Mathildoidea (Gastropoda, Heterostropha) from the Late Triassic St Cassian Formation

Klaus Bandel

Bandel, K. Mathildoidea (Gastropoda, Heterostropha) from the Late Triassic St Cassian Formation. — Scripta Geol., 111: 1-83, 19 pls, Leiden, November 1995.
Klaus Bandel, Geologisch-Paläontologisches Institut, Universität Hamburg, Bundesstraße 55, D-20146 Hamburg, Germany.

Key words: Gastropoda, Heterostropha, Late Triassic, evolution.
In the St Cassian fauna of Late Triassic (Early Carnian) age gastropods with protoconch coiled in opposite direction to the teleoconch are common and belong to a number of quite different taxa. Twenty nine of these are here described, 11 of them for the first time: *Promathilda misurinensis* sp. nov., *Turrithilda cassiana* sp. nov., *T. dockeryi* sp. nov., *Tirolthilda seelandica* gen. et sp. nov., *T. nuetzeli* sp. nov., *Tofanella cancellata* sp. nov., *Cristalloella cassiana* gen. et sp. nov., *C. sinuata* sp. nov., *C. delicata* sp. nov., *Stuorilda cassiana* gen. et sp. nov., and *S. tichyi* sp. nov. All are newly defined and placed in the Mathildoidea. This connects the Triassic species of that superfamily with the modern Heterostropha (= Heterobranchia). In the family Mathildidae the genera *Mathilda* and *Promathilda* are differentiated, two species of *Turrithilda* described, and *Tirolthilda* and *Schroederilda* are included as new genera, with the type species *T. seelandica* gen. et sp. nov. and *Pseudotritonium millierense* Zardini, 1978, respectively. The new family Anoptychiidae holds the genera *Anoptychia*, *Turristylus* and *Camponella* gen. nov. (type species *Coelostylina pianozensis* Zardini, 1985). Here the juvenile ornament resembles that of the Mathildidae but differs from the later smooth teleoconch. Protoconch morphology differentiates the new families Tofanellidae, Trachoecidae and Ampezzanildidae. In contrast to the Mathildidae, Dolomitellidae and Anoptychiidae, the sinistral shell of the protoconch changes its direction of coiling within the larval part of the shell and not at the transition from larval shell to teleoconch. The Trachoecidae with the genera *Trachoecus* and *Vallandroella* gen. nov. (type species *Tyrsoecus antorni* Zardini, 1985) have a fusiniform shell. The Tofanellidae, with the genera *Tofanella* gen. nov. (type species *Turritella decussata* von Münster, 1841), *Cristalloella* gen. nov. (type species *C. cassiana* gen. et sp. nov.) and *Camponaxis* gen. nov. [type species *Cerithium* (?) *lateplicatum* Klipstein, 1843], differ from the Ampezzanildidae, with the genera *Ampezzanilda* gen. nov. (type species *Promathildia aialensis* Zardini, 1980), *Cassianilda* gen. nov. (type species *Turritella margaritifera* von Münster, 1841) and *Stuorilda* gen. nov. (type species *S. cassiana* gen. et sp. nov.), by the ornament of their protoconch. A key differentiates all described species, and the evolutionary history of the group is discussed.

Contents

Introduction 2
Localities 3
Depository of material studied 3
General morphology of mathildoid shells 4
Systematic part 4
Mathildidae 4
Anoptychiidae 16
Tofanellidae 21
Trachoecidae 29
Ampezzanildidae 32
Classification of the Mathildoidea 37

Key to the Mathildoidea of the St Cassian Formation 38
General discussion on heterostrophic gastropods of the mathildoid type 40
Acknowledgement 42
References 43

Introduction

Heterostrophic gastropods may form a monophyletic unit within the Gastropoda that can presently be traced back to the Early Carboniferous (Donald, 1898; Yoo, 1988, 1989; Bandel, 1992a) and probably even to the Middle Devonian (Bandel, 1994a). The Heterostropha probably originated during Early Paleozoic times, most likely during the Ordovician. In the modern fauna three large units of Heterostropha can be distinguished. These are the Allogastropoda, Opisthobranchia and Pulmonata. The anatomy of the Allogastropoda is intermediate between that of the Euthyneura (Opisthobranchia and Pulmonata) and the Caenogastropoda. The nervous system of the Allogastropoda is streptoneurous like that of the Caenogastropoda, and ganglia are not concentrated as is typical for the Euthyneura (Haszprunar, 1985a, b). The early ontogenetic shell is sinistrally coiled. During the growth of the larval shell or at the end of its formation, the shell switches to dextral coiling. The same change in the mode of shell coiling during early ontogeny is also characteristic of shell-bearing Euthyneura and is not found in the other subclasses of the Gastropoda such as the Caenogastropoda, Neritimorpha and Archaeogastropoda.

Modern Allogastropoda include the Architectonicoidea, Omalogyroidea, Pyramidelloidea, Valvatoidea, and Rissoelloidea according to the classification presented by Ponder & Warén (1988). According to this classification the Architectonicoidea are composed of the Architectonicidae with a low spirally coiled shell and the Mathildidae with a high turreted shell. The living members of both groups feed on coelenterates and live in fully marine environments. The Pyramidelloidea include numerous extant genera and species that exhibit a rather wide variety of shell forms. Relatively few of these have been studied anatomically, and their mode of life is little known. It appears that they are parasites which extract blood from a wide variety of marine invertebrates (see Fretter & Graham, 1986). The Valvatoidea contain the freshwater Valvatidae, feeding on algae and the marine Cornirostridae that live among seagrass in shallow water (Ponder, 1991). Ponder & Warén (1988) and Ponder (1990) tentatively placed the marine Orbitestellidae here as well. Rissoelloidea hold very small helicoid forms that live in littoral algal growths and have a non-planktotrophic development (Ponder, 1967).

A previous study of Late Triassic gastropods from the St Cassian Formation of the Dolomites near Cortina d'Ampezzo and St Cassian in the Italian Alps had shown these gastropods to include members of the Architectonicidae that had been misinterpreted as offshoots of the Palaeozoic Euomphaloidea (Bandel, 1988a). The presence of a number of species belonging to the Mathildidae had been known since Koken's (1889) reinterpretation of von Münster's (1841) originals. Several species of the genus *Promathilda* were described by Kittl (1894), most of which are well illustrated by Zardini (1978, 1980, 1985). Outside this genus the presence of a heterostrophic protoconch was noticed only in members of the genus *Acteonina*, which is considered

to represent an opisthobranch (Acteonoidea of Knight et al., 1960; Cephalaspidea of Wenz & Zilch, 1960).

Bizzarini et al. (1986) have dated the St Cassian Formation as Late Ladinian to Early Carnian. The gastropods represented in this study have lived in shallow water. Wendt & Fürsich (1980) demonstrated that basins and carbonate platforms existed very close to each other at the times of St Cassian deposition. Gastropods lived in great numbers on reefs growing on the transition from shallow warm carbonate lagoons to the open Tethys Ocean. They were preserved in clay-rich, often tuffaceous sediments of the basins into which they were slumped down along more or less steep slopes. The gastropods thus must be collected from basin sediments that have formed alongside with the carbonate platforms and their fringing reefs and from larger slumps that have moved down steep slopes (Blendinger & Blendinger, 1989). Localities rich in fossils have been described and located on a map by Zardini (1978).

Localities

The Cordevol Member of the St Cassian Formation is of Late Triassic (Early Carnian) age (Urlichs, 1994). The studied gastropod shells were found at several localities close to the towns of St Cassian in Southern Tirol and Cortina d'Ampezzo in the province Ampezzo, both in the Dolomites (Northern Italy)

The locality Alpe di Specie (Seelandalpe) is situated west of Schluderbach (Carbonin) on the road from Cortina d'Ampezzo to Toblach. Here the outcrops lie on a meadow below the Rifugio Vallandro (Dürrenstein Hütte) at a height of c. 2000 m.

Locality Misurina indicates outcrops along a ski lift at a height of c. 1800 m west of the Lago di Misurina situated east of Cortina d'Ampezzo.

Campo lies c. 1200 m high in the forest above Campo di Sotto, a part of the town of Cortina d'Ampezzo and is represented by a small foxhole-like outcrop.

Dibona represents strata of the St Cassian Formation exposed on the slope and in the forest at a height of c. 1800 m below Rifugio Dibona situated above the road from Cortina d'Ampezzo to the Passo Falzarego. This locality may be the same as the one called Milieres by Zardini (1978). Zardini also presented a map giving all mentioned localities.

Stuores and Pralongia are situated near St Cassian c. 15 km west of Cortina d'Ampezzo. Here the outcrops lie to the northwest of Settsass Mountain southwest of St Cassian. Their situation is illustrated by Urlichs (1994, fig. 1). Stuores is an ever-changing slump outcrop at the northern side of Pralongia ridge at a height of c. 2100 m and Pralongia represents the steep slope below the ridge toward Corvara. With the exception of the Pralongia locality which belongs to the *Trachyceras aon* Zone, the other localities expose beds of the *Trachyceras aonoides* Zone (Urlichs, 1994).

Depository of material studied

Samples studied in this paper are housed mainly in the Geologisch-Paläontologisches Institut, Universität Hamburg, Hamburg (Germany) (GPIH). Holotypes are stored in the Naturhistorisches Museum at Vienna (Austria) (NHM) with registration numbers 1994/162-172. Paratypes and additional material of various species has been

deposited into the collections of the Nationaal Natuurhistorisch Museum (Palaeontology Department) (= former Rijksmuseum van Geologie en Mineralogie) at Leiden (The Netherlands) (registration numbers RGM 219 001-056 and RGM 344 963).

General morphology of mathildoid shells

The shells here described usually have a slender turriform teleoconch with spiral sculpture often much stronger than the axial sculpture and a protoconch of very different shape and ornament. The teleoconch was produced by the metamorphosed animal throughout its life in the benthos.

The protoconch consists of an embryonic and a larval shell. The embryonic shell portion can be distinguished from the larval shell portion in such species that hatched from the egg mass as planktotrophic veliger larvae. In cases where the larval stage was nearly completed within the egg mass or where the young left the egg mass after metamorphosis, the embryonic shell cannot be differentated from the larval shell, but both are included in the protoconch. In all cases studied here the protoconch is clearly differentiated from the teleoconch by a drastic change in ornamentation.

The visible portions of the whorls of the teleoconch within the spire are the flanks which have the upper parts in apical position and the lower parts in apertural position. The aperture is usually of somewhat drop-shaped outline with an indistinct broad anterior groove or canal that lies between columellar and outer lip which may be called the apertural notch.

Systematic part

Superfamily Mathildoidea Dall, 1889

Description — Elongated shell with many whorls. Teleoconch ornament of spiral and axial elements. The protoconch has a sinistral embryonic shell and twists into dextral coiling at or before the end of the larval shell.

Diagnostic difference — Streptacidoidea Knight, 1931 have a similarly high-spired shell but an ornament of spiral lirae and/or growth lines, but no axial ribs (Bandel, in press). The Architectonicoidea Gray, 1840 consist of low-spired to flatly coiled species (Bieler, 1988; Bandel, in press). In the Nerineoidea Zittel, 1873 the internal whorl diameter is decreased by plicae arising from columellar and outer walls.

Family Mathildidae Dall, 1889

Diagnosis — The shell is slender, turriform and ornamented. The whorls are rounded and aperture is subcircular in outline with a short anterior canal. The protoconch twists into dextral coiling at the end of the larval shell.

Description — The small elongated shell with many whorls is sculptured by spiral carinae that may be crossed by collabral costae or growth lines. The aperture is subcircular. The protoconch is sinistral and rests on the dextral teleoconch at a right angle or an angle smaller than 90° between the axis of the larval shell and the axis of

the adult shell. The larval shell is low conical with rounded whorls that may show some axial folds on the apical and umbilical sides. Just before the onset of the dextral teleoconch the shell twists into planispiral coiling. The onset of the teleoconch is always abrupt and connected with a change in sculpture.

Genus *Mathilda* Semper, 1865

Type species — *Turbo quadricarinatus* Brocchi, 1814.

Description — The elongated shell may reach 3 to 4 cm in height, but may also be small, has more than 10 whorls, and shows a sculptural pattern consisting of strong spiral costae crossed by fine to coarse collabral radial ribs, forming a reticulated pattern. The first 5-9 whorls show at least two main spiral carinae, and additional and secondary ones may be added later. The aperture is roundish, and the margin of the apertural lip is not continuous at the inner lip, which represents only a thin shell layer on the prior whorl. The protoconch is sinistral, forms a low helical coil, and is immersed in the apex of the teleoconch at 90° or less. The embryonic shell may lie free at the apex or may be partly covered by the first whorl of the teleoconch.

Most modern species of the genus are smaller than the type species and have a shell of less than 30 mm height. A factor uniting all is the reticulate sculptural pattern of usually dominant spiral cords and axial costae that may be of different width. The size of the larval shell varies from c. 0.2 to 0.5 mm in width. The type species *Mathilda quadricarinata* (Brocchi, 1814) lives in the sublittoral rubble down to 30 m depth in the Mediterranean Sea off southern Italy (Sabelli & Spada, 1978), and reaches a height of 30 mm. It has quite a large larval shell that is c. 0.5 mm in width (Gründel, 1973, 1976).

Remarks — Based on data presented by Koken (1889), Kittl (1894), Cossmann (1912), and Wenz (1939), Haas (1953) expressed the opinion that the growth lines of *Mathilda* differ from those of *Promathilda*. The lines of the first are supposed to be straight, and the second are described to be bent toward the main keel. Such a difference does not exist, and growth lines of *Promathilda* and *Mathilda* are similar to each other; for genuine differences see *Promathilda*.

Mathilda biserta (von Münster, 1841)
Pl. 1, figs. 1-8.

1841 *Cerithium bisertum* von Münster, p. 122, pl. 13, fig. 44.
1869 *Cerithium Koninckeanum* Laube, p. 5, pl. 29, fig. 6.
1894 *Promathildia biserta* Kittl, p. 220, pl. 9, figs. 18-23.
1978 *Promathildia subnodosa*, Zardini, p. 50, pl. 35, fig. 5.

Description — The protoconch, general character and sculpture of the teleoconch are conform to the the generic description. The embryonic shell measures c. 0.1 mm in diameter and is almost totally covered by the first whorl of the teleoconch. The larval shell is up to 0.3 mm wide and forms one additional whorl that has an ornament of axial folds on the umbilical side. Folds appear where the coiling changes from sinistral to dextral. The apertural margin of the pediveliger is thickened forming a rounded rim.

The first whorls of the teleoconch are sculptured by two spiral keels of about equal size, which are crossed by 20 (first postnuclear whorl) to 30 (fourth whorl) regularly spaced axial ribs. Additional spiral keels may appear after the 6th whorl. The base of early teleoconch whorls carries only one spiral rib, but ribs increase in number at later whorls. With 4 teleoconch whorls two basal spiral lines are present and with 7 whorls five such lines are seen. The spiral keels are crossed by the axial costae without forming tubercules or ridges on the first 4-5 whorls of the teleoconch. Later 8 costules form rounded projections of variable size with the axial ribs.

The apical angle of the teleoconch decreases somewhat with growth of the shell and amounts to c. 21° when fully grown. The aperture is higher than wide, almost straight at its columellar side, forms a shallow notch at its frontal end, and has a rounded outer lip that forms an angle with the uppermost spiral keel.

Diagnostic differences — *Mathilda biserta* differs from the species of *Promathilda* by two about equally strong spiral keels on the juvenile teleoconch that succeeds the protoconch. From *Promathilda subnodosa* and *P. decorata* it also differs by the slope of the whorl section that is of trapezoidal shape. *Mathilda bolina* differs from *M. biserta* by its larger apical angle and less inclined protoconch. *Tirolthilda seelandica* has a smaller apical angle, the protoconch deviates more strongly from the early teleoconch, and it develops no axial ribs in the later teleoconch. *Cassianilda* has an ampezzanildid protoconch while its teleoconch resembles that of *Mathilda biserta*.

Material — Alpe di Specie (numerous specimens, GPIH; 13 specimens, RGM 219 001); Misurina (2 specimens, GPIH; 1 specimen, RGM 219 002); Campo (several specimens, GPIH).

Remarks — Koken (1889, p. 459, fig. 25) noted and illustrated the heterostrophic protoconch of *Mathilda biserta*. Gründel (1976) thought that *M. biserta* had only a spiral sculpture and no axial costae in the first whorl of the teleoconch. This assumption, based on statements by Koken (1889), cannot be confirmed. Kittl (1894) even doubted the possibility of an exact identification of the young shell studied by Koken (1889) since (in his opinion) only older shells allow the exact identification of the species. This statement can also not be supported. According to Kittl (1894) *Mathilda biserta* shells without the protoconch are difficult to distinguish from those of *Cassianilda margaritifera* (*'Promathildia'*), and the only distinctive character of the adult shell is supposed to be the presence of three keels on all adult whorls in *C. margaritifera*, whereas only two keels should be present in *M. biserta*. This cannot be confirmed.

Mathilda bolina (von Münster, 1841)
Pl. 2, figs. 1-4, 6.

1841 *Turritella Bolina* von Münster, p. 118, pl. 13, fig. 11.
1894 *Promathildia Bolina*, Kittl, p. 217, pl. 9, figs. 6-9.
1912 *Teretrina bolina*, Cossmann, p. 6, fig. 3.
1978 *Promathildia bolina*, Zardini, p. 50, pl. 35, fig. 3.

Description — This species very closely resembles *Mathilda biserta* in ornament, but differs in apical angle, which is larger (40-50°). The apical angle decreases in the younger whorls, so that the tangents of the teleoconch are slightly concave. The protoconch lies flatly on the top of the teleoconch with the embryonic whorl totally

covered. The protoconch measures 0.27 mm in diameter and consists of 1.7 whorls which are smooth and coiled along almost the same axis as the teleoconch, but in the opposite way. Coiling switches to dextral in the last fourth of the larval whorl. Here some individuals have weak axial folds, others are smooth. The inner lip of the aperture may form a narrow pseudumbilicus with the columella.

Diagnostic differences — Among those mathildids of the St Cassian Formation that have two strong keels of almost equal strength on the whorls of their teleoconch *Mathilda bolina* has the widest shell. *M. biserta* is of intermediate shape while *Tirolthilda seelandica* is the most slender form. Regarding protoconch morphology that of *Mathilda bolina* lies flat on the apex, that of *M. biserta* shows part of the embryonic whorl between larval shell and first teleoconch, and that of *T. seelandica* forms an angle of c. 45° with the teleoconch. Whilst *M. bolina* and *T. seelandica* have only regular fine axial lines, in *M. biserta* some of these increase in width with age and form axial ribs. *Turrithilda cassiana* resembles *Mathilda bolina* in the sculpture of the teleoconch, but is more slender and has four spiral ribs on the first teleoconch whorl.

Material — Alpe di Specie (numerous specimens, GPIH; 1 specimen, RGM 219 004); Misurina (numerous specimens, GPIH; 2 specimens, RGM 219 003).

Remarks — Cossmann (1912) prepared a new drawing of *Turritella bolina* von Münster, 1841 from Kittl's (1894, pl. 9, figs. 6-9) illustrations idealising the aperture which became larger than in the original drawings. He used this species as the base for his new genus *Teretrina*. In the diagnosis he differentiated *Teretrina* from *Promathildia* by having two carinae crossed by fine axial threads on a shell of wider angle than in *Promathildia* and with subpentagonal aperture. Perhaps the taxon *Teretrina* can be of use when the extant *Mathilda* is to be differentiated from the Triassic species here regarded to represent members of this genus.

Genus *Promathilda* Andreae, 1887

Type species — Koken (1889) (not Cossmann, 1912, as suggested by Gründel, 1976) designated '*Cerithium bisertum* von Münster, 1841' as type species of *Promathilda* Andreae, 1887, but he actually figured and described a shell of *Fusus subnodusus*. Type species of *Promathilda* therefore is *Cerithium bisertum* Koken, 1889, non von Münster, 1841 = *Fusus subnodosus* von Münster, 1841.

Description — The protoconch is essentially like that of *Mathilda*. The early whorls of the teleoconch, in contrast, have only one dominant spiral keel that is crossed by minor axial elements. It is accompanied by none to several minor spiral elements. Axial collabral costules and growth lines may form tubercules and raised ridges where they cross the spiral keels and costae.

Diagnostic difference — In *Promathilda* teleoconch sculpture starts with one dominant spiral rib, while *Mathilda* and *Tirolthilda* have here two subequal ribs, and *Turrithilda* has four such ribs. In general teleoconch shape and sculpture these genera are similar to each other. *Promathilda* also differs from *Mathilda* by a continuation of dominance of one spiral keel over the other spiral elements in later whorls, and in the formation of tubercules and ridges where axial folds intersect spiral elements.

Remarks — According to Schröder (1995) the correct spelling is *Promathilda* and not *Promathildia*, as commonly used for example by Kittl, Cossmann, and Zardini.

Kittl (1894) described this species in detail as *Promathildia biserta*, but figured a juvenile specimen of *Promathilda subnodosa* to characterise the early ontogenetic shell. Cossmann (1912), in his description of the genus *Promathildia*, figured the adult shell of *P. biserta*, redrawn from an unknown source and the young shell of *P. subnodosa* redrawn from Kittl (1894, pl. 9, fig. 36). Cossmann expressed the opinion, that the young shell of *P. subnodosa* demonstrates the characteristics of the genus and that it also applies for *P. biserta*. This argument has been repeated by Gründel (1976) who expressed the opinion that the *Mathilda* type of early shell sculpture arose from that of *Promathilda* not earlier than the Jurassic. This is clearly not the case, and the difference is noted in the Triassic species. To preserve the genus *Promathilda* and differentiate it from *Mathilda*, the type has to be changed from *M. biserta* to *P. subnodosa*. Members of both genera lived in the shallow waters of the St Cassian sponge reefs.

Promathilda subnodosa (von Münster, 1841)
Pl. 1, figs. 5, 6; Pl. 2, figs. 1-4, 6, 7.

