suggests that most of aforementioned species do not belong to this genus. These species share a zygoileuroid habitus i. e., they are more or less high-spined with a teleoconch ornament of axial ribs. Most are probably caenogastropods, however, the protoconch is known only from *K. sciaphostera* and thus, the higher systematic placement of the other species is tentative. Many of the taxa assigned to *Kittliconcha* have an additional ornament of distinct spiral lirae or a spiral micro-ornament. Such features have not been observed in the type species of *Kittliconcha* (see above and Pl. 1). *Kittliconcha obliquecostata* may show only a very faint spiral lineation which is obviously result of intraspecific variation and cannot be considered diagnostic. BONARELLI (1927: 60) excluded a spiral ornament in his discussion of *Kittliconcha*: "... el ejemplar de referencia no presenta estrías espirales y la falta absoluta de este tipo de ornamentación acompañando a las cóstulas, permite excluir del todo su pertenencia al género *Katosira*" (translation: "... the specimen in question [holotype of *Kittliconcha cassiana*] shows no spiral striae and the complete absence of such an ornament in connection with the ribs facilitate to exclude an assignment to the genus *Katosira* entirely.").

In the following, the species which have been assigned to *Kittliconcha* are discussed and re-assigned whenever possible.

4.1 Re-assignment of *Kittliconcha contraria* ZARDINI, 1978

Kittliconcha contraria does not belong to *Kittliconcha* and it is designated here as a type species of the new genus *Triadosinister*.

Triadosinister n. gen.

Etymology: For the Triassic period and sinistrality.

Diagnosis: High-spined sinistral shells with prominent axial ribs and a reticulate micro-ornament of fine spiral grooves and threads intersected by strengthened growth lines; whorls convex, pendant; relatively few axial ribs per whorl; axial ribs not reaching the adapical suture; aperture seemingly with wide siphonal opening.

Type species: *Kittliconcha contraria* ZARDINI, 1978 (Carnian, Cassian Formation).

Remarks: *Triadosinister* differs from *Kittliconcha* in being left coiled and in having a reticulate micro-ornament. *Allostrophia* KITTL, 1894 with the type species *Allostrophia perversa* (MÜNSTER, 1841) from the Cassian Formation is another high spired sinistral genus with axial ribs on the teleoconch whorls. MÜNSTER's type specimen (BSPG AS VII 1681) is so poorly preserved (encrusted and abraded) (Textfig. 2) that the species and consequently also the genus are considered here to be *Nomina dubia*. According to KITTL (1894) and KNIGHT et al. (1960), *Allostrophia* has less convex whorls, continuous axial ribs and lacks a reticulate micro-ornament. The relatively well-preserved specimens illustrated as *A. perversa* by ZARDINI (1978: pl. 26, figs 2–4) show straight axial ribs, the whorls are not pendant (i.e., they do not have their maximum width below mid-whorl) and obviously lack a micro-ornament. A siphonal notch which is present in *Triadosinister* is obviously absent in *Allostrophia* (MARSHALL 1990). The protoconchs of *Allostrophia* and *Triadosinister* are unknown so far. BANDEL (1994: 138) mentioned that he observed that the protoconch of *Allostrophia* it is not typical for *Zygopleuridae*. The Early Jurassic high-spined sinistral genus *Virgella* DEGREGORIO, 1930 has numerous fine axial ribs.

Triadosinister contrarius (ZARDINI, 1978)
Textfig. 1

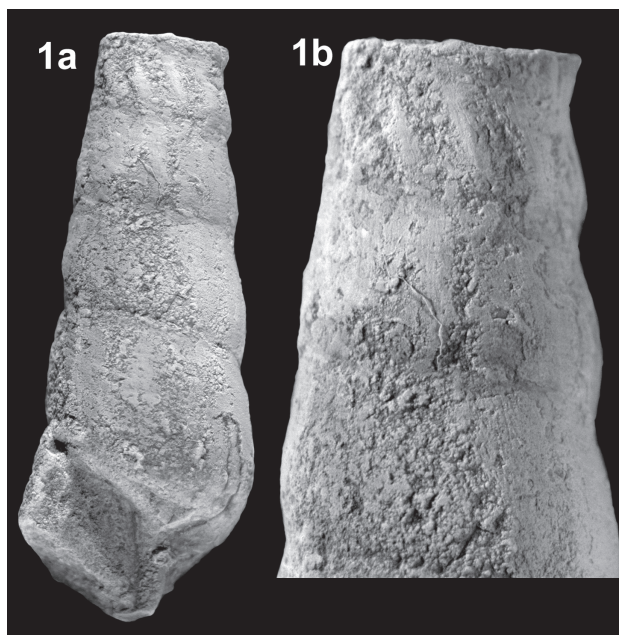
* 1978 *Kittliconcha contraria* n. sp. – ZARDINI: 42, pl. 26, figs 5, 6 (?fig. 7).