1841 *Fusus subnodosus* von Münster, p. 124, pl. 13, fig. 51.
1894 *Promathildia subnodosa* Kittl, p. 224, pl. 9, figs. 36-45.
1978 *Promathildia tyrsoecus* Kittl-Zardini, p. 51, pl. 35, fig. 15.
1980 *Promathildia subnodosa* Zardini, p. 10, pl. 5, figs. 1-3.
For an extended synonomy see Kittl (1894).

Description — The slender turriform shell bears a median to submedian spiral keel, and two smaller spiral ribs, one within or just above the suture, and the other some way below the suture. The spiral keels dominate over collabral elements in early whorls of the teleoconch. Spiral costae above and below the suture as well as the median keel appear in the first whorls that succeed the protoconch. Eight axial folds appear in the fourth whorl and slowly increase in number in succeeding whorls until they are 16 per whorl. Folds cross the spiral costae forming acute tubercules with them. In shells of almost 20 mm length, rows of tubercules become the most prominent sculptural element. Such a shell is illustrated by Zardini (1978, pl. 35, fig. 15) and identified as *Promathildia tyrsoecus* Kittl, 1894. The aperture is as wide as high and bears a straight columellar lip and a rounded outer lip. The apical angle in the first four whorls of the teleoconch is c. 25° and later decreases to 21°.

The protoconch measures c. 0.17 mm in width and height and consists of an embryonic whorl, largely covered and hidden by the subsequent smooth larval shell. Weak folds may appear near the wide umbilicus of the protoconch that is oriented upwards. Transition into the dextral whorl occurs in the final portion of the larval shell as is the case in *Mathilda bolina*. The axis of coiling of the larval shell forms an angle of c. 25° or less with the axis of coiling of the adult shell.

Diagnostic differences — *Promathilda subnodosa* differs from *P. sculpta* and *P. decorata* by the smooth early whorls of the teleoconch. These are decorated by axial ribs in the two latter species. Later teleoconch whorls of *P. subnodosa* develop stronger axial ribs than the two other species. *Promathilda misurinensis*, in contrast, has no axial ribs.

Material — Alpe di Specie (1 specimen, GPIH; 5 specimens, RGM 344 963); Misurina (2 specimens, GPIH; 1 specimen, RGM 219 005).

Promathilda decorata (Klipstein, 1843)
Pl. 4, figs. 1-5, 7.

1843 *Turritella decorata* Klipstein, p. 175, pl. 11, fig. 12.
1869 *Cerithium decoratum*, Laube, p. 7, pl. 29, fig. 9.
1894 *Promathildia decorata*, Kittl, p. 219, pl. 9, figs. 11-17.
1978 *Promathildia subnodosa*, Zardini, p. 50, pl. 35, figs. 4, 6-8.
1980 *Cheilotoma ampezzana* Zardini, p. 14, pl. 6, fig. 6.

Description — A 3.5 mm high shell has 7.5 whorls in the teleoconch and a maximum width of a little more than 1 mm. The apical angle is c. 22° in the juvenile shell and 15° in the adult shell that may reach a height of 8 mm. The whorls of the early teleoconch have a central keel flanked above and below by smaller spiral ribs. From the beginning of the teleoconch the dominant median keel and the upper spiral rib below the suture and the lower rib right in the suture are crossed by fine, regular, collabral ribs. An additional pattern of spiral threads is present between the ribs. At later whorls of the teleoconch axial ribs produce an undulating pattern of the median keel which may migrate slightly downward or remain in the centre of the whorl. It continues to produce a triangular shape in whorl section. The aperture is higher than wide and ends in a distinct siphonal notch. An additional strong spiral rib and several smaller ribs are present on the base and become covered by the inner lip of the subsequent whorl.

The protoconch is almost 0.35 to 0.4 mm wide and is shaped like that of *Mathilda biserta*. It displays radial folds around the umbilicus that do not cross the rounded flank but reappear on the apical side of the larval shell. The smooth embryonic whorl is largely covered by the first whorl of the teleoconch. The boundary with the teleoconch and thus the apertural margin of the former pediveliger is thickened by a rim.

Diagnostic differences — *Promathilda decorata* differs from *Mathilda biserta* by the ornament of the early teleoconch where the central keel is flanked on each side by spiral ribs. The ornament of the teleoconch of *Promathilda subnodosa* differs even more. In *P. decorata* the switch from left to right coiling occurs in the transition from protoconch to teleoconch, while at *P. subnodosa* this change is within the last part of the larval shell.

Material — Alpe di Specie (7 specimens, GPIH; 6 specimens, RGM 219 008); Misurina (4 specimens, RGM 219 006); Campo (numerous specimens, GPIH; c. 30 specimens, RGM 219 007).

Promathilda sculpta (Kittl, 1894)
Pl. 3, fig. 8; Pl. 4, figs. 6, 8, 9; Pl. 5, figs. 1, 3.

1894 *Promathildia sculpta* Kittl, p. 227, pl. 10, figs. 18-19.

Description — A shell with 6 whorls of the teleoconch is c. 4 mm high and has an apical angle of c. 30°. A smaller subsutural keel above the central one appears on the fifth whorl. Kittl (1894) based this species on a larger shell that had no younger (juvenile) whorls. The prominent central keel moves from central position to the lower flank in older (more basal) whorls. Fine spiral costae and the median keel are trans-

sected by numerous collabral costulae forming a fine network of rectangles and tubercules on the keel.

The protoconch measures almost 0.4 mm in diameter and consists of a smooth embryonic shell that is largely covered by the first whorl of the teleoconch and more than one larval whorl with well rounded sides. While the marginal flank is smooth, the apical and umbilical flanks are ornamented by rounded folds. The aperture of the pediveliger is thickened by a rim.

Diagnostic differences — The adult shell of *P. sculpta* has fine and dense spiral striation below the keels which contrasts to *Promathilda subnodosa*. The protoconch is larger than that of *Promathilda decorata* but quite similar in shape, ornament and position on the teleoconch. The teleoconch of *P. sculpta* differs from that of *P. decorata* by the presence of more coarsely developed spiral striation.

Material — Alpe di Specie (1 specimen, RGM 219 009); Campo (1 specimen, RGM 219 010); Misurina (2 specimens, RGM 219 011).

Remarks — Kittl (1894, pl. 9, fig. 36) demonstrated the heterostrophic protoconch of *Promathildia subnodosa*, and his observations are supported here. At his drawing the onset of the teleoconch sculpture is indicative of *Promathilda subnodosa* as well as *P. sculpta* of which he did not know the juvenile shell. Zardini (1978) illustrated shells without the juvenile portions that may possibly belong to *Promathilda subnodosa*, under a number of names, like *P. margaritifera* (von Münster) (pl. 35, fig. 10), *P. decorata* (Klipstein) (pl. 35, fig. 12), *P. biserta* (von Münster) (pl. 36, figs. 16,17), *P. perarmata* (von Münster) (pl. 36, fig. 20).

Promathilda misurinensis sp. nov.
Pl. 5, figs. 2, 4, 5.

Holotype — Specimen of Pl. 5, figs. 2, 4 (NHM 1994/162).

Locus typicus — Misurina (see details in the Introduction).

Stratum typicum — Cordevol Member, St Cassian Formation (Late Triassic, Early Carnian).

Derivatio nominis — This species is named after the type locality Misurina.

Diagnosis — This species of the genus *Promathilda* has spiral ribs like *P. subnodosa* but no axial ribs added to it later. The median keel is the more prominent one of the three spiral ribs present on the sides. The whorl profile is lower than is the case in *P. subnodosa*.

Description — The slender shell with c. 9 whorls measures c. 2.5 mm in height and 0.8 mm in width with an apical angle of c. 20° in the early teleoconch decreasing to 14° in the later part. The protoconch measures almost 0.2 mm across and consists of c. 1.5 whorls situated almost flatly on the apex of the teleoconch. It resembles the larval shell of *Promathilda sculpta*. Initially, the teleoconch is sculptured by a strong spiral rib which rapidly develops into the keel that features the top of the lower third of the flank of the whorl. It is accompanied by a spiral rib below the suture and another one just above it partly covered by the subsequent whorl, as is the case in *P. decorata*. Only simple growth lines cross the spiral ornament. The aperture is about as wide as high, and the inner lip is somewhat thickened and convex.

Diagnostic differences — *P. misurinensis* resembles the other three species of the

genus *Promathilda* described above in general shape of the shell, but differs in its lack of an axial ornament. *Mathilda tomaszina* Schröder, 1995, from the Early Cretaceous, is similar due to its having only simple growth lines as axial sculptural elements, but its median keel is stronger, and the protoconch not as flat as it is in *P. misurinensis*. *Gymnothilda levata* Schröder, 1995, from the same Early Cretaceous occurrence in Poland, differs by the two spiral ribs that accompany the keel.

Paratypes — Misurina (several specimens, GPIH; 3 specimens, RGM 219 012); Campo (several specimens, GPIH; 1 specimen, RGM 219 013).

Genus *Turrithilda* Schröder, 1995

Type species — *Turritella opalina* Quenstedt, 1858 from the Middle Jurassic (Aalenian) of northern Germany.

Description — The turriform shell has a teleoconch with 4 or more spiral ribs present at the beginning of the teleoconch. These spirals are overrun by collabral ribs forming a regular pattern of rectangles. The whorls are convex, and therefore the sutures are deep. The aperture is rounded, with the inner lip slightly thickened and almost straight. The protoconch is sinistrally coiled and clearly separated from the teleoconch.

Diagnostic difference —*Turrithilda* is distinguished from the other genera of the Mathildidae from the St Cassian Formation by the onset of the teleoconch with an ornament of four spiral lirae succeeding a mathildid protoconch.

Turrithilda cassiana sp. nov.
Pl. 7, figs. 1-5.

1978 *Promathildia bolina*, Zardini, p. 50, pl. 41, fig. 6.

Holotype — Specimen of Pl. 7, fig. 3 (NHM 1994/163).

Locus typicus — Dibona (see details in the Introduction).

Stratum typicum — Cordevol Member, St Cassian Formation (Late Triassic, Early Carnian).

Derivatio nominis — This species of the genus *Turrithilda* is named after the St Cassian Formation.

Diagnosis — The description of the genus *Turrithilda* applies to this species. The slender shell with an apical angle of 17° has four spiral ribs visible on the flanks and two more on the base. Spiral ribs are crossed by collabral ribs forming a regular network of rectangles. The upper flank is flattened and bears very fine spiral lirae which increase in number with growth. The aperture is as wide as high. The protoconch is smooth with rounded whorls. The axis of coiling of the protoconch is almost the same as that of the teleoconch, but coiling modes are opposite to each other.

Description — A shell with almost 3 mm length has 6.5 teleoconch whorls. The apical angle remains the same from the first whorl of the teleoconch onward, whereas the protoconch forms a flattened apex. It consists of almost 1.5 whorls with the embryonic part dipping sinistrally below surface. The simple rounded margin of the pediveliger is thickened by a rim, and the shell is almost 0.2 mm wide. The portion

of the protoconch that had been formed by the planktotrophic larva becomes planispiral prior to its change into the teleoconch. The axis of coiling deviates a little from that of the teleoconch. The ornament of the teleoconch starts abruptly. The main ornament consists of spiral ribs, there is also a fine spiral liration. Axial elements are not quite as regular on the early teleoconch whorls as on later ones. The aperture has a rounded outer lip, a straight columellar lip and a flattened apertural notch. A narrow pseudumbilicus lies next to the upturned columellar lip.

Diagnostic difference — *Turrithilda cassiana* closely resembles *T. opalina* from the Middle Jurassic (Schröder, 1995). It differs in having a smaller protoconch and a less regularly reticulate ornament of the teleoconch.

Paratypes — Dibona (6 specimens, RGM 219 014).

Turrithilda dockeryi sp. nov.
Pl. 7, figs. 6-8.

1894 ? *Rhabdoconcha triadica* Kittl, p. 180, pl. 8, figs. 9-10.

Holotype — Specimen of Pl. 7, fig. 8 (NHM 1994/164).

Locus typicus — Alpe di Specie (see details in the Introduction).

Stratum typicum — Marls of the Cordevol Member, St Cassian Formation (Late Triassic, Early Carnian).

Derivatio nominis — The species is named after David T. Dockery III (Jackson, Mississippi, USA), a good friend and colleague.

Diagnosis — The description of the genus *Turrithilda* applies to this species. The turreted shell with an apical angle of 35° has 4 spiral ribs visible on the flanks of the first teleoconch whorl. The number of ribs increases with growth of the teleoconch. Spiral ribs are crossed by collabral ribs, and both form a regular net of rectangles to each other. The aperture is as wide as high. The protoconch is smooth with rounded whorls, and its axis of coiling deviates only little from that of the teleoconch.

Description — A shell with 5 whorls is 1.2 mm high. The ornament of the rounded whorls of the teleoconch consists of spiral and axial ribs at increasing numbers that form a net of rectangles to each other. The aperture is a little wider than high with a straight inner lip and reflected columellar lip. The anterior part of the outer lip forms a broad notch whilst its remainder is well rounded. Whorls are wider than high.

The protoconch consists of 1.6 smooth and rounded whorls of which the embryonic portion is clearly sinistral and dips below the apical surface. At the larval portion of the protoconch the sinistral coiling changes into planispiral coiling, and dextral coiling begins with the onset of the teleoconch. The protoconch measures c. 0.2 mm in diameter and deviates with a small angle from the axis of the teleoconch.

Diagnostic difference — The larger apical angle of the teleoconch, the increasing number of spiral ribs with teleoconch growth, and the more evenly convex whorl profile distinguishes *Turrithilda dockeryi* from *T. cassiana*. *T. opalina* from the Middle Jurassic has a protoconch that forms almost an angle of 90° with the teleoconch. Its teleoconch is more slender than that of *T. dockeryi*, but otherwise very similar. Differences to *Echinimathilda parvula* (Sohl, 1960) from the Ripley Formation of Mississippi are small. The protoconch of this Late Cretaceous species is slightly larger and its

axis is the same as that of the teleoconch (Dockery, 1993, pl. 30, figs. 1-3). At the later whorls of the teleoconch the spiral ornament dominates over axial ribs with the species of the genus *Echinimathilda* Sohl, 1964, in contrast to *Turrithilda* where both elements retain similar dimensions.

Material — One specimen from the type locality Alpe di Specie (GPIH). A further individual was found at Misurina (RGM 219 015) and three more were studied from Dibona (GPIH).

Remarks — The description and illustration of *Rhabdoconcha triadica* Kittl, 1894 are insufficient to compare it successfully with *Turrithilda dockeryi*. Both have a similar apical angle, but Kittl (1894) noted that the 6 shells studied by him from the St Cassian Formation have no apical whorls preserved. He placed his species in the genus *Rhabdoconcha* Gemmellaro, 1878, which is based on a slender species from the Early Jurassic of Sicily. The protoconch of that species is also unknown, but the genus is considered to belong to the Pseudomelaniidae of the Subulitoidea by Wenz (1939). Kittl (1894) had regarded *Rhabdoconcha* to represent a loxonematid genus. Neither true subulitids nor true loxonematids have heterostrophic shells (Bandel, 1993a).

Genus *Tirolthilda* gen. nov.

Type species — *Tirolthilda seelandica* gen. et sp. nov. from the St Cassian Formation.

Derivatio nominis — The genus is named after the Tirolian locality of the Seelandalpe (Alpe di Specie), south of Toblach (southern Tyrol, Italy).

Diagnosis — The high-spired, slender, turritelliform shell has flattened whorl flanks of the teleoconch and a sinistral protoconch. The early teleoconch succeeding the larval shell is sculptured by two keels of equal strength just above and below the suture and separated from each other by a plane area occupying most of the surface of the whorl. Numerous, fine collabral, axial ribs or growth lines are present. The keels of succeeding whorls and the suture between them form a regular V-shaped depression. The aperture is subcircular, and the base is rounded and covered by several spiral ribs.

Differences — The sculpture of the teleoconch consists of two dominant keels without nodes that results in a flat median ribbon. This ornament contrasts to the other mathildids and tofanellids from the St Cassian Formation that have also axial elements at their ornament and usually one spiral rib dominating over the others in magnitude.

Remarks — Kittl (1894) included specimens of *Tirolthilda seelandica* within the varieties of *Promathildia biserta*. Zardini (1978) placed this species with *Promathildia peracuta*, recognising a short and a long variety. He agreed with Leonardi & Fiscon (1959) who tentatively placed a short and a long form of similar shape under this heading and connected *Tirolthilda* with *Flemingia peracuta* Kittl. But *Flemingia* represents a member of the caenogastropods (Bandel, 1993b) so that this genus can not be utilised for a heterostrophic species.

Tirolthilda seelandica sp. nov.
Pl. 5, figs. 6, 8-10.

1894 *Promathildia biserta*, Kittl, p. 220, pl. 9, figs. 18-19.

1959 *Promathildia ? peracuta*, f. *elongata*, Leonardi & Fiscon, p. 86, pl. 9, figs. 14-15, 20.
1978 *Promathildia peracuta* forma *elongata*, Zardini, p. 52, pl. 35, figs. 24-25.

Holotype — Specimen of Pl. 5, fig. 6 (NHM 1994/165).

Locus typicus - Alpe di Specie (Seelandalpe) (see details in the Introduction).

Stratum typicum — Marls of the Cordevol Member, St Cassian Formation (Late Triassic, Early Carnian).

Derivatio nominis — This species is named after its type locality.

Diagnosis — Two strong spiral ribs turn into keels and have a flattened area of the whorl flank between them. Below and above this plane ribbon between keels the flank is concave and forms a V-shaped depression with the suture. The sinistral protoconch lies in inclined position on the dextral teleoconch, has umbilical folds and a thickened apertural margin.

Description — With 13 whorls of the teleoconch the shell is 9 mm high and almost 2 mm wide. The apical angle decreases during growth of the early teleoconch until it is c. 16°. The apex of the teleoconch thus appears pointed. The inclined protoconch measures 0.17-0.18 mm in diameter. It consists of c. 1.5 whorls with three quarter whorls that belong to the embryonic part. The larval shell bears strong folds where it twists into the dextral coiling mode. The aperture of the fully grown pediveliger shell is commonly thickened by a rounded rim. The teleoconch begins with an ornament of 2 equally strong spiral ribs and c. 16 axial riblets on smooth background forming a regular pattern of rectangles. From the third whorl of the teleoconch onward the two spiral ribs turn into keels while axial riblets remain narrow as before. The flank between the spiral keels becomes broader and flattened. The flanks of the keels in apical and apertural direction slope into a groove that contains the suture in its centre. A third spiral keel lies below the suture. The flattened base is ornamented by 3 fine spiral lirae, axial elements are absent. The aperture is about as wide as high with a short straight columella, a small siphonal notch, and a well rounded outer lip. There is a narrow pseudumbilicus in such cases where the thickened columellar lip forms a slit at the base of the body whorl.

Diagnostic differences — The presence of two keels on the flanks with a plane area between them reminds one of *Cassianilda margaritifera*. While *Tirolthilda seelandica* has a mathildid protoconch that of *Cassianilda* is ampezzanellid. *Tirolthilda nuetzeli* differs by having a flat apex. *Mathilda biserta*, *M. bolina* and *Turrithilda cassiana* also have two dominant keels on their flanks but they are less regular, connected to axial ribs and have a central depression between them.

Material — Alpe di Specie (> 40 specimens, GPIH; 11 specimens, RGM 219 016); Misurina (3 specimens, RGM 219 017).

Tirolthilda nuetzeli sp. nov.
Pl. 6, figs. 1-5.

Holotype — Specimen of Pl. 6, fig. 1 (NHM 1994/166).

Locus typicus - Misurina (see details in the Introduction).

Stratum typicum — Marls of the Cordevol Member, St Cassian Formation (Late Triassic, Early Carnian).

Derivatio nominis — This species is named after Alex Nützel (Hamburg) who assisted in discovering it.

Diagnosis — The small (less than 5 mm high) slender shell has a flattened apex. In it the first, smooth, rounded whorls are the sinistral protoconch that twists around the same axis as the dextral teleoconch. Teleoconch ornament consists of three spiral keels of which the lower one becomes covered by the next whorl. The keels produce a regular rectangular whorl profile.

Description — With 7 whorls the shell is 3.5 mm high and 1.2 mm wide. The apical angle amounts to c. 15°, and the apex is flattened. Flanks of the whorls of the teleoconch are straight, and the apical angle thus does not change with growth. The protoconch measures 0.18 mm in diameter, and lies as a smooth sinistral whorl in the flat first whorl of the teleoconch. The aperture of the protoconch is indistinct, and the onset of the teleoconch is indicated by the appearance of the upper keel of the flank. The teleoconch begins with an ornament of 2 equally strong spiral ridges on almost smooth background with minute straight growth lines. At the second whorl of the teleoconch the two keels have taken their median position on the flank. The area between the spiral keels is concave with an almost flat bottom. The flanks of the keels in apical and apertural direction slope into a V-shaped groove that contains the suture in its centre. The flank forms a sharp edge enforced by a spiral ridge with the weakly rounded base. This lowest spiral ridge may still be detectable within the suture or may be covered by the succeeding whorl. The aperture is about as wide as high with a short inclined columella and rounded frontal end and outer lip. There is no umbilicus.

Diagnostic difference — The flat protoconch differentiates the minute *Tirolthilda nuetzeli* from *T. seelandica* as well as from the other mathildoids from the St Cassian Formation.

Material — Alpe di Specie (5 specimens, GPIH; 2 specimens, RGM 219 018); Misurina (4 specimens, RGM 219 019).

Genus *Schroederilda* gen. nov.

Type species — *Pseudotritonium milierensis* Zardini, 1978 from the St Cassian Formation.

Diagnosis — This mathildid genus has an inclined sinistral protoconch on a teleoconch with rounded whorls and fine sinuating axial ribs.

Derivatio nominis — Named after Michael Schröder (Hamburg), who described many new mathildids and other gastropods from the European Jurassic.

Schroederilda milierensis (Zardini, 1978)
Pl. 9, figs. 4-6, 8.

1978 *Pseudotritonium milierensis* Zardini, p. 54, pl. 38, fig. 3.
1980 *Pseudotritonium milierensis* Zardini, p. 11, pl. 5, figs. 22-23.