Lectotype: Here designated, specimen illustrated in ZARDINI (1978: pl. 26, fig. 6a, b, MPRZ 1493) Cassian Formation, Early Carnian, from Alpe di Specie, Seelandalpe; ZARDINI's illustration is reproduced here (Textfig. 1.2).

Paralectotype: The specimen illustrated in ZARDINI (1978: pl. 26 fig. 5a, b, MPRZ 1492) from Rumerlo; ZARDINI's illustration is reproduced here (Textfig. 1.1).

Additional material: One specimen from the Misurina Skilift location (see NÜTZEL et al. 2010), BSPG 2010 III 1 (Textfig. 1.3).

Description: Shell high-spined, slender, sinistral; lectotype is a teleoconch fragment of about five whorls, 21 mm high, 8 mm wide; whorls distinctly convex; whorl profile somewhat pendant; whorls somewhat adpressed; sutures distinct; whorls



Textfigure 2: The holotype of *Turritella perversa* MÜNSTER, 1841, type species of *Allostrophia* KITTL, 1894; the preservation of the type specimen (illustrated in MÜNSTER 1841: pl. 9, fig. 41) is so poor that this taxon is considered to represent a *nomen dubium*; BSPG AS VII 1681; 2.1a: 16.1 mm high, 5.9 mm wide; 2.1b: detail of earliest preserved whorls showing faint, eroded axial ribs; 8.8 mm high.

ornamented with prominent axial ribs; number of ribs increasing during ontogeny from 8–9 to about 15 per whorl; ribs reduced on last whorl; ribs slightly opisthocline somewhat curving opisthocyrt; ribs much narrower than interspaces between ribs; ribs weak or reduced below adapical suture and absent on base; whorls with reticulate micro-ornament of fine spiral grooves and threads intersected by strengthened parasigmoidal growth lines; growth lines especially strong below adapical suture; aperture seemingly with wide siphonal opening; base flatly convex, covered with reticulate micro-ornament; protoconch unknown.

Remarks: The differences to other species and genera are discussed above. ZARDINI (1978: pl. 26, figs. 5–7) illustrated three specimens which he assigned to *Kittliconcha contraria*. The specimen in ZARDINI (1978: pl. 26, fig. 7) is poorly preserved and its identity is questionable. The shell figured here in Textfigure 1.3 is the first known from the location Misurina Skilift near Cortina d'Ampezzo. It shows a well-preserved micro-ornament. The three specimens of *Triadosinister contrarius* illustrated here seem to exhibit a considerable intraspecific variability in number and strength of the ribs. However, these specimens represent different growth stages and the pronounced ontogenetic change of the ornament of *T. contrarius* (increase of the number of ribs per whorl and reduction of ribs on mature whorls) is suggestive of this apparent variability. However, there is no doubt that these specimens represent a single species.

4.2 Re-assignment and discussion of *Kittliconcha cassiana* sensu ZARDINI (1978) and *Kittliconcha giauensis*

ZARDINI (1978: pl. 28, figs 3–4) illustrated two specimens from the early Carnian Cassian Formation and assigned them to *Kittliconcha cassiana* BONARELLI, 1927. These specimens represent a new species and probably a new genus. This new species is described herein and tentatively assigned to *Katosira*. *Kittliconcha giauensis* ZARDINI, 1978 also does not belong to *Kittliconcha* and is tentatively transferred to *Katosira* herein.

Genus *Katosira* KOKEN, 1892

Type species: *Katosira periniana* (ORBIGNY, 1851), Early Jurassic, France.

Katosira? *cortinensis* n. sp.
Textfig. 3.1, 3.2

*1978 *Zygopleura* (*Kittliconcha*) *cassiana* BONARELLI, 1927 – ZARDINI: 42, pl. 28, figs 3, 4.