Description — According to Zardini (1978) the species has a very small fusiform and apically pointed shell. Whorls are rounded and separated by shallow sutures.

The last whorl of the fully grown shell is much higher than the spire. The ornament consists of numerous densely arranged narrow axial ribs. The aperture is oval and high, and the columella covered by a thick inner lip.

The adult shell consists of c. 5.5 whorls of the teleoconch, with the last two whorls greatly expanding in height. The c. 3 mm high adult shell of the holotype figured by Zardini (1978) resembles in ornament the last whorl of a juvenile shell found at Alpe di Specie. Here the early whorls are well developed and show that the protoconch is of mathildid type. It consists of a sinistral, flatly coiled shell of c. 1.5 whorls and a largest diameter of c. 0.2 mm. The embryonic shell is largely covered by the first whorl of the teleoconch. Axial folds on the larval shell are present adjacent to its suture with the embryonic whorl and along the umbilicus. Folds do not cross the flanks which are smooth and well rounded. The orientation of the protoconch is almost at right angle to the apex of the teleoconch. At the contact between larval shell and first teleoconch sinistral coiling changes into dextral coiling. The sculpture of the first and second whorls of the juvenile teleoconch consists of simple narrow axial ribs that are well spaced from each other and transected by fine spiral lirae; 15 ribs are present on the first teleoconch whorl, 25 on the second, and with beginning of the third whorl the number of axial ribs greatly increases while the space between them decreases. The adult whorl has c. 35 axial ribs that are also connected to closely spaced fine spiral lirae.

Diagnostic difference — *Pseudotritonium venustum* (von Münster, 1841) is larger than *Schroederilda milierensis*, has a different sculpture, and represents a caenogastropod with dextral protoconch (Bandel,1993a).

Material — Zardini (1978, 1980) described *Schroederilda milierensis* on the basis of an individual found at Milieres, near Cortina d'Ampezzo. The two new specimens were washed from material collected 1989 in Alpe di Specie (RGM 219 020) and from Campo (GPIH).

Family Anoptychiidae Bandel, 1994

Diagnosis — The shell is slender, cylindrical, and has many whorls, which are flat-sided when fully grown. The aperture is angular in outline with a short anterior canal and a slightly twisted spindle. The early whorls of the teleoconch are sculptured by axial collabral ribs, spiral ribs, or a combination of both. On later whorls of the teleoconch the sculpture decreases and disappears. The protoconch is heterostrophic with the axis of the larval shell forming an angle of between 20° and 80° with the axis of the teleoconch.

Differences — The early portion of the slender teleoconch is strongly sculptured, while the later parts are smooth or nearly so. This differentiates members of this family from most of the usually highly ornamented Mathildidae, Tofanellidae and Ampezzanildidae. It also distinguishes them from smooth Ebalidae, spirally striped Donaldidae, Dolomitellidae and Zardinellidae from the St Cassian Formation (Bandel, 1994b; 1995). The heterostrophic protoconch distinguishes them from slender Caenogastropoda of similar teleoconch shape. The absence of a posterior sinus or slit and a smooth, non-folded columella differentiates the Anoptychiidae from the Nerineidae.

Genus *Anoptychia* Koken, 1892

Type species — *Melania supraplecta* von Münster, 1841 from the St Cassian Formation.

Description — The shell is slender and turriform with numerous whorls. The protoconch is a sinistral shell of the *Mathilda* type. Ornament of the juvenile teleoconch consists of axial ribs and traces of spiral ribs. In later whorls the sculpture disappears, and the shell is smooth.

Diagnostic differences — *Anoptychia* differs from *Turristylus* by a less slender shell and from *Camponella* by the predominantly axial ornament of the early teleoconch.

Anoptychia supraplecta (von Münster, 1841)
Pl. 8, figs. 1-6.

1841 *Melania supraplecta* von Münster, p. 96, pl. 9, fig. 40.
1869 *Chemnitzia supraplecta*, Laube, p. 55, pl. 23, fig. 18.
1894 *Loxonema (Anoptychia) supraplecta*, Kittl, p. 155, pl. 4, figs. 54-55, pl. 8, fig. 40.
1894 *Eustylus Koninckı* (von Münster, 1841), Kittl, p. 213, pl. 6, figs. 39-47.
1978 *Anoptychia multitorquata*, Zardini, p. 43, pl. 27, figs. 5,14.
1978 *Anoptychia supraplecta*, Zardini, p. 42, pl. 26, fig. 21.

Description — The shell with c. 10 whorls has a length of 4.5 mm. The protoconch measures c. 0.25 mm across and consists of c. 1.5 whorls. It twists strongly from the sinistral first whorl into the planispiral whorl before the onset of the teleoconch. Here the protoconch is ornamented with some axial folds while it is otherwise smooth. Its margin is clearly demarcated from the sculptured onset of the teleoconch. The axis of the larval shell forms an angle somewhat larger than 45° with that of the adult shell. The embryonic shell is partly covered by the first whorl of the teleoconch. The four first whorls of the teleoconch are sculptured by c. 18 axial ribs. These increase in size as the diameter of the whorls increases. In the first whorl axial ribs are crossed by two spiral ribs of the same dimension, which end before the begin of the second whorl. From the fifth whorl onward ornament disappears, and whorls are only weakly convex. They are separated from each other only by impressed sutures. The apical angle of the teleoconch is c. 27-30°. The base is less rounded in juveniles than in larger individuals, and the aperture is of considerably lower width than height and inclined. Growth lines form the only sculpture of the later teleoconch and retrace the inclination of the apertural lip from the suture forward to the base.

Diagnostic differences — The dominant axial ornament of the early teleoconch whorls distinguishes *A. supraplecta* from *Camponella* and *Cristalloella* where spiral ribs or keels are stronger. The change from ornamented early teleoconch to smooth later teleoconch differentiates *Anoptychia* from *Schroederilda* which is ornamented up to the final whorl.

Material — Seven individuals from Campo and two from Alpe di Specie were studied. One individual from Alpe di Specie (RGM 219 021) and five from Campo (RGM 219 022) are deposited at Leiden.

Discussion — See *Camponella pianozesis*.

Genus *Turristylus* Blaschke, 1905

Type species — *Eustylus triadicus* Kittl, 1894 from the St Cassian Formation.

Description (altered from Blaschke, 1905) — The shell is slender to needle-like with a whorl profile which is at first gently convex, and later becomes flat. The sutures are shallow, and the ornamentation consists of axial costation, extending from suture to suture, which is not continuous onto the adult shell. The protoconch lies inclined on the shell axis.

Differences — *Turristylus* is more slender than *Anoptychia* and *Camponella* and differs from the other mathildoids of St Cassian Formation by the flattened flanks of the later teleoconch. The teleoconch of *Kittlistylus* is ornamented with axial ribs throughout (Haas, 1953). Its heterostrophic shell distinguishes it from similarly slender conical shells as found in *Protorcula* (Bandel, 1991) and some other Caenogastropoda from the St Cassian Formation.

Turristylus triadicus (Kittl, 1894)
Pl. 8, figs. 8-9.

1894 *Eustylus triadicus* Kittl, p. 214, pl. 8, figs. 26-27.
1905 *Trypanostylus (Turristylus) triadicus*, Blaschke, p. 205, pl. 20, fig. 23.
1978 *Euthystylus triadicus*, Zardini, p. 48, pl. 33, figs. 18-19.

Description — A teleoconch of 11 whorls is up to 4.5 mm long and of slender, needle-like shape. The axis of the protoconch forms an angle of less than 45° with that of the teleoconch. The protoconch, of mathildid shape, is a little more than 0.2 mm wide and smooth. Whorl profile of the teleoconch is gently convex at first and becomes flat later. The first 6 whorls of the teleoconch are provided with c. 8 axial ribs. The sutures become shallower and indistinct so that the sides of the shell appear straight. The base is smooth and flat with a rounded shoulder. The aperture is of rhomboidal shape with a short anterior notch that points anteriorly.

Diagnostic differences — See the genus description above.

Material — Misurina (1 specimen, Pl. 8, figs. 8-9, RGM 219 023).

Genus *Camponella* gen. nov.

Type species — *Coelostylina pianozesis* Zardini, 1985 from the St Cassian Formation.

Derivatio nominis — Named after the locality Campo at Cortina d'Ampezzo where these small shells were collected by Rinaldo Zardini.

Diagnosis — The small shell has a high spire with numerous flat-sided whorls and distinct sutures. The protoconch is sinistrally coiled and inclined with respect to the axis of the teleoconch. The first (5) whorls of the juvenile teleoconch are covered with axial and spiral costae, of which the spiral ones are dominant. Later whorls are smooth or have indistinct spiral threads up to the edge of the base, while the base is covered by spiral carinae. The umbilicus is narrow and may form the opening to a hollow columella.

Diagnostic differences — The ornament of the juvenile shell consisting of axial and

spiral ribs distinguishes *Camponella* from *Anoptychia* with its predominantly axial ornament and from the more slender *Turristylus* with only axial ribs.

Camponella pianozesis (Zardini, 1985)
Pl. 8, figs. 7, 10; Pl. 9, figs. 1-3.

1980 *Coelostylina infrastriata*, Zardini, p. 6, pl. 3, fig. 2.
1985 *Coelostylina pianozesis* Zardini, p. 10, pl. 3, figs. 15-19.

Description — The diagnosis of the genus *Camponella* applies fully to this species. A shell with 8 whorls measures 4 mm in height and almost 2 mm in maximal width. The larval shell is deeply immersed within the first whorl of the teleoconch, and the apical portion of the embryonic whorl is covered by the first whorl of the teleoconch. The axes of the sinistral larval shell and the dextral adult shell point in almost opposite directions and are offset by only a small angle. The twist of the final portion of the larval shell into the first whorl of the teleoconch is accompanied by several axial folds. The protoconch consists of c. 1.5 whorls and measures c. 0.2 mm in maximum width. The juvenile whorls are sculptured by three spiral keels that are crossed by numerous straight collabral ribs. The latter ones are not regularly spaced and of different size, while the spirals are regularly developed. The central one of these is usually the most prominent. The umbilicus is narrow. In a shell with 5-8 whorls, the columella is hollow. The rounded base is ornamented with 5 to 6 low spiral costae. The aperture is almost round.

Diagnostic differences — The juvenile teleoconch ornament distinguishes this species from the other three species of the Anoptychiidae here described.

Material — Alpe di Specie (1 specimen, GPIH; 5 specimens, RGM 219 026); Misurina (3 specimens, RGM 219 025); Campo 3 specimens, GPIH, 35 specimens, RGM 219 024).

Remarks — The systematic placement of slender shells of the type of the three here documented Anoptychiidae from the St Cassian Formation is quite complex, due to the activities of Kittl (1894), Cossmann (1895), Wenz (1939), and Haas (1953). With regard to *Anoptychia* Koken, 1892 (type species *Melania supraplecta* von Münster, 1841) Wenz (1939, fig. 924) considered *Zygopleura (Anoptychia) supraplecta* (von Münster) as type of the subgenus *Anoptychia*, but figured *Zygopleura (Anoptychia) carinata* (von Münster). He assumed that *Turritella carinata* von Münster, 1841 represented a synonym of *T. supraplecta*. This is not correct as these two species can be distinguished by the presence (*carinata*) or absence (*supraplecta*) of a keel above the sutures on the teleoconch. Koken (1892) selected *supraplecta* and *multitorquata* as possible types. These two species were placed by Kittl (1894) in *Anoptychia*, but he was not able to separate them. The same has happened when Zardini (1978) named a juvenile shell *Anoptychia supraplecta* and the fully grown shell of the same species *Anoptychia multitorquata*. Since *Anoptychia supraplecta* is the better preserved and Kittl's pl. 8, fig. 6 can be compared well with the species described here, *Anoptychia supraplecta* (von Münster, 1841) seems to be the best choice for a type species of this genus.

Trypanostylus Cossmann, 1895 is based on *Eustylus militaris* Kittl, 1894. The generic name *Eustylus* was replaced because of preoccupation. If *Euthystylus triadicus*

(Kittl) by Zardini (1978, pl. 34, fig. 7) is a fragment of a larger shell of this species, the species could have reached 5 cm in height. The type species *Eustylus triadicus* Kittl, 1894 of *Turristylus* Blaschke, 1905 is not the same as *Eustylus militaris*, as was assumed by Wenz (1939).

Similarly the genus *Heterogyrella* Wenz, 1938 replaces *Heterogyra* Kittl, 1899 (because of preoccupation of the latter generic name). The type species of *Heterogyrella* is *Eustylus ladinus* Kittl, 1894 from the Marmolata Limestone. It has two spiral ribs on the lower flanks of its early juvenile shell. This could indicate a relation with *Camponella*. It resembles *Camponella* in respect to the general shell shape and the presence of a hollow columella. Kittl (1895) described another fossil from the Marmolata Limestone as *Heterogyra ladina* with spiral keels present on the first whorls. It is very doubtfull whether the species from the Marmolata Limestone is the same as that of the St Cassian Formation since it is more slender and has no spiral costae on its base.

Kittlistylus Haas, 1953 is based on *Turritella flexuosa* von Münster, 1841 and differs from the other forms discussed here in having an ornament of axial ribs on the whole teleoconch. In general shape *Turristylus* resembles *Kittlistylus* but it shows the ornament of axial ribs only in its juvenile shell portions. *Kittlistylus semiglaber* (von Münster, 1841) seems to be intermediate in having more whorls of the teleoconch covered with axial ribs than *T. triadicus*. Comparing with the illustrations of the three species provided by Kittl (1894), *Eustylus triadicus* resembles the here described shell closely, also with respect to its small apical angle (15 to 16°). The protoconch of *Kittlistylus flexuosus* is described as smooth and inclined at an unusual high degree toward the shell axis and strongly alloiostrophic. This could well represent a heterostrophic protoconch similar to that found in *Turristylus triadicus* and would than be an indication for a close relation between *Kittlistylus* and *Turristylus*.

Spirochrysalis Kittl, 1894 with the type species *Melania nympha* von Münster, 1841 is of more spindle-like fusiform shape than the species of *Anoptychia*, *Turristylus* and *Camponella* here described and early whorls do not have the characteristic sculpture, and the protoconch is unknown.

Wenz (1939) considered also the genus *Protorcula* Kittl, 1894, based on *Turritella subpunctata* von Münster, 1841 to be related to the genera *Trypanostylus*, *Anoptychia*, *Turristylus*, *Heterogyrella*, and *Spirochrysalis*. This genus belongs to the Protorculidae Bandel, 1991, a family of the Caenogastropoda, and thus it is not related to the Anoptychiidae. All these genera together are representatives of the Loxonematoidea from the St Cassian group, the Coelostylinidae in the classification presented by Wenz (1939). If we consider the genus in the St Cassian fauna that comes closest to what is known about the Silurian type species of *Loxonema*, it is *Polygyrina* Koken, 1892. It is so close in shape to *Loxonema* that it was considered a subgenus of it by Wenz (1939). *Polygyrina lommeli* (von Münster, 1841), the type species and thus the type of the family Polygyrinidae Bandel, 1991, belongs to the Caenogastropoda. *Coelostylina* Kittl, 1894, based on *Melania conica* von Münster, 1841, also represents a caenogastropod, but is quite unrelated to the Polygyrinidae (Bandel, 1993). *Kittlistylus* belongs to the Procerithiidae according to Haas (1953). This family is based on the Jurassic genus *Procerithium* that has a quite distinct caenogastropod protoconch (Schröder, 1995) but differs markedly from its fellow caenogastropod groups the Polygyrinidae and the Coelostylinidae.

Family Tofanellidae Bandel, 1994

Diagnosis — The small, slender, turritelliform shell has a spiral and collabral ornament with spiral ribs or keels dominating. Whorl flanks are angular or slightly convex. The aperture is angular or rounded and provided with a short, shallow anterior canal. The distinctive feature of this family is the protoconch. The embryonic shell is sinistral and immersed in the apex of the larval shell. The rounded whorls of the larval shell gradually change from sinistral coiling to planispiral and finally to dextral coiling. The pediveliger shell is thus dextral. Apertural margin of the protoconch is usually thickened, and a hook-like projection of the outer lip may or may not be present. The larval shell is smooth or indistinctly ornamented by growth lines of straight outline and axial or spiral lirae. The Tofanellidae are based on *Tofanella* from the St Cassian Formation.

Difference — The predominantly smooth protoconch forms a 180° angle with the teleoconch unlike many mathildids with protoconch axis deviating from the teleoconch axis (Bandel, 1994b). Sinistral coiling grades into dextral coiling still within the larval whorls unlike the mathildids. The protoconch is smooth unlike the ampezzanildids where it is axially ribbed. The teleoconch is ornamented spirally with minor axial components unlike that of the Trachoecidae with axial ribs dominating.

Genus *Tofanella* gen. nov.

Type species — *Turritella decussata* von Münster, 1841.

Derivatio nominis — Named after the mountain La Tofana that dominates the scenery of Cortina d'Ampezzo.

Diagnosis — The turriculate shell has a major spiral keel on the first whorls of the teleoconch, which disappears on later whorls as they become almost flat. The spiral sculpture is crossed by few collabral elements. The protoconch has a smooth surface, and the embryonic shell is immersed in its apex. In the larval whorls the sinistral coiling changes into dextral coiling before the onset of the teleoconch. With transition from larval to adult shell sculpture and whorl shape change drastically.

Diagnostic differences — The protoconch of tofanellid type, which is connected to a slender teleoconch with a median keel in the early whorls and flattened flanks in later whorls, distinguishes this genus from all other slender mathildoid heterogastropods from the St Cassian Formation. St Cassian members of the Anoptychiidae also change from an ornamented early teleoconch to a smooth later teleoconch, but their protoconch deviates from the teleoconch in the mathildid way. *Cristalloella* has no flattened flank in the later teleoconch, retains the median keel and has a more delicate axial ornament.

Tofanella decussata (von Münster, 1841)
Pl. 9, fig. 7; Pl. 10, figs. 1-6.

1841 *Turritella decussata* von Münster, p. 119, pl. 13, fig. 14.
1894 *Promathildia decussata* Kittl, p. 247, pl. 10, fig. 13-16.
1978 *Promathildia decussata* Zardini, p. 52, pl. 5, figs. 27, 29.

Description — In Kittl's description the following characters are stated: the shell is non-umbilicate, turriculate and slender. The sutures are shallow, and flanks of the whorls are slightly convex to almost flat. Circa 12 fine spiral costae are crossed by c. 8 coarse axial folds. Two spiral costae are elevated and form tubercules with the crossing axial ribs. The base is flattened and sculptured by 5 spiral costae of which the outer is the strongest. The aperture is of oval shape.

Kittl did not know the juvenile shell, and therefore did not notice the change of sculpture from juvenile to adult shell. In the protoconch the first whorl is strongly sinistral and immersed within the second whorl that belongs to the larval shell. Within this second whorl the shell gradually turns into a dextral coil. The aperture of the protoconch is thickened and extends into a strong apertural hook that was added to the shell of the pediveliger when the larval shell had grown to its final size of c. 0.25 mm in width and 0.16 mm in height.

The onset of the teleoconch is characterised by the appearance of two spiral keels of which the upper is the strongest. It forms an angle on the flank of the first four whorls of the teleoconch. In the fifth whorl of the teleoconch the keels disappear, and the whorl flank becomes rounded in the fifth to seventh whorl. In following whorls, the flanks are flattened and spiral keels disappear. With 8 whorls of the teleoconch the shell measures a bit more than 3 mm in length and less than 1 mm in maximum width, and the apical angle is 18° in early teleoconch and 15° in the later teleoconch. With 15 mm length the shell has c. 20 whorls.

Diagnostic difference — The teleoconch with its keeled first 5 whorls and the flattened later whorls distinguish it from all other tofanellids and mathildids. Only the Anoptychiidae have a similar change in ornament but differ by their mathildid deviating protoconch. The smooth protoconch with distinct larval hook distinguishes *Tofanella decussata* from the ampezzanildids. In contrast to *T. cancellata*, the median keel of the early teleoconch whorls is undulating where axial ribs cross, and in later whorls this keel looses its dominance over other sculptural elements. *T. decussata* grows to a greater length than *T. cancellata*. *Kittlistylus* Haas, 1953 from the Late Triassic Pucará Group of Peru may be closely related to *Tofanella*, even though it was included in the Procerithiinae by Haas (1953). Its protoconch is similar to that of a mathildid (Bandel, 1994b).

Material — Alpe di Specie (numerous specimens, GPIH; 30 specimens, RGM 219 027), Misurina (2 specimens, GPIH; 15 specimens, RGM 219 028), Campo Campo (2 specimens, RGM 219 029).

Remarks — Juvenile shells of *Tofanella decussata* closely resemble those of *T. cancellata*, and they have been figured as separate species by Zardini (1978, pl. 35, figs. 17-18). Thus, *Promathildia* sp. (fig. 17) and *P. pygmaea* (von Münster) (fig. 18) could represent the early teleoconch of *P. decussata* figured on the same plate in figs. 27-29.

Tofanella cancellata sp. nov.
Pl. 11, figs. 4-9; Pl. 12, fig. 1.

Holotype — Specimen of Pl. 11, fig.4 (NHM 1994/167).
Locus typicus — Misurina (see details in the Introduction).
Stratum typicum — Marls of the St Cassian Formation, Cordevol Member, with

reef debris slumped from the shallow water into the basinal deposits (Late Triassic, Early Carnian).

Derivatio nominis — This species is named after its cancellate sculpture.

Diagnosis — The generic diagnosis of *Tofanella* applies to this species which has a hooked protoconch with c. 1.5 whorls. In the teleoconch the flanks of the median keel become flattened, increasingly in older whorls of the teleoconch. The ornament consists of a regular pattern of rectangles formed by a few spiral ribs, crossed by many axial ribs of equal strength.