?1978 *Zygopleura* (*Kittliconcha*) *cassiana* n. f. *fascicostata* – ZARDINI: 42, pl. 28, fig. 2.

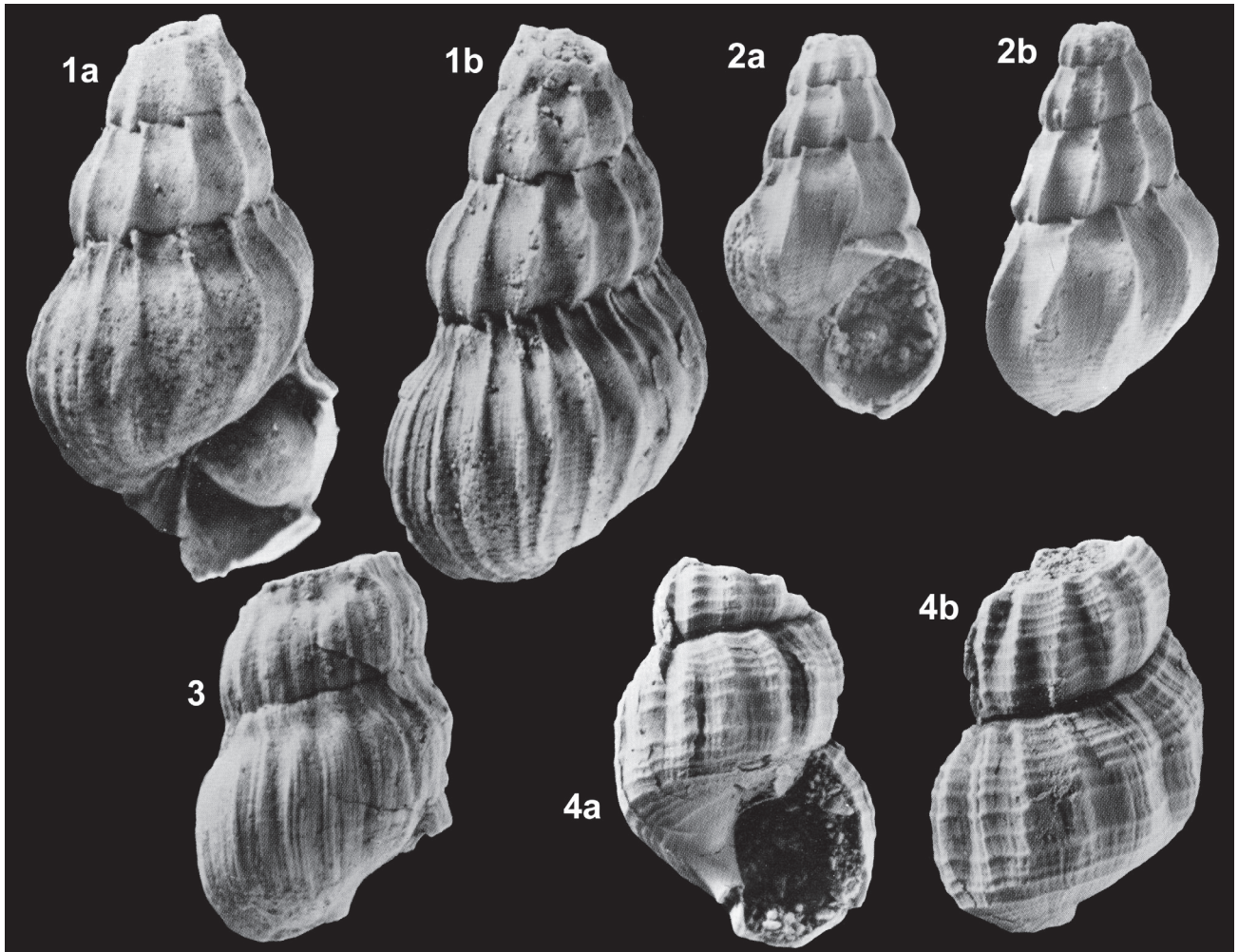
Diagnosis: Shell broad, relatively low-spired, last whorl somewhat higher than spire; whorls convex, somewhat adpressed; whorls ornamented with narrow, sharp, fold like axial ribs; axial ribs curving, opisthocyrt to opisthocline; early teleoconch whorls with few ribs, last whorl with numerous ribs; whorls with additional spiral micro-ornament; base convex.

Holotype: The specimen illustrated by ZARDINI (1978) in pl. 28, fig. 3a, b, reproduced here in Textfigure 3.1a, b, MPRZ 3706.

Paratype: The specimen illustrated by ZARDINI (1978) in pl. 28, fig. 4a, b, reproduced here in Textfigure 3.2a, b, MPRZ 3707.

Etymology: Atte Cortina d'Ampezzo (type locality)

Locus typicus: The holotype comes from Alpe di Specie



Textfigure 3: Reproduction of ZARDINI's (1978) illustrations of specimens which have been assigned to *Kittliconcha*; Late Triassic Cassian Formation. (3.1, 3.2): *Katosira?* *cortinensis* n. sp. (3.1): height 13 mm; from the location Alpe di Specie, from ZARDINI (1978: pl. 28, fig. 3a, b), MPRZ 3706. (3.2): height 9 mm; from the location Costalares, from ZARDINI (1978: pl. 28, fig. 4a, b), MPRZ 3707. (3.3): "*Zygopleura* (*Kittliconcha*) *cassiana* n. f. *fascicostata*", height 9.6 mm; from the location Sasso di Stria, from ZARDINI (1978: pl. 28, fig. 2), MPRZ 3705. (3.4): *Katosira?* *giauensis* (ZARDINI, 1978), height 9.8 mm; from the location Forcella Giau, from ZARDINI (1978: pl. 28, fig. 6a, b), MPRZ 3709.

near Cortina d'Ampezzo (South Tyrol, N Italy).

Stratum typicum: Early Carnian, Cassian Formation.

Description: Shell broad, relatively low-spined, last whorl somewhat higher than spire; holotype comprises about three whorls (apex missing), 13 mm high, 7.2 mm wide; whorls convex, somewhat adpressed; whorls ornamented with narrow, sharp, fold like axial ribs; axial ribs curving, opisthocyrt to opisthocline; early teleoconch whorls with about 9 ribs per whorl, last whorl of holotype with more than 15 ribs; distance between ribs much wider than width of ribs, especially in early whorls; ribs fade on base; whorls ornamented with additional spiral micro-ornament; base convex, not demarcated from whorl face, minutely phaneromphalous.

Remarks: The broad, stout shape, the sharp ribs and the spiral micro-ornament described by ZARDINI (1978) strongly suggest that these specimens do not belong to *Kittliconcha obliquecostata* alias *K. cassiana*. The generic assignment to *Katosira* is tentative until more information about the new species become available. *Katosira* encompasses generally more high-spined and slender species with axial ribs crossed by finer spiral threads. The genus is based on the *K. periniana* from the Early Jurassic of France. This species is based on a poorly preserved specimen (FISCHER & WEBER 1997). The variety *Zygopleura (Kittliconcha) cassiana* n. f. *fascicostata* described by ZARDINI (1978) could also belong to *Katosira? cortinensis* n. sp. but the single teleoconch fragment illustrated by ZARDINI (1978: pl. 28, fig. 2) differs in shape and ornament (Textfig. 3.3). It does not provide enough information for a meaningful systematic placement. *Kittliconcha giamensis* ZARDINI, 1978 from the Cassian Formation has broad, round axial ribs crossed by several distinct spiral ribs. The holotype, a fragment of two teleoconch whorls, is the only known shell (re-illustrated here in Textfig. 3.4). The strong spiral ribs suggest that it does not belong to *Kittliconcha*. It is tentatively transferred to *Katosira* but could also represent a cerithioid.

4.3 Discussion of *Kittliconcha obesa* from the Middle Triassic of South China

Kittliconcha obesa YU, PAN & WANG, 1974 from the Middle Triassic Qingyan Formation of South China as described and illustrated by YIN HONG-FU & YOCHELSON (1983) seems to be similar to the type species of *Kittliconcha*. It is a relatively broad shell with prominent axial ribs. It lacks any spiral ornament. As in *K. obliquecostata*, the earliest teleoconch whorls of *K. obesa* are smooth. The protoconch of *K. obesa* is unknown. Nevertheless, *K. obesa* can be assigned to *Kittliconcha* according to the current state of knowledge.