Description — A shell with 4 teleoconch whorls is c. 1.2 mm high. The first five whorls of the teleoconch have an apical angle of c. 35°, decreasing to c. 15° in the later whorls of the teleoconch. Whorls are almost twice as wide as high and have flanks of a triangular shape. The median spiral rib forms a keel and flat flanks continue into deep sutures. On the third whorl of the teleoconch a further spiral rib appears below the suture while a spiral rib above the suture is present as early as the second whorl. These spiral ribs are of the same width as the straight axial ribs. The base bears two further spiral ribs near its edge and is smooth further inward. The aperture is of angular outline, about as wide as high and provided with a short frontal notch.

The protoconch consists of 1.5 whorls and measures c. 0.2 mm in width and height. The switch in coiling mode from sinistral to dextral occurs c. 0.5 whorls before its aperture. A wide apical hook is added to the thickened apertural rim in its lower portion, below the keel that is present on the early teleoconch. A very fine spiral lination may be seen on the last portion of the pediveliger shell before its apertural margin that may or may not be thickened.

Diagnostic differences — The regular cancellate sculpture and the smaller protoconch differentiate *Tofanella cancellata* from *Cristalloella cassiana*. The strong keel differs from the more rounded flank of *C. delicata*, and the straight axial ribs differ from the sinuous ones of *C. sinuata*. From *Tofanella decussata* it is distinguished by the the shorter and wider apical part of the teleoconch, its smaller size, and the distinctly cancellate ornament.

Material — Alpe di Specie (13 specimens, GPIH; 12 specimens, RGM 219 031), Misurina (25 specimens, RGM 219 030), Campo (numerous specimens, GPIH, c. 40 specimens, RGM 219 032).

Genus *Cristalloella* gen. nov.

Type species — *Cristalloella cassiana* gen. et sp. nov. from the St Cassian Formation.

Derivatio nominis — Named after Monte Cristallo (3216 m) which dominates the area of Cortina d'Ampezzo.

Diagnosis — The diagnosis of the family Tofanellidae also applies to this genus. The shell is slender, small and multiple whorled with keeled flank and fine axial ribs crossed by spiral striae. The aperture is angular with a short siphonal fold. The protoconch has a sinistral first whorl that grades into the dextral whorl before the larval shell ends. Its margin is thickened and commonly bears a hook.

Diagnostic differences — The keeled flank of the teleoconch remains characteristic during all growth stages which differentiate *Cristalloella* from *Tofanella*. The tofanellid

protoconch differs from that of the mathildids, and especially the members of the genus *Promathilda* with a similar teleoconch. The very similar *Wonwalica* Schröder, 1995, from the Early Cretaceous of Poland differs only in regard to the embryonic portion of the protoconch, which has no clearly sunken and sinistrally coiled first whorl that dips below the larval shell.

Cristalloella cassiana sp. nov.
Pl. 10, figs. 7-10; Pl. 11, figs. 1-3.

1841(?) *Turritella trochleata* von Münster, p. 118, pl. 13, fig. 11.
1894(?) *Promathildia trochleata*, Kittl, p. 215, pl. 9, fig. 2.

Holotype — Specimen of Pl. 10, fig.9 (NHM 1994/168).

Locus typicus — Seelandalpe (Alpe di Specie) above Carbonin (for details see introduction).

Stratum typicum — Cordevol Member, St Cassian Formation, in reef debris slumped from the shallow water into the basinal marls (Late Triassic, Early Carnian).

Derivatio nominis — This *Cristalloella* is named after the St Cassian Formation.

Diagnosis — The protoconch consists of almost two whorls that end with a thickened apertural rim to which a larval hook is added. Whorls of the teleoconch are characterised by a median keel and two flattened to concave flanks bordering it and ending in the deep sutures. Ornament consists of regular collabral ribs crossed by finer spiral lirae forming a reticulate network. The aperture is angular.

Description — A shell with 10.5 whorls is 2.5 mm high, up to 0.8 mm wide and has an apical angle of 16-17° in the juvenile teleoconch and 11° in the fully grown shell. The protoconch consists of two whorls, is almost 0.3 mm high and 0.25 mm wide. The sinistral embryonic shell clearly dips below the apical surface. The planktotrophic larva produced 1.3 whorls which are dextral in their larger part and covered by a delicate ornament of flat grooves and bordering ridges that are arranged in undulating axial lines. The apertural margin of the fully grown pediveliger shell forms a broad varix. A hook-like projection was secreted at the middle of the outer lip in front of its thickened rim. After metamorphosis, a keel in the median position of the flank of the whorls forms the continuation of this apertural hook.

While larval whorls are evenly rounded, those of the postlarval shell are sculptured by the median keel, a concave flank, and a basal keel. The keels are crossed by fine axial ribs, which have a density of 4 per 0.1 mm. These collabral ribs reflect a small sinus connected to the concave flanks between the keels. They are crossed by finer spiral threads forming a fine pattern of rectangles on the whorl surface. The aperture is angular with a straight inner lip on the columella, a short anterior siphonal groove next to it, and an outer lip with a corner at the median keel.

Diagnostic differences — The other members of the genus are of rather similar shape. *Tofanella cancellata* has a smaller protoconch (1.5 whorls) and a coarser ornament, *Cristalloella sinuata* is characterised by more sinuous regular axial ribs and *C. delicata* has a less prominent median keel. *Promathilda sculpta* is less slender and has a mathildid protoconch. *Ampezzanilda aialensis* differs in regard to the protoconch that is axially ornamented and the teleoconch that has a keel further down in later whorls.

Material — Alpe di Specie (2 specimens, RGM 219 033), Campo (5 specimens, RGM 219 034).

Remarks — *Promathildia trochleata* as described by Kittl (1894) is based on two individuals which may represent a badly preserved individual of *Cristalloella cassiana* (pl. 9, fig. 2), that had been the original to the species presented by von Münster (1841), while the other individual (pl. 8, fig. 31) does not belong to this species. It is larger, with a more screw-like outline, and has a more flattened base.

Cristalloella sinuata sp. nov.
Pl. 12, figs. 2-8; Pl. 13, fig. 1.

1841(?) *Turbo crenata*, von Münster, p. 119, pl. 13, fig. 14.
1894(?) *Promathildia crenata* Kittl, p. 223, pl. 9, fig. 34-35.

Holotype — Specimen of Pl. 12, fig. 4 (NHM 1994/169).

Locus typicus — Misurina (details see in Introduction).

Stratum typicum — Cordevol Member, St Cassian Formation, in reef debris slumped from the shallow water into the basinal marls (Late Triassic, Early Carnian).

Derivatio nominis — This species is named after its ornament of sinuate ribs.

Diagnosis — This slender, narrow, small *Cristalloella* has a tofanellid protoconch and a teleoconch ornamented by a median spiral keel crossed by numerous sinuous fine collabral ribs.

Description — A c. 1.5 mm high shell consists of the protoconch and five teleoconch whorls. Its apical angle is 13°. The whorl profile is angular with a median keel accompanied by two slightly concave flanks of which the upper one is slightly wider than the lower. The whorls cover some of the stronger spiral lirae that are present on the rounded margin to the evenly rounded base. On the flanks a fine spiral striation is present forming the background on which the characteristic sinuous axial ribs are superimposed. They reflect in their outline the shape of the apertural outer lip and have a low lobe above the keel and a wide low saddle below the keel. The apertural outer lip forms an angle with the keel and is rounded. A simple and straight inner lip ends in a wide shallow siphonal notch that is slightly bend to the left.

The protoconch is smooth and lies slightly inclined on the top of the teleoconch. The transition from left to right coiling is marked by rounded folds. The anterior embryonic shell is covered by the larval shell, and the umbilicus is narrow or closed. Protoconch measures c. 0.21 mm across, is as high as wide, and consists of almost 1.5 whorls. Margin of the pediveliger shell is thin and extends into a larval hook in the lower part of the outer lip.

Diagnostic differences — See *Cristalloella delicata*.

Material — Misurina (2 specimens, GPIH; 4 specimens, RGM 219 035), Campo (10 specimens, RGM 219 036).

Remarks — The three individuals of *Promathildia crenata* studied by Kittl (1894) resemble *C. sinuata* in general shape, but are much larger and more coarsely sculptured. It may be that larger and more fully grown individuals of *C. sinuata* exist which would then resemble *Promathildia crenata*. A modern species from the shallow sea near Cebu in the Philippines is provided with a rather similar protoconch (Ban-

del, 1991b, pl. 8, fig. 6, 10), but an unkeeled teleoconch. This indicates that species similar to the Triassic *Cristalloella* may still be alive.

Cristalloella delicata sp. nov.
Pl. 13, figs. 2-8.

Holotype — Specimen of Pl. 13, fig. 6 (NHM 1994/170).

Locus typicus — Seelandalpe (Alpe di Specie) (for details see Introduction).

Stratum typicum — Cordevol Member, St Cassian Formation, in reef debris slumped from the shallow water into the basinal marls (Late Triassic, Early Carnian).

Derivatio nominis — This is a rather delicate species of *Cristalloella*.

Diagnosis — The very slender and tiny *Cristalloella* is characterised by spiral ribs that are present only below the low median keel.

Description — A 1 mm high shell consists of c. 6 whorls with an apical angle of c. 10°. The protoconch forms a flattened apex that is slightly wider than the first whorl of the teleoconch. It is smooth, c. 0.23 mm wide and consists of a little more than 1.5 whorls that may show some folds and strong growth increments or may be smooth. The twist from the weak sinistral coiling into dextral coiling appears after the first whorl and in the middle of the shell produced by the planktotrophic larva. The apertural rim of the protoconch is not thickened and has no larval hook, but is slightly inclined backwards. The teleoconch sculpture remains similar from the first whorl of the teleoconch onward. It consists of fine collabral ribs that have a shallow lobe on the flattened to slightly concave upper flank and a low saddle on the rounded lower flank. Here they are crossed by 4, and on later whorls increasingly more spiral ribs. They have the same width as the axial ribs and also cover the rounded base. The aperture is of rounded outline.

Diagnostic differences — The delicate sculptural pattern and low keel differentiate *Cristalloella delicata* from *C. cassiana* and *T. cancellata*. The smaller apical angle and the pattern of spiral ribs of the teleoconch distinguishes from *C. sinuata*. *C. delicata* is the smallest of the members of the genus found in the St Cassian Formation.

Material — Alpe di Specie (2 specimens, GPIH; 6 specimens, RGM 219 037).

Remarks — Schröder (1995) described *Wonwalica minuta* Schröder, 1995, from the Early Cretaceous of Poland which in essential features resembles *Cristalloella sinuata* and *C. delicata*. Not only the sculpture and dimensions of the adult shell are similar, but the larval shell is also of the tofanellid type, with two larval whorls present. The embryonic shell is less immersed in the apex as is the case among the Tofanellidae from St Cassian. *Wonwalica* appears to be related to *Tofanella* and *Cristalloella*, thus forming a connection with modern species still living in tropical seas (Bandel, 1991b).

Genus *Camponaxis* gen. nov.

Type species — *Cerithium* (?) *lateplicatum* Klipstein, 1843 from the St Cassian Formation.

Derivatio nominis — The name is a combination of the Campo locality and the word 'axis' referring to the main sculptural element.

Diagnosis — The teleoconch is ornamented by axial ribs that may or may not be crossed by spiral lirae of smaller size than the ribs. The protoconch is of the tofanellid type with a sinistral embryonic shell and twists into dextral coiling well within the larval shell.

Diagnostic differences — The dominant axial ornament of the teleoconch connected to a tofanellid protoconch differentiates this genus from the other Mathildoidea of the St Cassian Formation.

Camponaxis lateplicata (Klipstein, 1843)
Pl. 13, fig. 9; Pl. 14, figs. 1-5.

1843 *Cerithium* (?) *lateplicatum* Klipstein, p. 182, pl. 11, fig. 35.
1868 *Loxonema lateplicata*, Laube, p. 62, pl. 24, fig. 14.
1894 *Katosira* (?) *lateplicata*, Kittl, p. 164, pl. 4, figs. 27-28.
1894 *Coronaria subcompressa* Kittl, p. 164, pl. 4, figs. 31-32.
1978 *Katosira seelandica* Zardini, p. 43, pl. 28, fig. 1.
1978 cfr. *Coronaria zeuschneri*, Zardini, p. 41, pl. 25, fig. 25.

Description — The turreted shell has up to 9.5 whorls and measures 4.5 mm in height and a little more than 1 mm in width. Whorls have rounded flanks and are about twice as wide as high. The ornament consists of strong axial ribs that differ in number among individuals from 10 to 18 per whorl. Ribs are widest in central position on the whorl and end near the sutures as well as at the edge of the base. This edge is accompanied by a spiral costa and on the flattened base two or three more spiral costae are present. The flanks are ornamented also by spiral lirae, which differ in number and strength. The number of lirae increases with whorl dimension, and they are always much smaller than the axial ribs. The aperture is as wide as high, arranged in vertical position parallel to the axis of coiling; the inner lip is bend over so to form a slit with the columella, but there is no umbilicus.

The protoconch is smooth and c. 0.2 mm wide forming a sinistral and slightly deviating top to the dextral teleoconch.

Diagnostic differences — *Turrithilda* Schröder, 1995, with *T. opalina* (Quenstedt, 1858) from the Middle Jurassic has a larval shell of larger size (0.35 mm) and with a vertical orientation on the teleoconch. *Stuorilda tichyi* gen et sp. nov. has a similar teleoconch ornament but higher whorls and it differs strongly with regard to its ribbed ampezzanildid protoconch, while that of *Camponaxis* is smooth.

Material — Alpe di Specie (5 specimens, GPIH), Misurina (2 juvenile specimens, RGM 219 040), Campo (2 specimens, GPIH, 12 specimens, RGM 219 038), Dibona (2 specimens, RGM 219 039).

Camponaxis subcompressa (Kittl, 1894)
Pl. 14, figs. 6-8; Pl. 15, fig. 1.

1868 *Loxonema lateplicata* Laube, p. 34, pl. 24, fig. 14.
1894 *Coronaria subcompressa* Kittl, p. 185, pl. 4, figs. 31-32.
1980 *Coronaria subcompressa*, Zardini, p. 9, pl. 4, fig. 12.

Description — According to Kittl (1894) the turriform shell with convex whorls is

ornamented by coarse axial folds of which c. 14 are found on each whorl. The base is flattened and without umbilicus, and the aperture is circular. The protoconch consists of 1.7 whorls of which the first is sinistral, and the remainder twists into a dextral coil. It measures c. 0.18 mm in diameter and bears a thickened margin projecting in a hook that is largely covered by the first whorl of the teleoconch.

Diagnostic differences — The number of ribs that appear on the first whorl of the teleoconch remains similar in the next whorls of the teleoconch, whilst in *Camponaxis beneckei* there are more such axial ribs and they increase in number. In *C. lateplicata* the first whorls have indistinct axial ribs, the following whorls carry many of them, and it is only later that the ribs appear in a more regular number. The protoconch of *C. subcompressa* is smaller (below 0.2 mm) than that of the other two species of this genus (more than 0.2 mm). According to Kittl (1894), the aperture of *Coronaria compressa* (von Münster, 1841) is lower than that of *Camponaxis subcompressa* and not as circular.

Material — Misurina (3 specimens, RGM 219 041), Dibona (1 specimen, RGM 219 042).

Camponaxis beneckei (Kittl, 1894)
Pl. 15, figs. 2-7.

1894 *Katosira Beneckei* Kittl, p. 163, pl. 8, fig. 12.
1978 cfr. *Katosira beneckei*, Zardini, p. 43, pl. 27, fig. 15.

Description — According to Kittl (1894) who based his description on three individuals, the shell is conical, not umbilicate and has weakly rounded flanks with 20-24 straight axial folds on each whorl. The dominant axial ribs of the ornament are cut by a fine spiral liration. The base is flattened and spirally lirated. The aperture is angular.

The juvenile shells on which this study is based, fit into this description with regard to shell shape and ornament. The small shells, which have 5 whorls when 1 mm high, are juvenile shells that are considered to represent the apical portion of the fragmentary specimen without apex illustrated by Kittl (1894). The protoconch consists of 1.5 whorls with the c. 0.15 mm wide embryonic whorl forming a depression in the flattened apex. The larval whorl is smooth, 0.25 to almost 0.3 mm wide and rounded. Turn from sinistral to dextral coiling occurs within the central part of the larval whorl of the protoconch, and its aperture is thickened, forming a simple rim. The onset of the teleoconch is abrupt with several unequal spiral lirae appearing, and axial ribs are irregularly spaced. Where spiral lirae cross the axial ribs small tubercules appear. There are c. 26 to 29 narrow axial ribs on each whorl. They end at the rounded corner of the base which is ornamented by several spiral lirae. The aperture demonstrates a straightened columellar lip, a shallow anterior notch and rounded outline of the outer lip.

Diagnostic differences — The whorls of the teleoconch of *Camponaxis beneckei* are ornamented by a larger number of axial ribs than found in *C. lateplicata*, and the protoconch is larger than that of *C. subcompressa*.

Material — Alpe di Specie (1 specimen, RGM 219 044), Campo (1 specimen, GPIH, 1 specimen, RGM 219 043).

Remarks — The three species of *Camponaxis* gen. nov. described here are based on juvenile shells and they are thus difficult to compare with the species based on fragmental larger teleoconchs described by Kittl (1894). The genus *Katosira* Koken, 1892 is based on Jurassic material of which the juvenile shell is unknown. *Coronaria* Koken, 1892 (= *Stephanocosmia* Cossmann, 1895) is based on a Carnian type from the Raibler Formation. Of the type species the protoconch and early teleoconch ornament are unknown. *Vallandroella seelandica* has also been considered to belong to the genus *Katosira* by Kittl (1894). Laube (1868) figured *Loxonema lateplicata* in a drawing which coincides fairly closely with *Camponaxis lateplicata* studied here, but could also represent a fully grown *C. subcompressa*. The species is not similar to *Loxonema*, as suggested by Laube (1868), because among the St Cassian fauna *Polygyrina* is the closest to the Palaeozoic loxonematids, and it represents a caenogastropod (Bandel, 1991a, 1993a).

Family Trachoecidae Bandel, 1994

Diagnosis — The shells have a smooth protoconch with a sinistral initial whorl and change into the dextral coil within the larval whorl. The teleoconch is *Fusus* like in shape, has a short siphon and strong axial ribs crossed by finer spiral lirae as ornament.

Diagnostic difference — Among the St Cassian Heterostropha with a tofanellid type of protoconch the members of the Trachoecidae differ from members of the Tofanellidae by the siphonate aperture and the ornament of strong axial folds of the teleoconch (Bandel, 1994b).

Genus *Trachoecus* Kittl, 1894

Type species — *Trachoecus gemmellaroi* Kittl, 1894, from the St Cassian Formation.

Description — The slender high-ovate c. 1 cm high shell with a sharp spire is composed of weakly convex whorls ornamented by inclined axial folds on a background of fine spiral lirae. The aperture has a simple outer lip and a thickened inner lip forming a slit with the columella. A short anterior apertural notch is present. The protoconch is smooth and of tofanellid type.

Trachoecus gemmellaroi Kittl, 1894
Pl. 15, fig. 8; Pl. 16, figs. 1, 3-4.

1894 *Trachoecus gemmellaroi* Kittl, p. 240-241, pl. 11, figs. 20-21.
1978 *Trachoecus gemmellaroi*, Zardini, p. 54, pl. 37, figs. 10-12.
1994 *Trachoecus gemmellaroi*, Bandel, pl. 5, fig. 14.

Description — The fully grown shell has five whorls of the teleoconch and is 9 mm high and 4.5 mm wide. Dominant features of the ornament consist of 10-12 axial folds on each whorl. They are slightly inclined toward the base, quite straight and continue from one whorl to the next. Alternating stronger and weaker spiral lirae form the ribs, and c. 9 of them are visible on the flanks, and more are present on the extended base. The shell is of acutely conical shape with an apical angle of c. 37°. The

aperture narrows to a gutter-like siphonal canal twisting to the left. The protoconch of the tofanellid type consists of almost two whorls that measures 0.22 to 0.27 mm across. Its embryonic part dips below the apical surface. The margin of the pediveliger shell is thickened.

Diagnostic difference — *Trachoecus gemmellaroi* differs from members of the genus *Protofusus* from the Late Triassic of Peru by its heterostrophic protoconch. *Protofusus* has the protoconch of a caenogastropod (Bandel, 1994b). *Vallandroella* is not of ovoid-conical shape, and its ribs are not as inclined as is the case in *Trachoecus*.

Material — The type material (NHM 1899/VI) consisting of two individuals was studied. Further material: Alpe di Specie (3 specimens, RGM 219 046), Misurina (3 specimens, GPIH; 2 specimens, RGM 219 045).

Remarks — Kittl (1894) noted a similarity between *Trachoecus* and species of the cancellariids among the neogastropods. The latter make their first appearance in the Cretaceous (Bandel, 1993a). Kittl noted that folds are usually present on the columella of cancellariid species, but are absent in the case of *Trachoecus*. But the main difference lies in the shape of the protoconch, which is dextral in the Cancellariidae, but sinistral in the Trachoecidae. Wenz (1939, pl. 732, fig. 2121) placed *Trachoecus* as questionable genus in the subfamily Paracerithiinae of the Procerithiidae (superfamily Cerithioidea). *Trachoecus* resembles *Protofusus* from the Late Triassic of Peru so much that Haas (1953, pl. 14,15) accepted the opinion of Wenz (1939). Whilst *Protofusus* is a caenogastropod (Bandel, 1993a) and could represent a member of the cerithioids, *Trachoecus* is a representative of the Heterostropha and thus not related to *Protofusus* and the Caenogastropoda in general.

Genus *Vallandroella* gen. nov.

Type species — *Tyrsoecus antorni* Zardini, 1985, from the St Cassian Formation.

Derivatio nominis — This genus is named after the Rifugio Vallandro, which is near Alpe di Specie below the Pico di Vallandro, where the type species was found.

Diagnosis — The slender and less than 10 mm high, turriform shells bear a dominant sculpture of axial ribs which are crossed by fine spiral costae. Growth lines reflect a shallow bay on the upper portion of the outer lip. The protoconch is of tofanellid type. The larval shell twists into dextral coiling well in advance of the teleoconch.

Diagnostic differences — *Protofusus* Bonarelli, 1921 and *Paracerithium* Cossmann, 1902 with species described by Haas (1953) from the Peruvian Triassic have similarly shaped teleoconchs that are connected to caenogastropod protoconchs and not to a heterostrophic one as found in *Vallandroella*. Among the Mathildoidea of the St Cassian Formation only *Trachoecus* bears a similarity in regard to teleoconch ornament, but it has less angular whorls and a more regular rib pattern. *Canepina* Conti & Fischer, 1983 from the Early Jurassic of Umbria (Italy) is similar in teleoconch shape. It was considered to be a caenogastropod belonging to the Coelostylinidae by Conti & Fischer (1983) and should thus have a dextral protoconch. This has not been demonstrated.

Vallandroella antorni (Zardini, 1985)
Pl. 16, figs. 5, 7-8; Pl. 17, fig. 9

1978 *Katosira seelandica*, Zardini, p. 43, pl. 28, fig. 7.
1985 *Tyrsoecus antorni* Zardini, pp. 10-11, pl. 3, fig. 20.

Description — Zardini (1985) described a single individual without the early ontogenetic portion of the shell from Misurina near the 'Lago d'Antorni'. The shell is slender and high with convex whorls that are sculptured by 6 coarse axial ribs. In successive whorls the ribs are oriented in alternating position (as seen across the suture). A shell with c. 8 whorls is a bit more than 5 mm high and c. 1.5 mm wide. Coarse axial ribs are crossed by fine spiral costae and additional fine axial costae form a background ornament of a rectangular network. Two of the spiral costae are a bit larger and form a raised zone in the lower centre of the flank. The aperture has a rounded outer lip, and an almost straight inner lip that forms a callus on the spindle. Its anterior base forms a narrow short siphonal canal.

The holotype is 4.5 mm high and without the apical whorls. These whorls are present in the Alpe di Specie specimen. The ornamental pattern on the early teleoconch resembles that of the later teleoconch with the exception that only 7 strong axial folds are present. The protoconch measures 0.28 mm in width and less than 0.2 mm in height. The embryonic shell is immersed in the apex of the larval shell and clearly sinistral. The larval shell changes coiling direction in its first half, and in its second half it is dextral. The aperture of the pediveliger shell is thickened and has a large apertural projection of the lower margin of the outer lip. The protoconch margin is well differentiated from the sculptural pattern of the teleoconch that begins with two dominant spiral costae.

Diagnostic differences — The protoconch is narrower, smaller and has fewer whorls than that of *Vallandroella seelandica*.

Material — Alpe di Specie (1 juvenile specimen, RGM 219 048), Misurina (2 specimens, RGM 219 047).

Vallandroella seelandica (Kittl, 1894)
Pl. 16, figs. 2, 6, 9; Pl. 17, figs. 1-2, 4-5.

1894 *Katosira seelandica* Kittl, p. 162, pl. 4, figs. 33-34.
1985 unidentified species, Zardini pl. 3, figs. 13-14.

Description — The diagnosis of the genus fully applies to this species. The slender shell with 7 whorls measures 6 mm in height and a bit more than 2 mm in width. Whorl width is about twice whorl height. Circa 7-8 coarse axial ribs are crossed by 4-5 fine spiral costae of unequal strength. The base is covered by 5-7 additional spiral costae. A shallow ridge below the suture lies outside of the bulge of the flanks, and axial ribs end before they reach the sutures and the subsutural ridge. Fine regular growth lines demonstrate that the apertural lip has an upper low bay and a broad central saddle. The base is rounded. The aperture is about as wide as high with rounded outer lip, almost straight inner lip and broad shallow siphonal notch at the anterior end.

The protoconch consists of 2.5 whorls and is c. 0,5 mm high and wide. The embryonic shell with c. 0.1 mm width is sinistral and held within the apex of the larval shell that rapidly grades into dextral coiling so that the last larval whorl is dextral. The apertural margin of the pediveliger shell is not thickened, and it is extended into a larval hook which in its larger part became covered by the following first whorl of the teleoconch.

Diagnostic difference — The shell of *Vallandroella seelandica* is somewhat more slender than that of *V. antorni* and, in contrast to the latter, has more spiral costae on the flanks and less on the base. The protoconch is larger in size and has more whorls. The teleoconch of *Stuorilda tichyi* resembles that of *Vallandroella seelandica*, but lacks the ribbon below the suture. Regarding to the morphology and sculpture of the protoconch *Stuorilda* differs considerably from *Vallandroella*.

Material — Alpe di Specie (3 specimens, RGM 219 049), Misurina (2 specimens, RGM 219 050). Kittl (1894) also had individuals from Alpe di Specie (Seelandalpe) and, in addition, from Stuores above St Cassian.

Remarks — Kittl (1894) described and figured his *Katosira seelandica* so insufficiently that it could represent a mixture of *Vallandroella seelandica*, *Stuorilda tichyi* and *Camponaxis lateplicata*. Species of the genera *Trachoecus* and *Vallandroella* are siphonate gastropods with a tofanellid protoconch. They are convergent to *Protofusus* and *Pseudotritonium* of the Peruvian province (Bandel, 1994b) which also lived in the Late Triassic. Early neogastropods from the Cretaceous are likewise convergent regarding the shape of their teleoconchs. The protoconch of the cancellariids actually is also quite similar in general outline and usually has a smooth surface (Bandel, 1993a, pl. 15, fig. 3), but has no sinistral first whorl as is so clearly seen in *Trachoecus* and *Vallandroella*.

Family Ampezzanildidae fam. nov.

Diagnosis — Shells with mathildoid teleoconch connected to a protoconch that is formed like that of the Tofanellidae, but has an ornament of strong regular axial ribs.

Diagnostic difference — The protoconch with axial ribs on its larval whorls distinguishes the Ampezzanildidae from all other gastropods of mathildoid shape from the St Cassian Formation. The Dolomitellidae with a similarly ornamented protoconch differ by the morphology and ornament of their teleoconch (Bandel, 1994a,b).

Genus *Ampezzanilda* gen. nov.

Type species — *Promathildia aialensis* Zardini, 1980.

Derivatio nominis — A combination of Ampezzo (from Cortina d'Ampezzo) and *Promathilda* (from the type species).

Diagnosis — The diagnosis of the family applies to the genus. The shell is slender, elongate, and consists of many whorls. Whorl flanks are concave and covered by fine axial, collabral striae, crossed by spiral striae, forming a dense reticulate pattern that in later whorls becomes inclined into a pattern of rhomboids. The early ontogenetic shell consists of a smooth embryonic shell that is immersed in the first sinistrally

coiled portion of the larval shell. Within the first whorl of the larval shell, the sinistral coil changes into planispiral coiling and later grades into a dextral coil. The last whorl of the larval shell is dextrally coiled and ends with an apertural rim. The sculpture of the larval shell consists of a regular pattern of rounded axial costae that are crossed by very fine spiral threads.

Diagnostic differences — The ribbed protoconch of *Ampezzanilda* differs clearly from *Cristalloella* with a similar teleoconch but a smooth protoconch.

Ampezzanilda aialensis (Zardini, 1980)
Pl. 17, figs. 3, 7-8, 10; Pl. 18, figs. 2, 4-5.

1980 *Promathildia aialensis* Zardini, p. 11, pl. 5, figs. 7-10, pl. 6, fig. 20.
1985 *Protorcula aialensis* Zardini, p. 14, pl. 5, fig. 11.

Description — Zardini (1980) presented a description of this strange species of which he had found numerous individuals at the Campo locality near Cortina d'Ampezzo. Though he described the teleoconch, he did not pay attention to the morphology of the first whorls. A shell with more than 14 whorls is c. 4.5 mm high and very slender. The apical angle in the first 5 whorls is c. 50° and decreases to less than 10° with further growth. During growth of the teleoconch there is a relative decrease in whorl expansion. The flanks of the whorls of the fully grown teleoconch are concave.The keel at the corner to the base forms a ridge just above the suture. In juvenile whorls of the teleoconch this keel lies further from the suture, and there may be an additional smaller ridge below the suture. The fine collabral threads and spiral threads in the first whorls of the teleoconch form a regular pattern of minute rectangles. In later whorls the orientation of the aperture and associated collabral threads becomes inclined. The spiral threads also change to inclined orientation so that they cross the collabral threads at almost right angles. Thus an inclined reticulate pattern is characteristic from the 6th or 7th whorl onward. The outline of the aperture is angular as that of *Promathilda*. Due to this similarity Zardini (1980, pl. 5. figs. 8-9) had placed his species into that genus.

The embryonic shell measures c. 0.1 mm in diameter. The rounded whorls of the larval shell are covered with c. 20 regular and straight axial ribs in each whorl. The larval shell is c. 0.4'mm high and wide, and its pediveliger stage is well marked by the thickened aperture. The protoconch consists of a little more than two whorls with the change from sinistral into dextral coiling found at the begin of the second whorl.

Diagnostic differences — The morphology of the teleoconch clearly differentiates *Ampezzanilda aialensis* from any of the other ampezzanildids with similar protoconchs.

Material — The species was originally described from Campo near Cortina d'Ampezzo and one individual from this locality is deposited in Leiden (RGM 219 051). The species also occurs in Alpe di Specie (2 specimens, RGM 219 052). It occurs in Pralongia in graded beds with reef detritus from the Richthofen reef (Monte Settsass) washed down the slope by turbidity currents (5 specimens, RGM 219 053).

Genus *Cassianilda* gen. nov.

Type species — *Turritella margaritifera* von Münster, 1841, from the St Cassian Formation.

Derivatio nominis — The name *Cassianilda* represents a combination of a mathildoid shell from the St Cassian Formation.

Diagnosis — The teleoconch is that of a slender *Mathilda*. However, the larval shell resembles that of *Ampezzanilda*. The embryonic shell is deeply immersed in the apex of the larval shell. The earliest larval shell is sinistral, and within the first whorl changes its coiling from sinistral into planispiral and dextral. The sculptural pattern of the larval shell consists of evenly rounded straight axial costae crossed by fine spiral threads.

Diagnostic differences — The ampezzanildid protoconch, characterised by a regular ornament with strong axial ribs, differentiates *Cassianilda* from the members of *Mathilda* and *Tirolthilda* which show a quite similar sculpture of the teleoconch. The sculpture of the teleoconch with its two keels overprinted with regular axial ribs differs from other ampezzanildids.

Cassianilda margaritifera (von Münster, 1841)
Pl. 18, figs. 1, 3, 6-7.

1841 *Turritella margaritifera* von Münster, p. 120, pl. 3, fig. 45.
1869 *Cerithium quadrangulatum* Laube, p. 8, pl. 29, fig. 12.
1894 *Promathildia margaritifera* Kittl, p. 223, pl. 9, figs. 24-26.
1978 *Promathildia margaritifera* (von Münster), Zardini, p. 52, pl. 35, fig. 30, pl. 36, figs. 1-2.
1985 *Promathildia margaritifera* Zardini, p. 14, pl. 5, fig. 12.
An extended synonymy was assembled by Kittl (1894).

Description — Judging from Zardini's (1978, pl. 36, figs. 1-2) illustrations, the animals grew to a large size. The specimen illustrated in Zardini (1985, pl. 5, fig. 12) was c. 3 cm high. With 10 mm in height the slender shell consists of c. 14 whorls. The aperture is angular, and the sculpture remains basically the same from the first whorls of the teleoconch to the last ones; the only exception being some smaller spiral ribs that may appear below the suture.

The embryonic shell is smooth and measures c. 0.1 mm in width. It lies within the apex of the protoconch. The larval shell is sinistral for c. one half whorl and then becomes planispiral. It grades into a dextral coil with the completion of the first postembryonic whorl. The protoconch is c. 0.3 mm wide and less than 0.2 mm high. Its ornament consists of c. 22 sharp axial ridges which are crossed by c. 30 fine axial threads. The margin of the pediveliger shell may or may not be thickened by a collabral rim. Change of sculpture between protoconch and teleoconch is abrupt.

Diagnostic differences — *Cassianilda margaritifera* is differentiated by the presence of first two and later three spiral costae on the teleoconch from *Promathilda biserta* which has only two costae throughout in addition to the different protoconch. In contrast to *P. subnodosa*, the whorls of the teleoconch are more rounded. The teleoconch sculpture distinguishes it from *Ampezzanilda aialensis*.

Material — Zardini found specimens of this species at various localities near Cor-

tina d'Ampezzo. The specimens described here, which have the first whorls preserved, come from below the Pralongia ridge above St Cassiano (2 specimens, GPIH; 1 specimen, RGM 219 054).

Genus *Stuorilda* gen. nov.

Type species — *Stuorilda cassiana* gen. et sp. nov. from the St Cassian Formation.

Derivatio nominis — Named after the Stuores meadows where the small mathildoids occur below the Pralongia ridge in an ever-changing outcrop.

Diagnosis — The shape of the teleoconch resembles that of *Zygopleura* or *Ampezzopleura* with simple axial ribs and slender turriculate form, but the protoconch is of ampezzanildid type with change in direction of coiling occurring in the early part of the larval shell.

Diagnostic differences — The combination of an axially ornamented teleoconch with an ampezzanildid protoconch is unique among the Heterostropha and other gastropods of the St Cassian Formation.

Stuorilda cassiana gen. et sp. nov.
Pl. 18, fig. 8; Pl. 19, figs. 1-2, 5.

1978*Katosira seelandica*, Zardini, p. 43, pl. 25, fig. 8.

Holotype — Specimen of Pl. 18, fig. 8 and Pl. 19, fig. 2 (NHM 1994/171).

Locus typicus — Stuores meadows below Pralongia ridge (for details see Introduction).

Stratum typicum — Cordevol Member, St Cassian Formation, in thin beds of shallow water debris that has been transported downslope into basinal deposits from the nearby Settsass carbonate platform (Late Triassic, Early Carnian).

Derivatio nominis — This species of *Stuorilda* is named after the St Cassian Formation.

Diagnosis — The generic diagnosis can be applied to this species. The turriform and slender shell is regularly ornamented by c. 10 broad axial folds on each whorl which are widest at the whorl centre and decrease toward the sutures. The protoconch consists of almost two whorls with even axial folds and a fine spiral liration between them.

Description — A shell with 2.5 mm height has 6.5 teleoconch whorls and an apical angle of c. 18°. The protoconch is c. 0.33 mm wide and high. It is flattened at the top with the sinistral embryonic shell found within a central depression. The whole last whorl of the larval shell has a dextral coiling mode, and its aperture is thickened by a raised rim. It is ornamented with c. 20 axial ribs separated from each other by rounded depressions which show fine spiral lirae crossing over from rib to rib. Teleoconch ornament differs drastically from protoconch sculpture. Here on a smooth background 8 to 10 broadly rounded axial folds form straight ribs that are strongest in the central part of each whorl and disappear toward the suture as well as toward the base. The corner to the rounded base carries a spiral costa that becomes covered by the following whorl. The aperture is suboval, but poorly preserved.

Diagnostic differences — The very similarly shaped *Stuorilda tichyi* sp. nov. differs mainly by having a spirally lirated background on the teleoconch and broader axial ribs. Also the protoconch has more whorls than present in *S. cassiana*. Whorls are broader in *Camponaxis*, which also differs in having a smooth tofanellid protoconch. The protoconch of *Schroederilda* is of mathildid type with the axis of coiling not falling together with the axis of the teleoconch. Here axial ribs on the teleoconch whorls multiply much more rapidly than is the case in *Stuorilda*.

Material — Stuores (1 specimen, RGM 219 055), Campo (2 specimens, RGM 219 056).

Stuorilda tichyi sp. nov.
Pl. 19, figs. 3-4, 6-7.

Holotype — Specimen of Pl. 19, figs. 3-4, 6-7 (NHM 1994/172).

Locus typicus — Misurina (details see in introduction).

Stratum typicum — Cordevol Member, St Cassian Formation (Late Triassic, Early Carnian).

Derivatio nominis — This species is named after colleague G. Tichy (Salzburg).

Diagnosis — The generic diagnosis can be applied to this species. The turriform and slender shell is regularly ribbed by c. 10 broad axial folds on each whorl which are crossed by a fine spiral liration. The protoconch consists of almost 2.5 whorls with even axial folds and a fine spiral liration between them.

Description — A shell with 4 whorls of the teleoconch is 2 mm high and has an apical angle of c. 17°. The protoconch is almost 0.5 mm wide and high and has a rounded top with a central depression in which the sinistral embryonic shell is found. The embryonic shell measures c. 0.1 mm in width. The change in direction from sinistral to dextral coiling occurs within the first whorl of the larval shell, and the second whorl is dextral. The protoconch consists of almost 2.5 whorls, and its aperture is thickened by a raised and straight rim. Its last whorl is ornamented with c. 20 sharp axial ribs separated from each other by rounded depressions which show fine spiral lirae. The teleoconch ornament differs from the protoconch sculpture, but also demonstrates axial ribs on a spirally lirated background. On the teleoconch 10 narrow axial folds form straight ribs that usually continue across whorls and sutures. They cross the rounded corner to the rounded base and disappear on the base. The base carries the same pattern of flattened spiral lirae separated from each other by flattened grooves. The aperture is suboval, but poorly preserved.

Diagnostic differences — *Stuorilda cassiana* has a smooth whorl surface on which the axial ribs are found, in contrast to *S. tichyi* having a densely lirated background. In contrast to *Zygopleura* Koken, 1892 and *Ampezzopleura* Bandel, 1991, having a rather similar teleoconch, the ampezzanildid protoconch of *Stuorilda* strongly differs from that of the ctenoglossan caenogastropods (see Bandel, 1991a).

Material — The holotype is the only known specimen.

Remarks — The larger teleoconch fragment figured by Zardini (1978, pl. 28, fig. 8) probably represents *Stuorilda tichyi*, but not fig. 7, which belongs to *Vallandroella antorni*. Both were placed with *Katosira seelandica* by Zardini. What Zardini (1978, pl. 24, figs. 13-14) considered to represent *Zygopleura walmstedti* (Klipstein, 1843) is

shorter than *Stuorilda cassiana*, whilst the same species called *Loxonema walmstedti* by Kittl (1894, pl. 4, figs. 20-23) could also include individuals of *S. cassiana*. Kittl's individual of *L. walmstedti* figured on pl. 8, fig. 5 is not even related to the other individuals, but represents a species of *Pseudotritonium* Wenz, 1938, which is a caenogastropod (pers. obs.).

Classifiction of the Mathildoidea

Species of the '*Promathildia*' groups of Kittl

When Kittl (1894) discussed the genus *Promathildia*, he had to evaluate the original descriptions presented by von Münster (1841) and Laube (1868). He was unable to study the original material in all cases. A modern re-evaluation of Kittl's descriptions and figures of the 22 species he considered to belong to the genus *Promathilda* Andreae, 1887 is difficult and often impossible. This is largely due to the preservation of the material that usually represents larger more or less fragmental teleoconchs.

Kittl (1894) distinguished four groups. The first of these holds only *Promathildia intermittens* Kittl, 1894, which is not a member of the Heterostropha, but belongs to the genus *Protuba* Cossmann, 1912 and carries a caenogastropod protoconch (own observations).

The second group of Kittl's system is the *Promathilda bolina* group comprising three species. Of these *P. trochleata* (von Münster, 1841) may represent a strongly worn shell of *Ampezzanilda aialensis* or *Cristalloella cassiana*. *P. winkleri* (Klipstein, 1843) could not be studied and seems to be a rather large species with a smaller apical angle than found in *Mathilda bolina*. It is not clear whether this species has an early teleoconch that resembles *P. bolina* (von Münster, 1841) which is here considered to belong to the genus *Mathilda*. Kittl (1894, pl. 9, figs. 6-9) figured *P. bolina* as more slender than *Mathilda bolina* (here) and with a wider apical angle than is present in the newly described *Turrithilda cassiana*. Thus it seems that Kittl mixed the characters of both in his illustrations so that Zardini (1978) reproduced both species with the same species name. *P. stuorensis* Kittl, 1894 was based on only a single shell that looks rather similar to *P. bolina* and was not well defined by Kittl (1894, pl. 9, fig. 10). Zardini (1978, pl. 36, fig. 23) illustrated an almost even flanked specimen, called *P.* cfr. *stuoresensis* (Kittl), which resembles *P. misurinenses* as described here. A similar shell had been photographed by G. Tichy from the Zlambach Marls of the Northern Alpes, which is of a similar age as the St Cassian Formation. It has a similar protoconch to *Ampezzanilda aialensis* and may represent this or a related species.

The third group distinguished by Kittl (1894) was called the *P. biserta* group. Here *P. decorata* and *Mathilda biserta* demonstrate a close morphological similarity to modern representatives of the genus *Mathilda*. *P. margaritifera* has such a characteristic larval shell that it is considered to represent a separate genus *Cassianilda*, which is also close to *Ampezzanilda* and *Dolomitella* Bandel, 1994 in regard to the larval shell morphology but not regarding the adult shell. *P. subnodosa* and *P. sculpta* are here considered to represent members of the genus *Promathilda*, which is a close relative of the Triassic members of the genus *Mathilda*. *P. bittneri* Kittl, 1894 of the *P. biserta* group

does not belong to the Heterostropha. Its rounded larval shell resembles that of *Cassianozyga* Bandel, 1991 and it is redescribed as *Cerithiozyga bittneri* and placed within the family Popenellidae Bandel, 1992. These represent a group of the Cerithioidea within the Caenogastropoda (Bandel, 1992b). The status of Kittl's *Promathildia subcancellata* (von Münster, 1841) is problematic. Zardini (1978, pl. 36, fig. 4,5,13) figured shells that he considered to be transitional from *P. subcancellata* to *P. subcrenata* which represent fragments of larger teleoconchs of *Cerithiozyga bittneri*. The taxonomic status of *P. crenata* (von Münster, 1841), and *P. perarmata* (von Münster, 1841) is presently unknown. *Promathildia pulchella* (Laube, 1869) is probably a young individual of *Ampezzoscala ornata* (von Münster, 1841) which has a caenogastropod larval shell (Bandel, 1992b; Bandel & El Nakhal, 1993) and belongs to the Ladinulidae, representing another Triassic group of the Cerithioidea. Other described individuals of *P. pulchella* may be related to the tofanellid *Vallandroella antorni* as described above. *P. tyrsoecus* Kittl, 1894, could very well represent a fragment of a larger shell of *Cassianilda margaritifera* similar to the one described by Zardini (1978, pl. 35, fig. 10) as *P. tyrsoecus* and by the same author on pl. 36, fig. 1 as *P. margaritifera* (the latter represents a somewhat younger section of the shell than the former).