4.4 Discussion of *Kittliconcha doelloi*, *K. peruviana*, and *K. dissimilis* from the Upper Triassic of South America

Kittliconcha doelloi BONARELLI, 1927 is based on a single specimen from the Pertrolifera Formation, Carbajal, Argen-

tina. This material is probably not of Triassic age but much younger (Mariel Ferrari, written communication 2010). This teleoconch fragment is poorly preserved and poorly illustrated. It is considered here as nomen dubium until the holotype is re-studied and topotypical material is found and described.

Kittliconcha dissimilis HAAS, 1953 and *K. peruviana* HAAS, 1953, both from the Late Triassic Pucara Formation, Peru are also problematic. Judging from HAAS's illustrations of these species, the type material is poorly preserved. The zygopleuroid shells are relatively stout and do resemble *Kittliconcha*. However, HAAS mentioned a spiral striation of the whorls which does not become obvious from the illustrations. This character would not suggest a placement in *Kittliconcha*. BANDEL (1994: 138) mentioned that *Kittliconcha dissimilis* and *K. peruviana* have a small and simple protoconch. I suggest leaving both species tentatively in *Kittliconcha* until more information becomes available.

4.5 Re-assignment of *Kittliconcha sciaphostera* from the Lower Triassic of Utah

Kittliconcha sciaphostera BATTEN & STOKES, 1986 (Early Triassic, Utah) does not belong to *Kittliconcha* and it is included here in the genus *Pseudotrionium* WENZ, 1940.

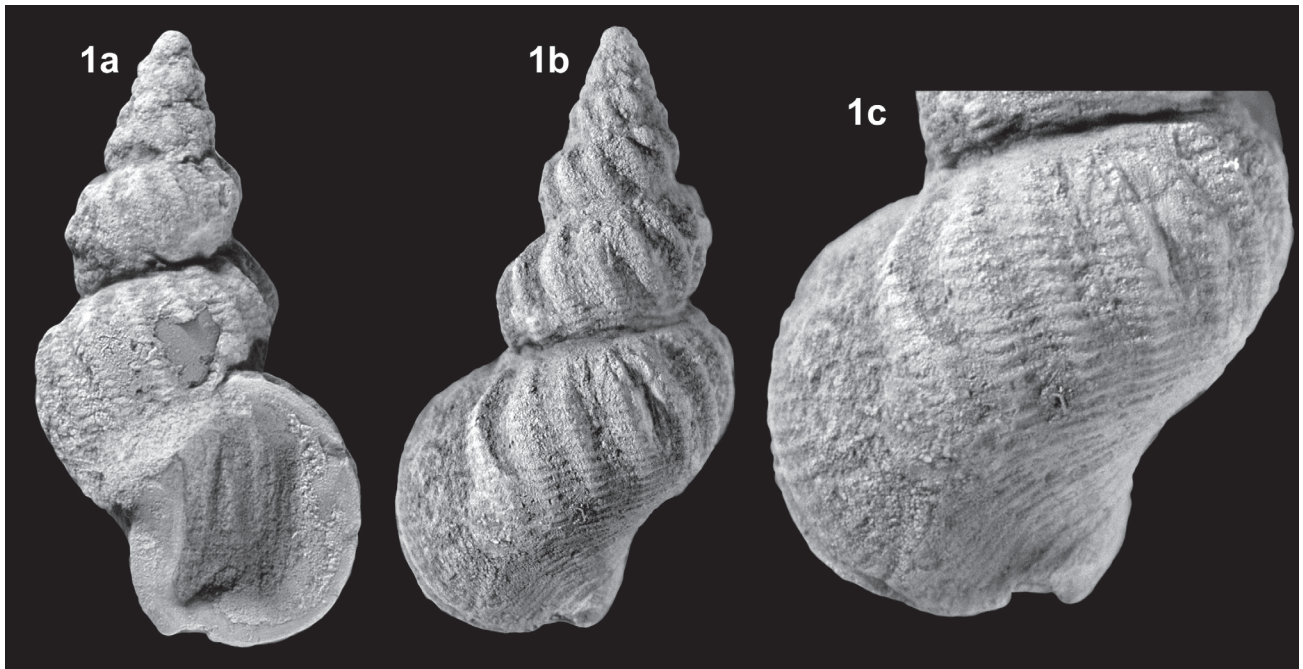
Family Maturifusidae GRÜNDEL, 2001
(= Pseudotrioninae GOLIKOV & STAROBOGATOV, 1987?)

Remarks: BANDEL (1994: 139) and BOUCHET et al. (2005) assigned *Pseudotrionium* (replacement name for *Palaeotrion* KITTL, 1894) to the family Purpurinidae. GOLIKOV & STAROBOGATOV (1987) erected the subfamily Pseudotrioninae based on this genus. Here, *Pseudotrionium* is preliminarily placed in the Maturifusidae. If *Pseudotrionium* and *Maturifusus* are really confamilial, then Maturifusidae GRÜNDEL would fall into the synonymy of Pseudotrionidae. However, synonymization should await a better knowledge of the type species of *Pseudotrionium*, *Scalaria venusta* from the Late Triassic Cassian Formation. So far, the protoconch of this species is insufficiently known (see below) and it would be important to document it better in order to clarify the relationship between *Pseudotrionium* and *Maturifusus*.

Genus *Pseudotrionium* WENZ, 1940
(replacement name for *Palaeotrion* KITTL, 1894)

Type species: *Scalaria venusta* MÜNSTER, 1841, Early Carnian, Cassian Formation; designation by Wenz (1940) (see Textfig. 4).

A lectotype for the type species *Scalaria venusta* MÜNSTER, 1841 from the Cassian Formation is selected here (BSPG AS VII 1871) (Textfig. 4). It is the specimen which was illustrated by MÜNSTER (1841: pl. 10, fig. 28) and KITTL (1894: pl. 11, fig. 3). *Pseudotrionium venustum* has a fusiform shell shape and a wide aperture. The aperture has a straight inner and a D-shaped outer lip. It seems to be siphonostomous. The teleoconch ornament is cancellate with oblique, opisthocline axial ribs which are crossed by numerous finer spiral lirae. The intersections of spiral lirae and axial ribs are not nodular at intersections



Textfigure 4: *Pseudotritonium venustum* (MÜNSTER, 1841), Lectotype, from the Late Triassic Cassian Formation, BSPG AS VII 1871; this species was illustrated by MÜNSTER (1841: pl. 10, fig. 28) and KITTL (1894: pl. 11, fig. 3); it resembles the Early Triassic *Pseudotritonium sciaphosterum*; 4.1a, b: 6.6 mm high, 3 mm wide; 4.1c: detail last whorl, 6.6 mm high.

which separates it from species of *Maturifusus* or *Astandes*. The Early Triassic *Pseudotritonium sciaphosterum* (BATTEN & STOKES), 1986 resembles *P. venustum* in general shape and in the cancellate teleoconch ornament.