The fourth group was centred around *Promathilda colon* (von Münster, 1841). Here *P. pygmaea* and *P. colon* are difficult to separate and may very well represent young portions of a shell of *Tofanella decussata*. Kittl's *P. decussata* represents a member of the Tofanellidae with rather differently keeled and nodulous early teleoconch, transitional intermediate whorls and flat-sided late teleoconch. The characteristic slender and flat-sided later shell portions have been recognised by Zardini (1978, pl. 35, fig. 27-29) as *P. decussata*, while earlier whorls were placed in *P. pygmaea* (fig. 18) or not recognised as belonging to *Tofanella* (fig. 17). Zardini followed Kittl's misleading illustrations and description. *P. subornata* (von Münster, 1841) may be more closely related to members of the Ctenoglossa in the morphology of the adult shell. This similarity has also been noted by Kittl (1894), but this needs to be confirmed by examining the early shell whorls in order to see if they have the characteristic juvenile Ctenoglossa sculpture (Bandel, 1991a) or whether there exists a relation to the ampezzanildid *Stuorilda*.

It is apparent that the concept of Kittl's groups of *Promathildia* cannot be maintained and must be replaced by a different system. It is also obvious that a classification that does not take all available shell features into consideration, can not reflect the order that is based on a natural system that comes close to the course of evolution in time. First all caenogastropods must be separated, like *Cerithiozyga bittneri* and *Ampezzopleura ornata*. The morphology of the protoconchs can group the remaining heterostrophic species into different lineages. Strong differences in the ornament of the early teleoconch and the late teleoconch are than still a problem as is seen in the case of *Tofanella decussata*. Thus, there is little that can remain of Kittl's four groups in the *Promathildia* genus as suggested by him a century ago.

Key to the Mathildoidea of the St Cassian Formation:

1a The change from sinistral to dextral coiling occurs at the transition from protoconch to teleoconch 2

b The change from from sinistral to dextral coiling occurs before the beginning of the teleoconch (Tofanellidae, Trachoecidae, Ampezzanildidae) 15

2a Sutures of teleoconch distinct and ornament the same throughout (Mathildidae) 3
b Sutures of teleoconch indistinct and ornament changes in the later teleoconch (Anoptychiidae) 13

3a Teleoconch begins with dominant axial ribs ..... *Schroederilda milierensis*
b Teleoconch begins with spiral ribs 4

4a Teleoconch begins with one dominating spiral rib (*Promathilda*) 5
b Teleoconch begins with more than one spiral rib 8

5a No axial ribs on early teleoconch (*P. subnodosa, P. misurinensis*) 6
b Axial ribs on early teleoconch (*P. decorata, P. sculpta*) 7

6a Later teleoconch with axial ribs ..... *Promathilda subnodosa*
b Later teleoconch without axial ribs ..... *Promathildia misurinensis*

7a Protoconch large and spiral lination of teleoconch fine ..... *Promathilda decorata*
b Protoconch small and spiral lination of teleoconch coarse ..... *Promathilda sculpta*

8a Teleoconch begins with 4 spiral ribs (*Turrithilda*) 12
b Teleoconch begins with 2 spiral ribs (*Mathilda; Tirolthilda*) 9

9a Spiral ribs on teleoconch subequal (*Mathilda*) 10
b Spiral ribs on teleoconch equal (*Tirolthilda*) 11

10a Shell angle low ..... *Mathilda biserta*
b Shell angle high ..... *Mathilda bolina*

11a Protoconch forms angle with axis of teleoconch ..... *Tirolthilda seelandica*
b Protoconch with same axis of coiling ..... *Tirolthilda nuetzeli*

12a Teleoconch with evenly rounded flanks ..... *Turrithilda dockeryi*
b Teleoconch with angular flanks ..... *Turrithilda cassiana*

13a Early teleoconch with predominant axial ribs ..... *Anoptychia supraplecta*
b Early teleoconch with spiral ribs 14

14a Teleoconch slender ..... *Turristylus triadicus*
b Teleoconch less slender ..... *Camponella pianozesis*

15a Protoconch predominantly smooth (Tofanellidae and Trachoecidae) 16
b Protoconch regularly ribbed (Ampezzanildidae) 26

16a Teleoconch with sculpture of axial and spiral ribs, aperture with short anterior notch (Tofanellidae) 17
b Ornament of strong axial folds, aperture with siphon or notch (Trachoecidae) 24

17a Teleoconch ornament changes during growth ..... *Tofanella decussata*
b Teleoconch ornament remains similar throughout 18

18a The ornament consists of keeled flank (*Cristalloella, Tofanella*) 19
b Ornament of predominant axial ribs (*Camponaxis*) 22

19a Ornament of straight axial ribs 20
b Ornament of sinuate ribs 21

20a Ornament of fine straight axial ribs ..... *Cristalloella cassiana*
b Ornament of equally coarse straight and axial ribs ..... *Tofanella cancellata*

21a Ornament with simple sinuate axial ribs ..... *Cristalloella sinuata*
b Ornament of cancellate pattern in lower whorl half ..... *Cristalloella delicata*

22a Ribs on teleoconch present throughout 23
b Axial ribs in teleoconch are indistinct at first ..... *Camponaxis lateplicata*

23a Number of ribs in teleoconch remain similar ..... *Camponaxis subcompressa*
b Number of ribs in teleoconch increase ..... *Camponaxis beneckei*

24a Teleoconch with ovoid shape and inclined axial folds continuous across sutures ..... *Trachoecus gemmellaroi*
b Teleoconch with *Fusus* like shape 25

25a Small protoconch ..... *Vallandoella seelandica*
b Large protoconch ..... *Vallandroella antorni*

26a Sculpture of teleoconch is keeled 27
b Sculpture of teleoconch is not keeled 28

27a Sculpture has one keel ..... *Ampezzanilda aialensis*
b Sculpture with two spiral keels ..... *Cassianilda margaritifera*

28a Sculpture of teleoconch with axial ribs on smooth background .... *Stuorilda tichyi*
b Sculpture of teleoconch with axial ribs on striped background .... *Stuorilda misurinensis.*

General discussion on heterostrophic gastropods of the mathildoid type

Heterostropha Fischer, 1885 hold all those species of gastropods that change from

sinistral to dextral coiling during their early ontogeny or have evolved from ancestors that had this development. They include the suborders Allogastropoda and Euthyneura (Opisthobranchia and Pulmonata).

The Allogastropoda Haszprunar, 1985, as used here, are the uniting taxon for superfamilies such as Streptacidoidea, Pyramidelloidea, Mathildoidea, Architectonicoidea, Nerineoidea, and Valvatoidea.

The Pyramidelloidea Gray, 1840 were considered by Knight et al. (1960) to belong to the Opisthobranchia and were interpreted to hold such ancient groups as the Streptacididae Knight, 1931 and the Donaldinidae Bandel, 1995 that range back in time at least to the Devonian (Bandel, 1994a, 1995). Wenz (1939) considered these Heterostropha of Palaeozoic times to belong to the Loxonematoidea. But Donald (1898) and Knight (1941) reported on a heterostophic protoconch among the Palaeozoic genera *Donaldina* and *Streptacis*. Its presence in *Donaldina* and *Streptacis* has since been confirmed for Carboniferous species by Anderson et al. (1985), Yoo (1988, 1994), Herholz (1992), and our own research (pers. obs., Bandel, 1994a). The Ebalidae Bandel, 1994 are present in the St Cassian fauna from the Late Triassic (Bandel, 1994b, 1995) as well and they are also known from the Early Jurassic of Northern Germany (Schröder, 1995). *Ebala* belongs to a separate group not related to the bulk of the Pyramidellidae. But since very similar shells are also found in Palaeozoic deposits there may well exist a connection with the Streptacididae. The related Donaldinidae form an ancient group with characteristic shell shape and size and they have representatives in the St Cassian fauna (Bandel, 1995). Modern species belonging to this family are still living in the shallow water of the tropical Indo-Pacific and can well be differentiated from members of the Pyramidellidae (Bandel, 1991b, 1995). True Pyramidellidae Gray, 1840 appear in the Campaninian and Maastrichtian Gulf Coast faunas of the USA with genera such as *Creonella* Wade, 1917 and *Lacrimiformia* Sohl, 1960.

The core of the superfamily Mathildoidea Dall, 1889, the Mathildidae Dall, 1889, have remained basically unchanged in their shell morphology since Triassic times. The presence of larval shells with mathildid and architectonicid characteristics in the Late Carboniferous sea of Central Europe has been documented by Herholz (1992). Bieler (1988) reconstructed the derival of Mathildidae and Architectonicidae from a common ancestral group living in Mid-Mesozoic times. But since the Late Triassic Mathildoidea and Architectonicoidea are present without any transitional forms (Bandel, 1995), this relation must be older. *Mathilda*, *Promathilda*, and *Turrithilda* are present in the Late Triassic St Cassian Formation and in deposits of the same age in Peru (Haas, 1953, Bandel, 1994b) as well as in the Jurassic of Northern Germany and Poland (Schröder, 1995; Gründel, 1973, 1976). In the Early Cretaceous of Poland representatives of *Gymnothilda* Schröder, 1995, and *Gegania* Jeffreys, 1884 make their first appearance (Schöder, 1995).

In the St Cassian Formation the family Mathildidae contains representatives of the genera *Mathilda*, *Promathilda*, *Tirolthilda*, *Turrithilda* and *Schroederilda*, the Tofanellidae holds the genera *Tofanella*, *Cristalloella*, and *Camponaxis*, the Trachoecidae the genera *Trachoecus*, and *Vallandroella*, the Ampezzanildidae genera such as *Ampezzanilda*, *Cassianilda*, and *Stuorilda*. A similar protoconch is also found among the Zardinellidae Bandel, 1994 based on the genus *Zardinella* from St Cassian. The Tofanellidae

may include species of the genus *Chevallieria* from the Jurassic (Schröder, 1995) as well as of younger age. In the Early Cretaceous of Poland *Wonwalica* Schröder, 1995 represents the group. Most probably there are still some members of this group living in the Indopacific Ocean (Bandel, 1991b).

The family Anoptychiidae is based on the genus *Anoptychia* Koken, 1892 and holds the genera *Turristylus* and *Camponella* from the St Cassian Formation. The superfamily Nerineoidea Zittel, 1873 may have developed from representatives of the Anoptychiidae. According to Vaughan (1988) the Nerineoidea contain the families Ceritellidae, Nerineidae, Nerinellidae, and Itieriidae and are restricted to Jurassic and Cretaceous strata. Whilst the ancestors of the Ceritellidae may have been closely related to the genus *Dolomitella* Bandel, 1994, the Nerineidae and Nerinellidae have slender conical shells with many whorls and a turritelliform shape and a heterostrophic protoconch (Vaughan, 1988). Their presence in the group was verified in several species from the Late Cretaceous of the Northern Alps and the Pyrenees (Harbeck, 1989; pers. obs.). They also have a slit or sinus in the apertural margin at the posterior end of the aperture. This feature clearly differentiates the Nerineidae and Nerinellidae from the Anoptychiidae of the St Cassian Formation. Most members of both families were initially specialised as lagoonal inhabitants, and later became closely associated with the rudist lagoons (Mustafa & Bandel, 1992).

The Valvatoidea also have their oldest known representatives in the St Cassian Formation (Bandel, 1995), which closely resemble their modern relatives especially those still living in the sea (Ponder, 1990, 1991; Bandel, 1991c). The superfamily Streptacidoidea belongs to the Allogastropoda and known representatives lived in Palaeozoic times. Modern species belonging to this taxon have been erroneously placed in the Pyramidelloidea and/or the Aclididae. Members of the Streptacidoidea represent the oldest known Heterostropha. It is only in the late Mid-Triassic of the St Cassian Formation that members of the superfamilies Architectonicoidea, Mathildoidea and Valvatoidea appear side by side. Similarly the first clearly recognisable Opisthobranchia make their appearance in this formation (Bandel, 1994a). A transition from Valvatoidea to Architectonicoidea in regard to shell form could be constructed (Bandel, 1995), but there is no indication of intermediate shell forms between Architectonicoidea and Mathildoidea. Thus intermediate forms, if present at all, should have lived before Carnian times. The Nerineoidea appear in the Jurassic and could be connected to the Anoptychiidae with regard to external shell shape. The Pyramidelloidea can be documented in the fossil record only from Cretaceous times onward.

Acknowledgements

Material collected by Rinaldo Zardini and made available to the author has been of great value in this evaluation of the Mathildoidea of Ladinian/Carnian times. This material was accumulated during a life time of collecting. Additional material was collected by Frank Riedel, Nikolaus Lehmann and myself during the summer of 1989, aided by financial support of DFG grant Ba 675/3. Sabrina Crafton, Frederike Stichert, Alex Nützel, Klaus Harbeck and myself continued work during the summer of 1991 aided by Rolando Lanzedelli. During the summer of 1993 collecting was

resumed together with Fredericke Stichert and Alex Nützel and financial support came from DFG grant Ba 675/12. Additional information was extracted from material preserved in and loaned from the Naturhistorisches Museum in Vienna with the assistance of Heinz Kollmann and Ortwin Schultz and from photographs of shells from the Zlambach Marls provided by G. Tichy (Salzburg). Plates were assembled by Eva Vinx and Dörte Kortum, and the text improved by Marlies Becker. Arie Janssen (Leiden) greatly improved the key and the clarity of the text. Thanks are expressed to all people and institutions involved in this study.

References

Anderson, J.R., R.D. Hoare & M.T. Sturgeon, 1985. The Pennsylvanian genera *Orthonema* Meek and Worthen and *Streptacis* Meek from the Appalachian Basin. — J. Paleont., 59: 1011-1027.

Bandel, K., 1988a. Repräsentieren die Euomphaloidea eine natürliche Einheit der Gastropoden ? — Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 67:1-33.

Bandel, K., 1988b. Early ontogenetic shell and shell structure as aid to unravel gastropod phylogeny and evolution. In: W.F. Ponder (ed.). Prosobranch Phylogeny. Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh Scotland. — Malacol. Rev., Suppl., 4: 267-272.

Bandel, K., 1991a. Über triassische 'Loxonematoidea' und ihre Beziehungen zu rezenten und paläozoischen Schnecken. — Paläont. Z., 65: 239-269.

Bandel, K., 1991b. Character of the microgastropod fauna from a carbonate sand of Cebu (Philippines). — Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 71: 441-485.

Bandel, K., 1991c. Gastropods from brackish and fresh water of the Jurassic Cretaceous transition (a systematic evaluation). — Berliner geowiss. Abh., A, 134: 9-55.

Bandel, K., 1992a. Die Evolution der Gastropoden aus biologischer und paläontologischer Sicht. — Veröff. Übersee Mus., Natur-Wissensch., 11: 17-25.

Bandel, K., 1992b. Über Caenogastropoda der Cassianer Schichten (Obertrias) der Dolomiten (Italien) und ihre taxonomische Bewertung. — Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 73: 37-97.

Bandel, K., 1993a. Caenogastropoda during Mesozoic times. In: A.W. Janssen & R. Janssen (eds.). Proceedings of the Symposium 'Molluscan Paleontology', 11th International Malacological Congress, Siena, Italy, 30th August-5th September 1992. — Scripta Geol., Sp. Issue, 2: 7-56.

Bandel, K. 1994a. Triassic Euthyneura (Gastropoda) from St Cassian Formation (Italian Alps) with a discussion on the evolution of the Heterostropha. — Freiberger Forschungsh., C, 452: 79-100.

Bandel, K., 1994b. Comparison of Upper Triassic and Lower Jurassic gastropods from the Peruvian Andes (Pucará Group) and the Alps (Cassian Formation). — Palaeontographica, A, 233: 127-160.

Bandel, K., in press. Some heterostrophic gastropods from Triassic St Cassian Formation with a discussion on the classification of the Allogastropoda. — Paläont. Z. (submitted).

Bandel, K. & H.A. El-Nakhal, 1993. The history and relationship of *Scaliola*, a gastropod that cements particles to its shell. — Mitt. Geol.-Paläont. Inst. Univ. Hamburg, 75: 171-191.

Bieler, R., 1988. Phylogenetic relationships in the gastropod family Architectonicidae, with notes on the family Mathildidae (Allogastropoda). — Malacol. Review, 1988, Suppl. 4: 205-240.

Bizzarini, F., R. Laghi, F. Russo & M. Urlichs, 1986. Preliminary biostratigraphic correlation between Ampezzo Basin sections and their Cordevolian stratotype (Late Triassic, Italian Dolomites). — Lavori Soc. Ven. Sc. Nat., 11: 151-158.

Blaschke, 1905. Gastropodenfauna der Pachycardientuffe der Seiseralpe in Südtirol nebst einen Nachtrag zur Gastropodenfauna der roten Raibler Schichten von Schlernplateau. — Beitr. Pal. Österr.-Ung. Orients, 17: 161-222.

Blendinger, W. & E. Blendinger, 1989. Windward-leeward effects on Triassic carbonate bank margins in the Dolomites, northern Italy. — Sedim. Geol., 64: 143-166.

Conti, M.A. & J.C. Fischer, 1983. Revisione della fauna mesogiurassico de Acque Fredde (Lago die Garda) descritto da Parona. — Boll. Mus. Civ. Storia Nat. Verona, 9: 489-522.

Cossmann, M., 1895. Essais de Paléoconchologie comparée, 1. — Cossmann, Paris: 1-159.
Cossmann, M. 1912. Essais de Paléoconchologie comparée, 9. — Cossmann, Paris: 1-215.
Dockery, D.T. III, 1993. The streptoneuran gastropods, exclusive of the Stenoglossa, of northeastern Mississippi. — Bull. Miss. Dep. Environm. Quality, Office Geol. (Jackson), 129: 1-191.
Donald, J., 1898. Observations on the genus *Aclisina* de Koninck, with descriptions of British species and of some other Carboniferous Gastropoda. — Quart. Journ. Geol. Soc. London, 54: 45-72.
Fretter, V., & A. Graham, 1986. The prosobranch molluscs of Britain and Denmark, 9. Pyramidellacea. — J. Moll. Stud., suppl. 16: 556-649.
Gründel, J., 1973. Zur Gastropodenfauna aus dem Dogger, 1. Die Gattungen *Mathilda* und *Eucycloidea* (Gastropoda). — Z. Geol. Wissensch., 1: 947-965.
Gründel, J., 1976. Zur Phylogenie und Umgrenzung der Gattungen *Mathilda* und *Promathildia* (Gastropoda). — Jb. Geol., 7-8 (1971-1972): 337-351.
Haas, O., 1953. The Late Triassic gastropods from Central Peru. — Bull. Amer. Mus. Nat. Hist., 101: 9-328.
Harbeck, K., 1989. Palökologische und mikrofazielle Untersuchungen an Küstensumpfablagerungen aus dem Maastricht bei Isona (Becken von Tremp, Südpyrenäen, Spanien). — Masters Thesis, Dept. Geol.-Paleont., Univ. Hamburg: 1-167 (unpubl.).
Haszprunar, G., 1985a. On the anatomy and systematic position of the Mathildidae (Mollusca, Allogastropoda). — Zool. Scripta, 14: 201-213.
Haszprunar, G., 1985b. The fine morphology of the osphradial sense organs of the Mollusca, 2. Allogastropoda (Architectonicidae, Pyramidellidae). — Phil. Trans. R. Soc. London, B, 307: 497-505.
Haszprunar, G., 1988. On the origin and evolution of the major gastropod groups, with special reference to the Streptoneura. — J. Moll. Stud., 54: 367-441.
Herholz, M., 1992. Mikromorphe Gastropoden aus dem rheinisch-westfälischen Steinkohlerevier (Oberkarbon). — N. Jb. Geol. Paläont, Mh., 1992: 242-256.
Kittl, E., 1894. Die Gastropoden der Schichten von St Cassian der südalpinen Trias, 3. — Ann. k.k. naturhist. Hofmus., 9: 144-277.
Kittl, E., 1895. Die triadischen Gastropoden der Marmolata und verwandter Fundstellen in den weißen Riffkalken Südtirols. — Jb. k.k. geol. Reichsanst. Wien, 44: 99-182.
Klipstein, A. von, 1843. Beiträge zur geologischen Kenntnis der östlichen Alpen. — Giessen: 1-144.
Knight, J.B., 1941. Paleozoic gastropod genotypes. — Bull. Geol. Soc. Amer., Spec. Pap., 32: 1-510.
Knight, J.B., R.L. Batten & E.L.Yochelson, 1960. Part I, Mollusca, 1. In R.C. Moore (ed.). Treatise on invertebrate paleontology. — Geol. Soc. Am. & Univ. Kansas Press, Lawrence/Kansas: I 169-I351.
Koken, E., 1889. Über die Entwicklung der Gastropoden vom Cambrium bis zur Trias. — N. Jb. Miner. Pal. Geol., B, 4: 305-484.
Koken, E., 1892. Über die Gastrpoden der rothen Schlernschichten nebst Bemerkungen über Verbreitung und Herkunft einiger triassischer Gattungen. — N. Jb. Miner. Pal. Geol., 1892: 25-36.
Laube, G. C., 1868-1869. Die Fauna der Schichten von St. Cassian. — K. Akad. Wiss. Wien, Denkschr., 28: 29-94 (1868); 30, 2: 1-106 (1869).
Leonardi, P. & F. Fiscon, 1959. La fauna Cassiana di Cortina d'Ampezzo, 3. Gasteropodi. — Mem. Ist. Geol. Min. Univ. Padova, 21: 1-103.
Münster, G.G. von, 1841. Beschreibung und Abbildung der in den Kalkmergelschichten von St. Cassian gefundenen Versteinerungen. In: Wissmann & G.G. von Münster (eds.). Beiträge zur Geologie und Petrefacten-Kunde des südöstlichen Tirol's vorzüglich der Schichten von St. Cassian. — Beitr. Petrefacten-Kunde, 4: 1-152.
Mustafa, H., & K. Bandel, 1992. Gastropods from lagoonal limestones in the Upper Cretaceous of Jordan. — N. Jb. Geol. Paläont., Abh., 185: 349-376.
Ponder, W.F., 1967. The classification of the Rissoidea and Orbitestellidae with description of some new taxa. — Trans. roy. Soc. New Zealand, Zool., 9: 193-224.
Ponder, W.F., 1990. The anatomy and relationship of marine valvatoideans (Gastropoda: Heterobranchia). — J. Moll. Stud., 56: 533-555.
Ponder, W.F., 1991. Marine Valvatoideans, implications for heterobranch phylogeny. — J. Moll. Stud., 57: 21-32.