Pseudotritonium sciaphosterum (BATTEN & STOKES, 1986)
Textfig. 5

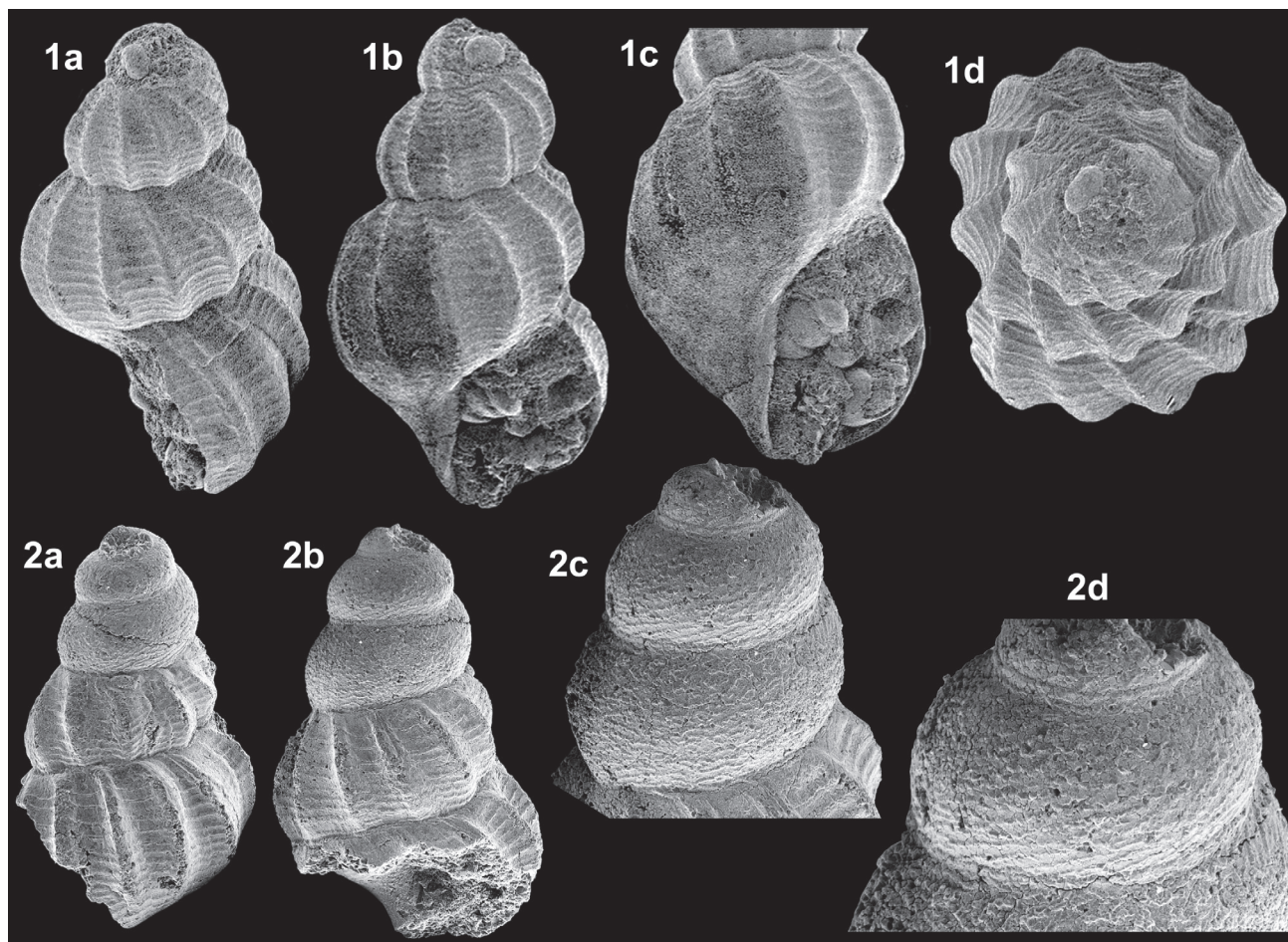
* 1986 *Kittliconcha sciaphostera* n. sp. BATTEN & STOKES: 19, figs 26–28.

Material: A paratype still fixed on a SEM-stub (AMNH 46314) (Textfig. 5.1) and a topotypical specimen with well preserved protoconch (BSPG 2010 IV 1) (Textfig. 5.2).

Description: *Pseudotritonium sciaphosterum* is a high-spired gastropod with an ornament of strong axial ribs crossed by finer spiral threads. The axial ribs are oblique, especially near the adapical suture; on later whorls, they may be almost orthocline to slightly opisthocyrt.

BATTEN & STOKES (1986) described the aperture as holostomous. However, the specimen from the type collection figured here (Textfig. 5.1b, c) shows an elongated aperture which seemingly has a siphonal notch. The protoconch was described as smooth and evenly inflated and is illustrated in BATTEN & STOKES (1986: fig. 28). The topotypical juvenile specimen illustrated here (Textfig. 5.2) is better preserved and shows the protoconch in detail. It consists of almost three whorls and is 0.44 mm high and 0.27 mm wide; the initial whorl has a diameter of 0.15 mm. The larval whorls are convex and somewhat adpressed so that a spiral band is present in a subsutural position. The larval shell is densely ornamented with faint, oblique threads.