Ponder, W.F., & A. Warén, 1988. Classification of the Caenogastropoda and Heterostropha - A list of the family group and higher category names. In: W.F. Ponder (ed.). Prosobranch phylogeny. Proceedings of a Symposium held at the 9th International Malacological Congress, Edinburgh Scotland. — Malac. Rev., Suppl. 4: 88-128.

Sabelli, B., & G. Spada, 1978. Guida illustrata all'identificazione delle conchiglie del Mediterraneo. Fam. Mathildidae; Fam. Turritellidae — Conchiglie, 14, 3-6, suppl. (2 unnumbered pages).

Schröder, M., 1995. Frühontogenetische Schalen jurassischer und unterkretazischer Gastropoden aus Norddeutschland und Polen. — Paläontographica (in press).

Urlichs, M. 1994. *Trachyceras* Laube 1869 (Ammonoidea) aus dem Unterkarn (Obertrias) der Dolomiten (Italien). — Stuttg. Beitr. Naturk., B, 217: 1-55.

Vaughan, P.G., 1988. Cretaceous nerineacean gastropods: Systematics, affinities and palaeoecology. — Doctor's Thesis, Open Univ., London: 1-264 (unpubl.).

Wendt, J. & F.T. Fürsich, 1980. Facies analysis and paleogeography of the Cassian Formation, Triassic, Southern Alps. — Riv. Ital. Paleont., 85: 1003-1028.

Wenz, W. 1939. Gastropoda, 1. — In: O.H. Schindewolf (ed.). Handbuch der Paläozoologie, 6, 1: 1-1639.

Wenz, W., & A. Zilch, 1960. Gastropoda Euthyneura. — In: O.H. Schindewolf, (ed). Handbuch der Paläozoologie, 6, 2: 1-853.

Yoo, E.K., 1988. Early Carboniferous Mollusca from Gundy, Upper Hunter, New South Wales. — Rec. Austr. Mus., 40: 233-264.

Yoo, E.K., 1994. Early Carboniferous Mollusca from the Tamworth Belt, New South Wales, Australia. — Rec. Austr. Mus., 46: 63-120.

Zardini, R., 1978. Fossili Cassiani. — Cortina d'Ampezzo: 1-58.

Zardini, R., 1980. Fossili Cassiani. — Cortina d'Ampezzo: 1-16.

Zardini, R., 1985. Fossili Cassiani. — Cortina d' Ampezzo: 1-16.

Manuscript received 23 November 1994, revised version accepted 16 May 1995.

Plate 1

Mathilda biserta (von Münster, 1841)

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Fig. 1. Adult specimen from Alpe di Specie; height 5.5 mm (RGM 219 001).
Fig. 2. Protoconch from Alpe di Specie (detail of fig. 3), diameter 0.3 mm. The teleoconch begins with an ornament of two keels.
Fig. 3. Adult specimen from Campo; height 3.8 mm (GPIH).
Fig. 4. Juvenile specimen from Alpe di Specie, height 1.3 mm (GPIH).
Fig. 5. Juvenile shell from Misurina with two keels on the early teleoconch; height 0.8 mm (GPIH).
Fig. 6. Juvenile specimen from Alpe di Specie; height 0.9 mm (GPIH).
Fig. 7. Protoconch from Campo; height 0.3 mm (GPIH).
Fig. 8. Early teleoconch from Misurina seen from above; diameter of protoconch 0.35 mm (GPIH).

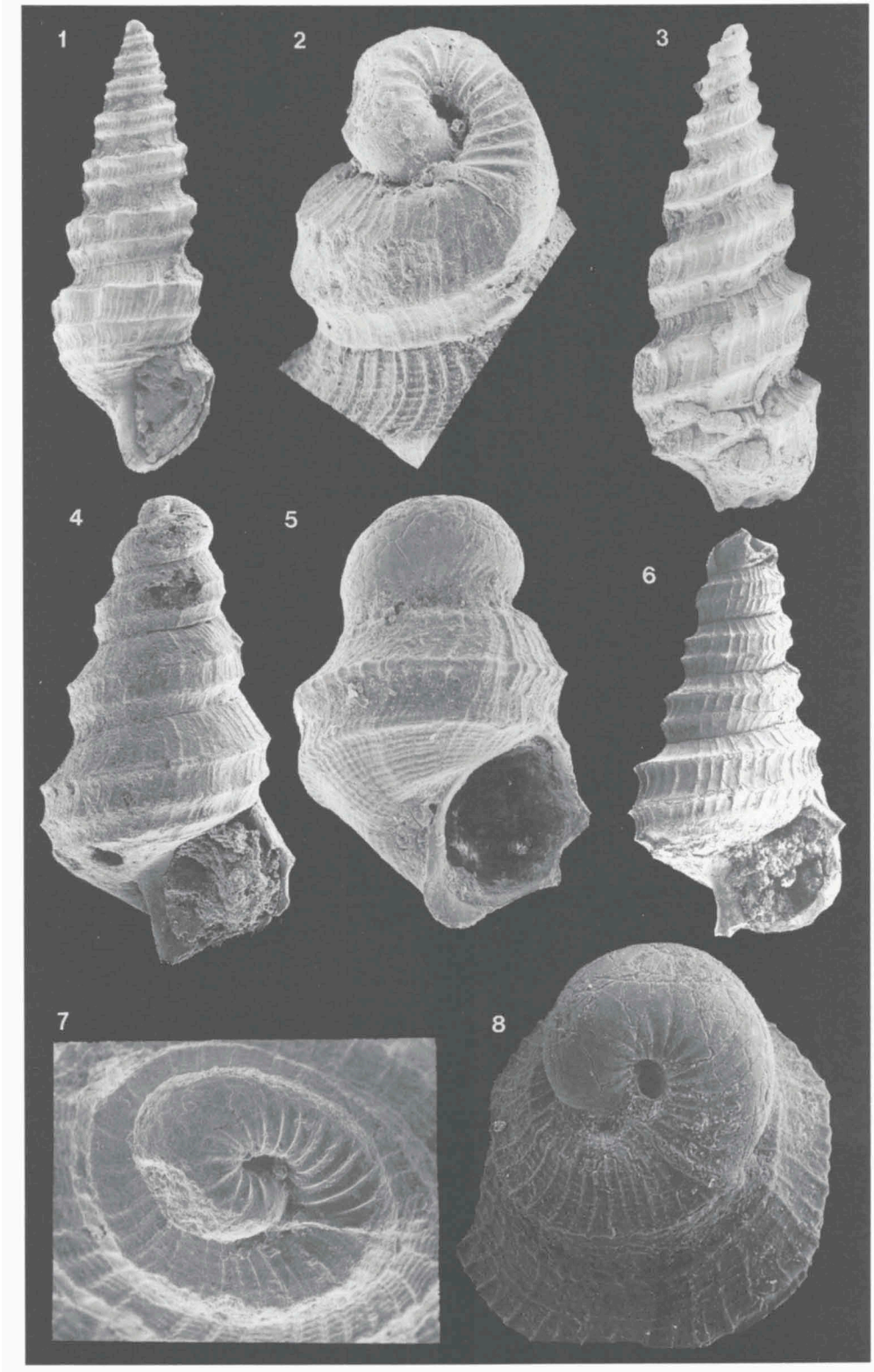

1
2
3
4
5
6
7
8

Plate 2

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Mathilda bolina (von Münster, 1841)
Fig. 1. Apex from Misurina with 0.25 mm wide and smooth protoconch (RGM 219 003).
Fig. 2. Protoconch from Alpe di Specie measuring 0.22 mm across (GPIH).
Fig. 3. Apical view from Alpe di Specie (detail of fig. 4) with protoconch of 0.22 mm in diameter and begin of the teleoconch with two dominant spiral keels.
Fig. 4. Juvenile shell from Alpe di Specie measuring 0.75 mm in height (RGM 219 004).
Fig. 6. Juvenile shell from Misurina of 1.3 mm height (RGM 219 003).

Promathilda subnodosa (von Münster, 1841)
Fig. 5. Juvenile shell from Misurina of 0.55 mm height (GPIH).
Fig. 7. Apex from Alpe di Specie that has a 0.22 mm wide protoconch (RGM 344 963).

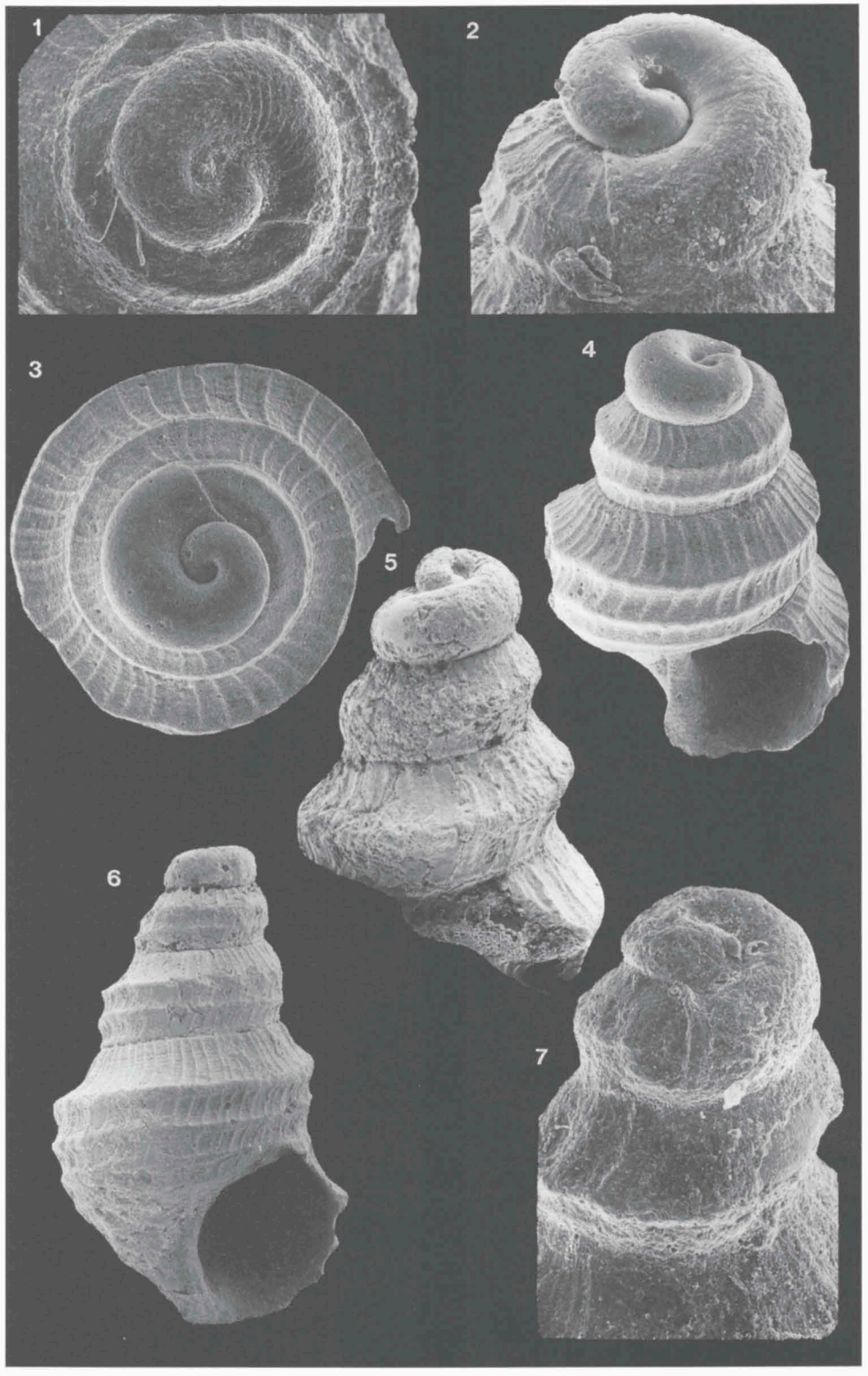

1
2
3
4
5
6
7

Plate 3

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Promathilda subnodosa (von Münster, 1841)

Figs. 1, 3. Apical shell of 0.7 mm height from Misurina (GPIH).

Fig. 2. Shell from Alpe di Specie, 2.9 mm high, with first whorls of the teleoconch ornamented more simply than later whorls (RGM 344 963).

Fig. 4. Apical shell from Alpe di Specie with 0.22 mm wide protoconch (detail of fig. 3) on teleoconch with small deviation (RGM 219 005).

Fig. 6. Juvenile shell from Misurina with 1.6 mm high shell (GPIH).

Fig. 7. Protoconch from Misurina (detail of fig. 6) that is almost 0.2 mm wide.

Promathilda decorata (Klipstein, 1843)

Fig. 5. Shell 2.2 mm high, from Stuores near St Cassiano (GPIH).

Promathilda sculpta (Kittl, 1894)

Fig. 8. Protoconch from Alpe di Specie (detail to Pl. 4, fig. 6), 0.37 mm wide and resting with apex down on the top of the teleoconch.

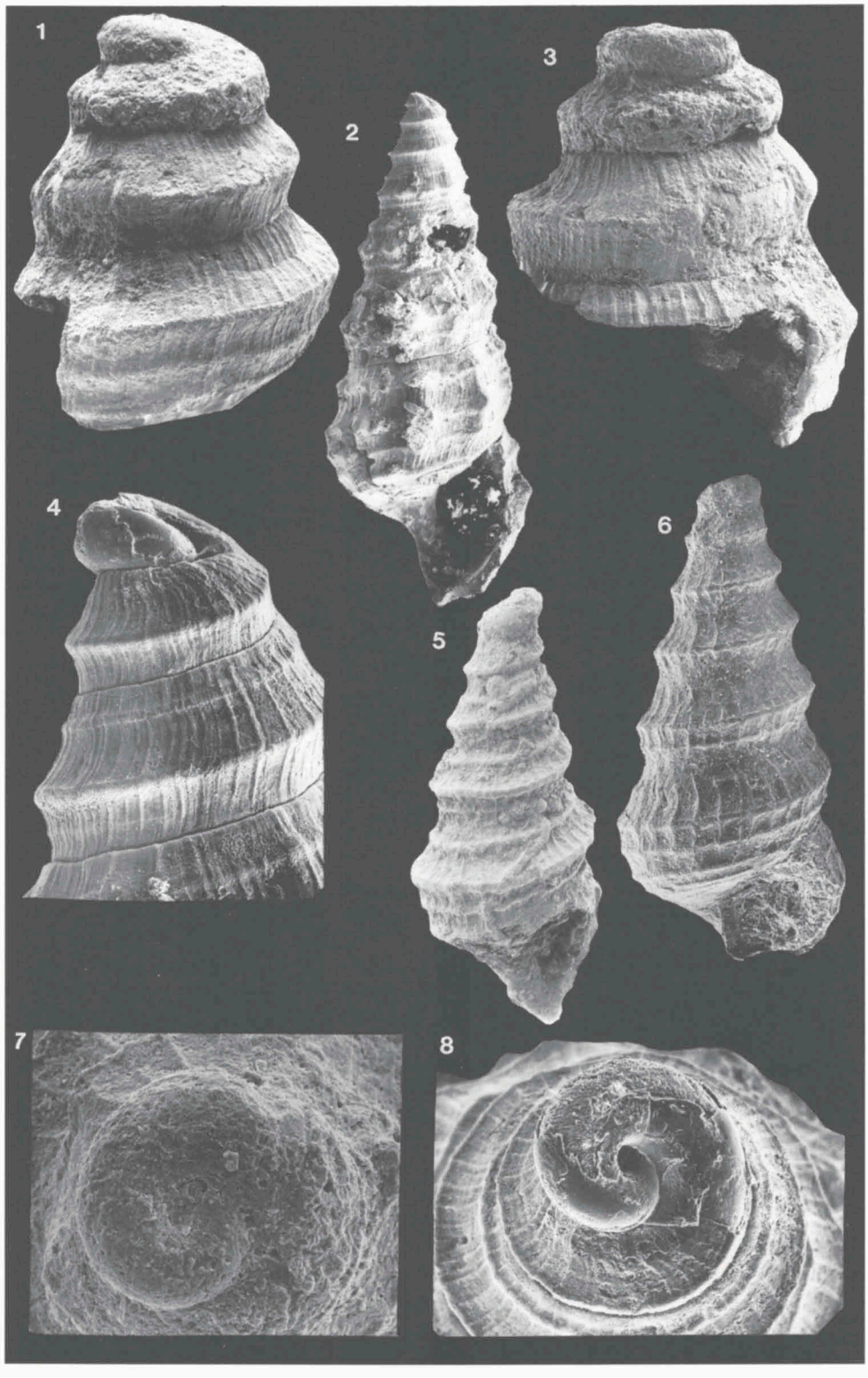

1
2
3
4
5
6
7
8

Plate 4

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Promathilda decorata (Klipstein, 1843)
Fig. 1. Apex from Misurina (detail to fig. 4) that has an almost 0.4 mm wide protoconch with embryonic shell (points to the right) largely covered by the first whorl of the teleoconch.
Fig. 2. Protoconch from Cortina d'Ampezzo (Italy) of almost 0.4 mm width that forms an angle with the teleoconch. Its umbilicus is surrounded by axial folds (GPIH).
Fig. 3. Protoconch from Dibona, 0.4 mm wide, forming an angle with the teleoconch. The upper flank is ornamented by axial folds (GPIH).
Fig. 4. Shell from Misurina, 3.8 mm high(RGM 219 006).
Fig. 5. Shell from Alpe die Specie, 3.5 mm high (RGM 219 008).
Fig. 7. Protoconch from Alpe di Specie, 0.4 mm wide, embryonic shell (lower left) is almost hidden by the teleoconch (RGM 219 008).

Promathilda sculpta (Kittl. 1894)
Fig. 6. Shell from Alpe di Specie, 4 mm high (RGM 219 009).
Fig. 8. Protoconch from Alpe di Specie (detail of fig. 6), 0.37 mm wide.
Fig. 9. Protoconch from Alpe di Specie, with its apex (central right) resting on the first whorl of the teleoconch (same as in fig. 8).

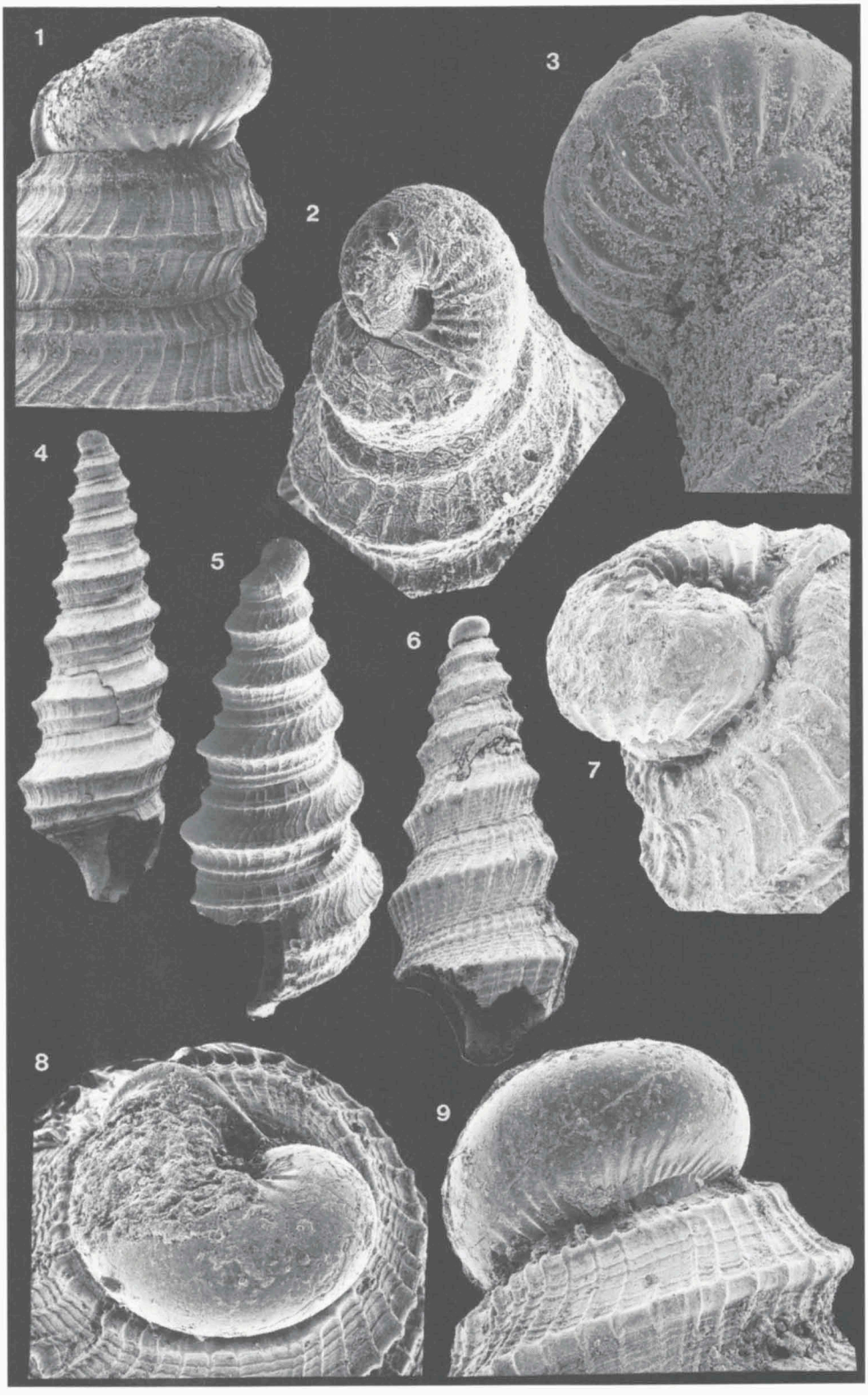

1
2
3
4
5
6
7
8
9

Plate 5

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Promathilda sculpta (Kittl, 1894)
Figs. 1, 7. Juvenile shell from Misurina, with c. 1 mm high shell, but wider apical angle than the adult teleoconch (RGM 219 011).
Fig. 3. Protoconch from Misurina (detail of figs. 1 and 7), smooth and c. 0.2 mm wide.