Remarks: BATTEN & STOKES (1986) correctly pointed out that the teleoconch ornament of *Pseudotritonium sciaphosterum* closely resembles that of the Late Palaeozoic genus *Plocezyga* und *Gamizyga* (Pseudozygopleuridae) (see HOARE & STURGEON 1980; NÜTZEL 1998). They even synonymised these genera with *Kittliconcha*. However, *Plocezyga* and *Gamizyga* have a larval shell with strong parasigmoidal, collabral axial ribs which are typical for Pseudozygopleuridae. In contrast, *Kittliconcha* has a smooth larval shell (Pl. 1) and *Pseudotritonium sciaphosterum* has a non-collabral micro-ornament of oblique threads (Textfig. 5.2). The reticulate teleoconch ornament and the overall shape of *Pseudotritonium sciaphosterum* resemble that of the Jurassic/Cretaceous family Maturifusidae (e.g., KAIM 2004). The protoconchs of most *Maturifusus* species are largely smooth but have angulations accompanied by spiral ribs which gives them a step-like whorl profile. However, A. Kaim (written communication) showed me unpublished micrographs of a maturifusid larval shell with relatively strong non-collabral ornament. The protoconch of the species from the Cassian Formation which have been assigned to the genus *Pseudotritonium* (including that of the type species) are insufficiently known. According to KITTL (1894: pl. 11, figs 5, 9) the protoconch is heliciform and has an oblique axis to the teleoconch axis (but not heterostrophic). Such oblique protoconchs have been documented for some caenogastropods e. g., for the Jurassic species *Plocezyga gruendeli* KAIM, 2004. The teleoconch morphology of members of the Mesozoic caenogastropod family Purpurinidae resembles that of *Pseudotritonium sciaphosterum*. However, Purpurinidae normally have a subsutural ramp or shelf. The Hettangian type species of the cerithioid genus *Paracerithium* also resembles that of *Pseudotritonium sciaphosterum* (see GRÜNDEL 1997; HIKUROA & KAIM 2007). However, the axial ribs of *Paracerithium* are much stronger and form almost spines.



Textfigure 5: *Pseudotritonium sciaphostera* (BATTEN & STOKES, 1986) formerly assigned to *Kittliconcha*, Sinbad Limestone, Moenkopi Formation, San Rafael Swell Utah, Early Triassic. (5.1): Paratype, AMNH 46314; 5.1a, b: height 3.1 mm; 5.1c: detail last whorl and aperture, height 2.5 mm; 5.1d: apical view, diameter 1.8 mm. (5.2): Topotypical juvenile specimen with well-preserved protoconch, BSPG 2010 IV 1; 5.2a, b: height 0.83 mm; 5.2c: protoconch, height 0.47 mm; 5.2d: detail larval shell with non-collabral micro-ornament, height 0.24 mm.

5. Conclusions

Zygopleuroid caenogastropods play an important role in Mesozoic gastropod faunas. This group is difficult because high-spired teleoconchs with a dominant axial ornament have obviously evolved in various groups as a convergent feature. The re-study of the holotype of the type species of *Kittliconcha* helps clarify the systematic placement of some involved taxa. Ironically, the characters which were initially used to characterize *Kittliconcha* resulted from a repaired shell fracture. Only later it turned out that the genus is nevertheless valid because the protoconch morphology of *Kittliconcha* alias its junior synonym *Settsassia* is unlike that of other gastropods with zygopleuroid habitus. *Kittliconcha* is probably a representative of the cerithimorph stem line as is indicated by its small, smooth larval shell (see also BANDEL 1992). Similar protoconchs have been found in the Mesozoic basal cerithimorph genera *Campanile*, *Metacerithium*, and *Dzikella* (the latter is probably a synonym of *Metacerithium*) (KIEL et al. 2000; KAIM 2004; KIEL 2006). Therefore, a close phylogenetic relationship of Campanilidae and Settsassiidae seems to be possible. A relationship with Littorinimorpha or other basal caenogastropods is also possible. Only a single additional

Triassic species may actually represent *Kittliconcha*: *K. obesa* from the Middle Triassic of China. Three South American species which have been assigned to *Kittliconcha* are based on so poorly preserved and documented material that any generic assignment is basically speculative. The material from the Late Triassic Cassian Formation which was assigned to *Kittliconcha* by ZARDINI (1978) does not belong here. It represents the new sinistral genus *Triadosinister* and two species (including one new species) are tentatively assigned to the genus *Katosira*. The early Triassic species *Kittliconcha sciaphostera* also does not represent *Kittliconcha*. It is transferred to the purpurinid genus *Pseudotritonium*. Its cancellate ornament, shape, aperture, and the protoconch morphology suggest that this is one of the earliest members of an evolutionary line which leads to the Mesozoic family Maturifusidae which could be the stem-group of Neogastropoda (RIEDEL 2000; KAIM 2004; PONDER et al. 2008).

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