Promathilda misurinensis sp. nov.
Fig. 2. Holotype from Misurina, 2.3 mm high (NHM 1994/162).
Fig. 4. Protoconch from Misurina (detail of fig. 2), 0.2 mm wide and with the same axis of coiling as the teleoconch.
Fig. 5. Shell from Campo, 2.2 mm high (RGM 219 013).

Tirolthilda seelandica sp. nov.
Fig. 6. Holotype from Alpe di Specie, 4.3 mm high (NHM 1994/165).
Fig. 8. Protoconch from Misurna, c. 0.3 mm wide (RGM 219 017).
Fig. 9. Juvenile shell from Alpe di Specie, c. 0.9 mm high (RGM 219 016).
Fig. 10. Apical part of shell from Alpe di Specie with 0.25 mm wide protoconch that rests with an angle apex down on the teleoconch (GPIH).

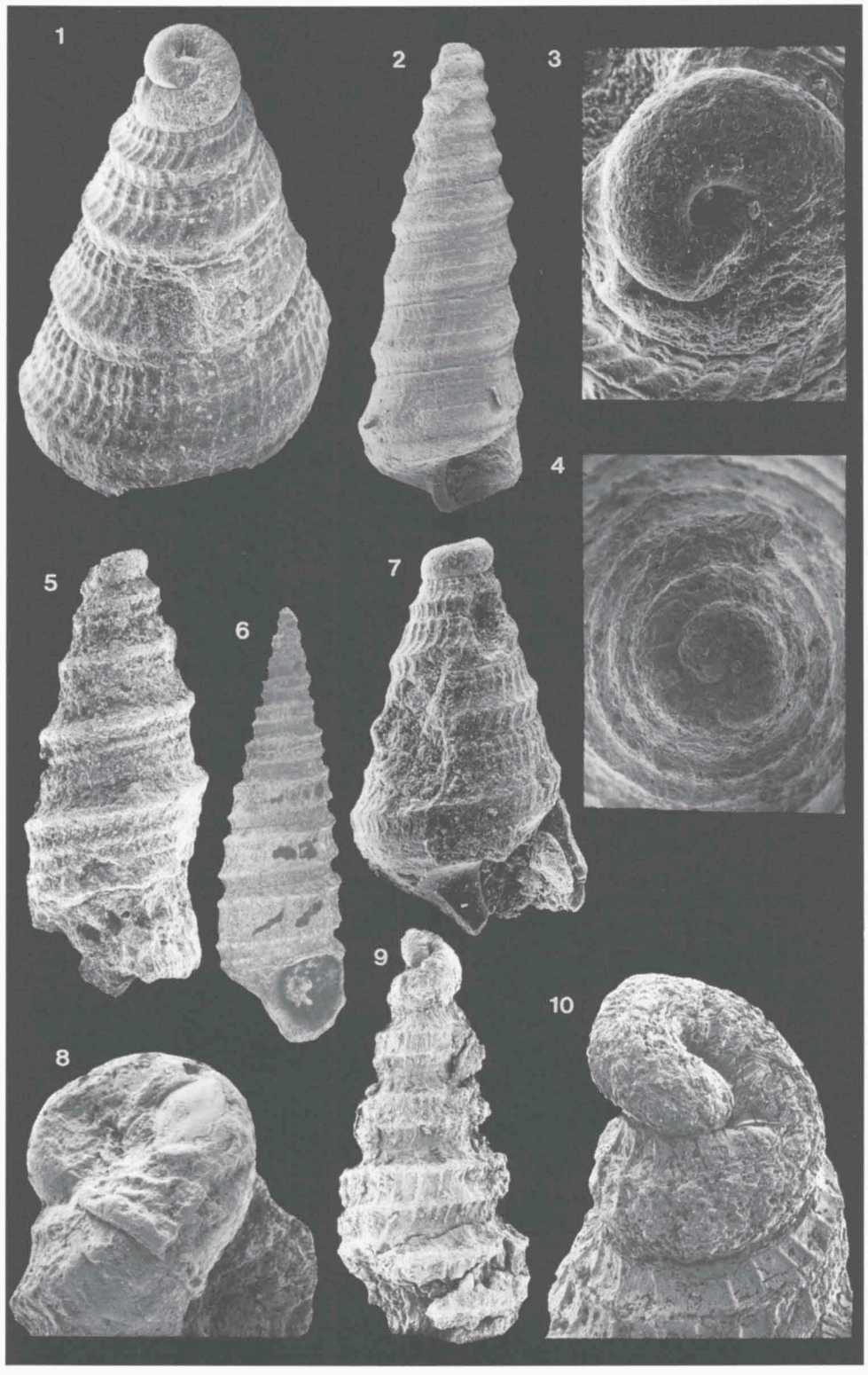

1
2
3
4
5
6
7
8
9
10

Plate 6

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Tirolthilda nuetzeli sp. nov.
Fig. 1. Holotype from Misurina, with 4.3 mm long shell (NHM 1994/166).
Fig. 2. Juvenile shell from Alpe di Specie with flattened apex and 0.75 mm height (RGM 219 018).
Fig. 3. Detail of fig 2 with the sinistral protoconch measuring 0.26 mm across.
Fig. 4. Juvenile shell from Misurina with 1.5 mm long shell (RGM 219 019).
Fig. 5. Apical view of fig. 4 with 1.2 mm wide shell.
Fig. 6. Protoconch from Dibona with a thickened shell margin (detail of Pl. 7, fig. 4).
Fig. 7. Shell from Misurina, 1.8 mm high (RGM 219 019).


1
2
3
4
5
6
7

Plate 7

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Turrithilda cassiana sp. nov.
Fig. 1. Protoconch of from Dibona, 0.2 mm wide (detail of fig. 3).
Fig. 2. Ornament of the teleoconch from Dibona with spiral ribs and fine spiral lirae (detail of fig. 3).
Fig. 3. Holotype from Dibona, with 1.5 mm high shell (NHM 1994/163).
Fig. 4. Shell from Dibona, 2 mm high (RGM 219 014).
Fig. 5. Sinistral protoconch on the apex of the teleoconch that is c. 0.2 mm wide (detail of fig. 3).

Turrithilda dockeryi sp. nov.
Fig. 6. Shell from Misurina, smooth and with c. 0.2 mm wide protoconch (detail of fig. 7).
Fig. 7. Juvenile shell from Misurina with 0.55 mm height (RGM 219 015).
Fig. 8. Holotype with juvenile shell from Alpe di Specie, 1.2 mm high, ornament of teleoconch in last whorl consists of equal spiral and axial ribs (NHM 1994/164).

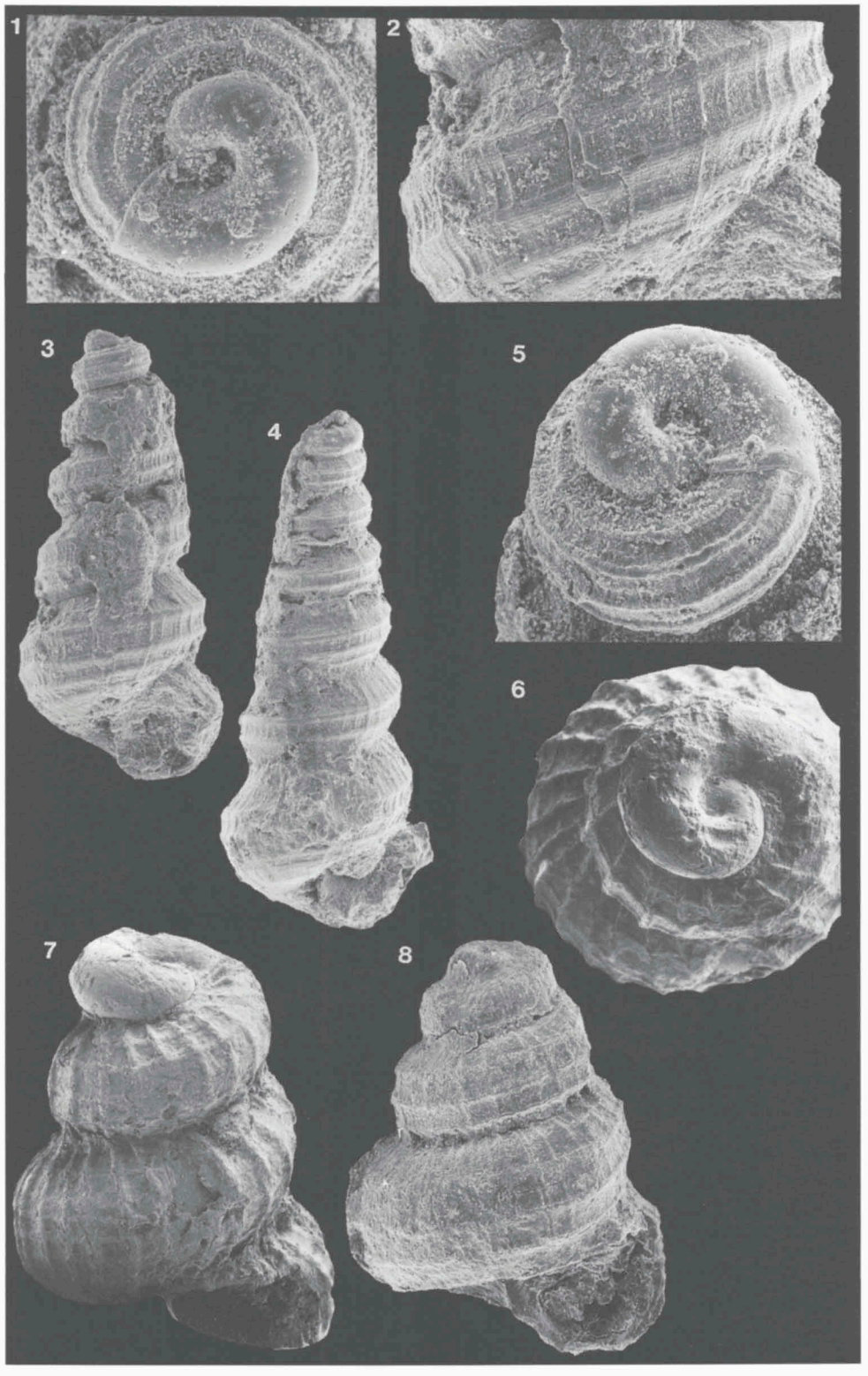

1
2
3
4
5
6
7
8

Plate 8

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Anoptychia supraplecta (von Münster, 1841)
Fig. 1. Apex from Alpe di Specie, with a 0.26 mm wide protoconch (GPIH).
Fig. 2. Protoconch from fig. 1 that forms an angle of more than 45° with the teleoconch.
Fig. 3. Shell from Alpe di Specie shown in fig. 5 demonstrates the axial ornament of the juvenile teleoconch (GPIH).
Fig. 4. Slightly compressed shell from Alpe di Specie with 4.4 mm high shell (details see figs. 1-2, 6) (RGM 219 021).
Fig. 5. Shell from Alpe di Specie, 4.8 mm high (detail see fig. 3).
Fig. 6. Protoconch and ornamented early teleoconch (detail to fig. 4).

Camponella pianozesis (Zardini, 1985)
Fig. 7. Juvenile shell from Campo with 4 mm high shel (RGM 219 024).
Fig. 10. Shell from Campo, 3.8 mm high (RGM 219 024).

Turristylus triadicus (Kittl, 1894)
Fig. 8. Protoconch (detail of fig. 9), 0.2 mm wide.
Fig. 9. Shell, 4.5 mm high, from Misurina (RGM 219 023).

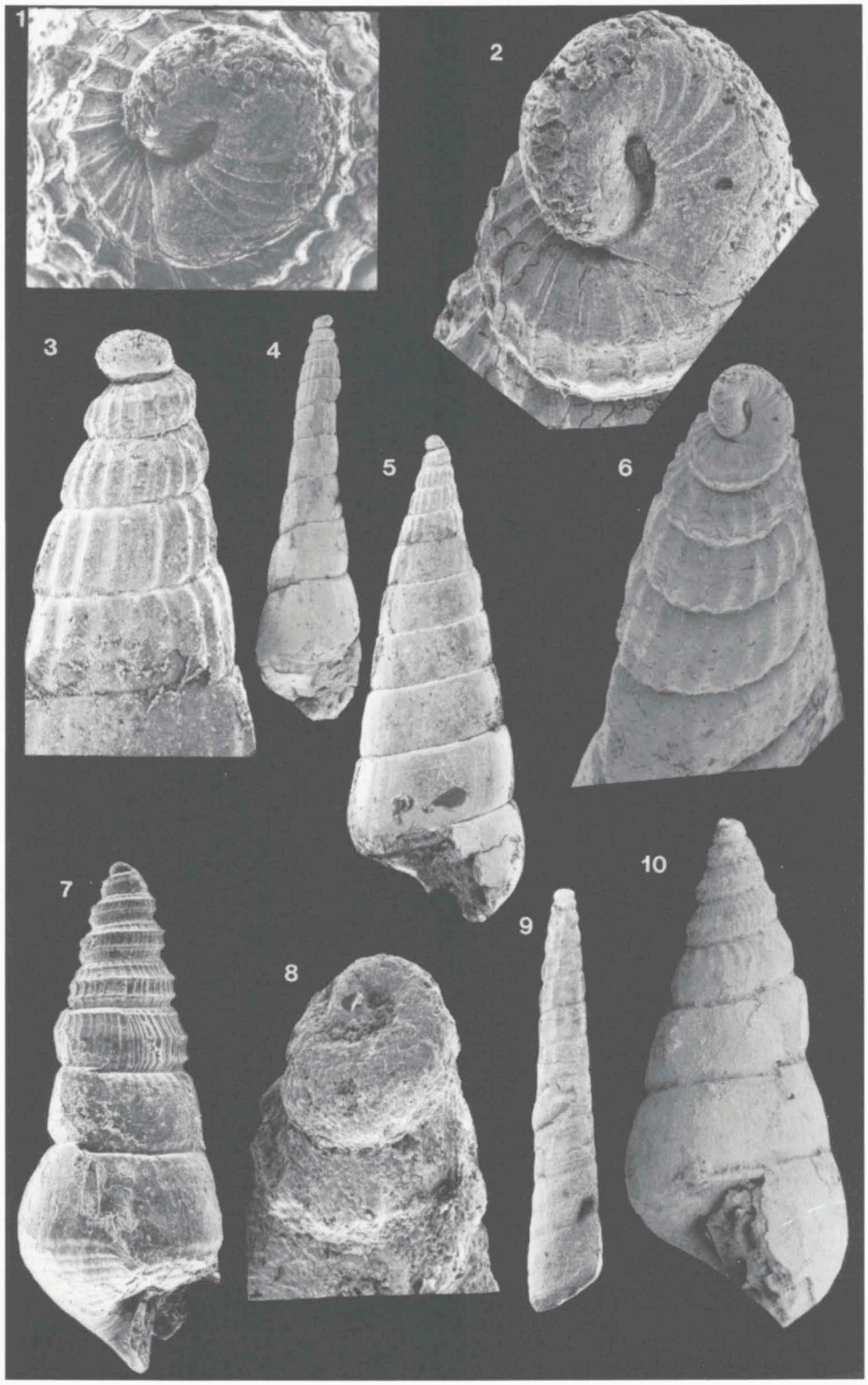

1
2
3
4
5
6
7
8
9
10

Plate 9

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Camponella pianozesis (Zardini, 1985)

Fig. 1. Shell from Campo, apex (detail of Pl. 8, fig. 8) with 0.2 mm wide protoconch (RGM 219 024).

Fig. 2. Juvenile shell from Dibona, 1.8 mm high (GPIH).

Fig. 3. Shell from Campo (detail of Pl. 8, fig. 7), with apex that has a 0.2 mm wide protoconch with axial folds.

Schroederilda milierensis (Zardini, 1978)

Fig. 4. Apical view (same specimen as fig. 5) of a 0.55 mm wide shell.

Fig. 5. Juvenile shell from Alpe di Specie with inclined sinistral protoconch and 0.7 mm height (RGM 219 020).

Fig. 6. Juvenile shell from Campo that is 0.9 mm high (GPIH).

Fig. 8. Same shell as in fig. 5 from Alpe di Specie seen from the back with increased number of ribs on the last whorl.

Tofanella decussata (von Münster, 1841)

Fig. 7. Apex (detail of Pl. 10, fig. 4) from Alpe di Specie and 0.25 mm wide protoconch that ends with a thickened apertural rim (RGM 219 027 Leiden).

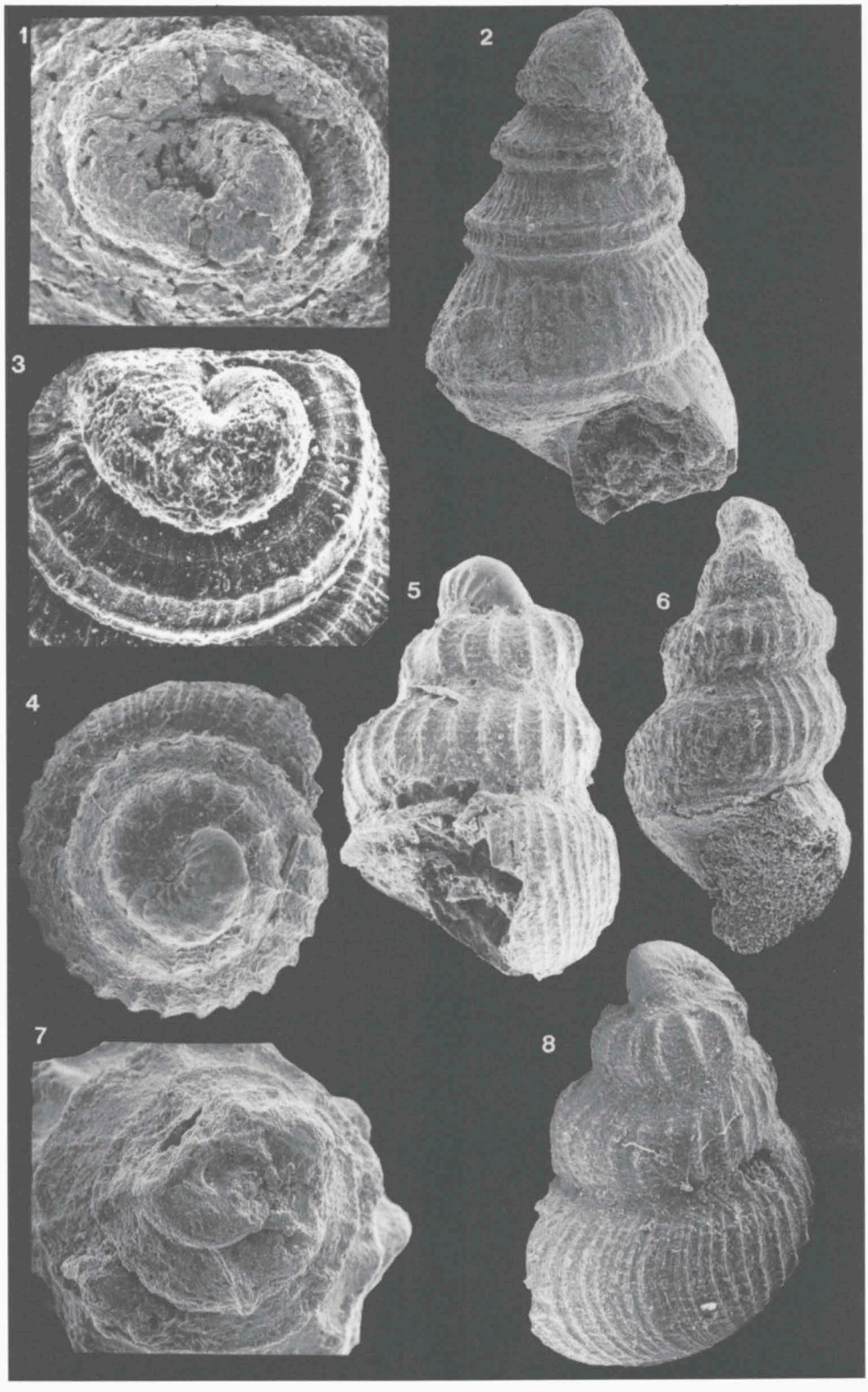

1
2
3
4
5
6
7
8

Plate 10

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Tofanella decussata (von Münster, 1841)
Fig. 1. Shell from Alpe di Specie, 3.5 mm high (RGM 219 027).
Fig. 2. Shell from Alpe di Specie, 4.5 mm high, with last whorls more flattened than juvenile whorls (RGM 219 027).
Fig. 3. Juvenile shell from Alpe di Specie, height c. 1 mm (RGM 219 027).
Fig. 4. Juvenile shell from Alpe di Specie, height 0.9 mm (RGM 219 027).
Fig. 5. Apex of fig. 3, showing 0.5 mm wide protoconch with an apertural projection.
Fig. 6. Margin of the protoconch shown in figs. 3 and 5 that is thickened and drawn out into a projection of the apertural lip.

Cristalloella cassiana sp. nov.
Fig. 7. Shell from Campo, 2.6 mm high (RGM 219 034).
Fig. 8. Shell from Campo, 2 mm high (RGM 219 034).
Fig. 9. Holotype from Alpe di Specie, 2.7 mm high (NHM 1994/168).
Fig. 10. Protoconch (detail of fig. 9), 0.3 mm high and provided with a median projection of the apertural lip.

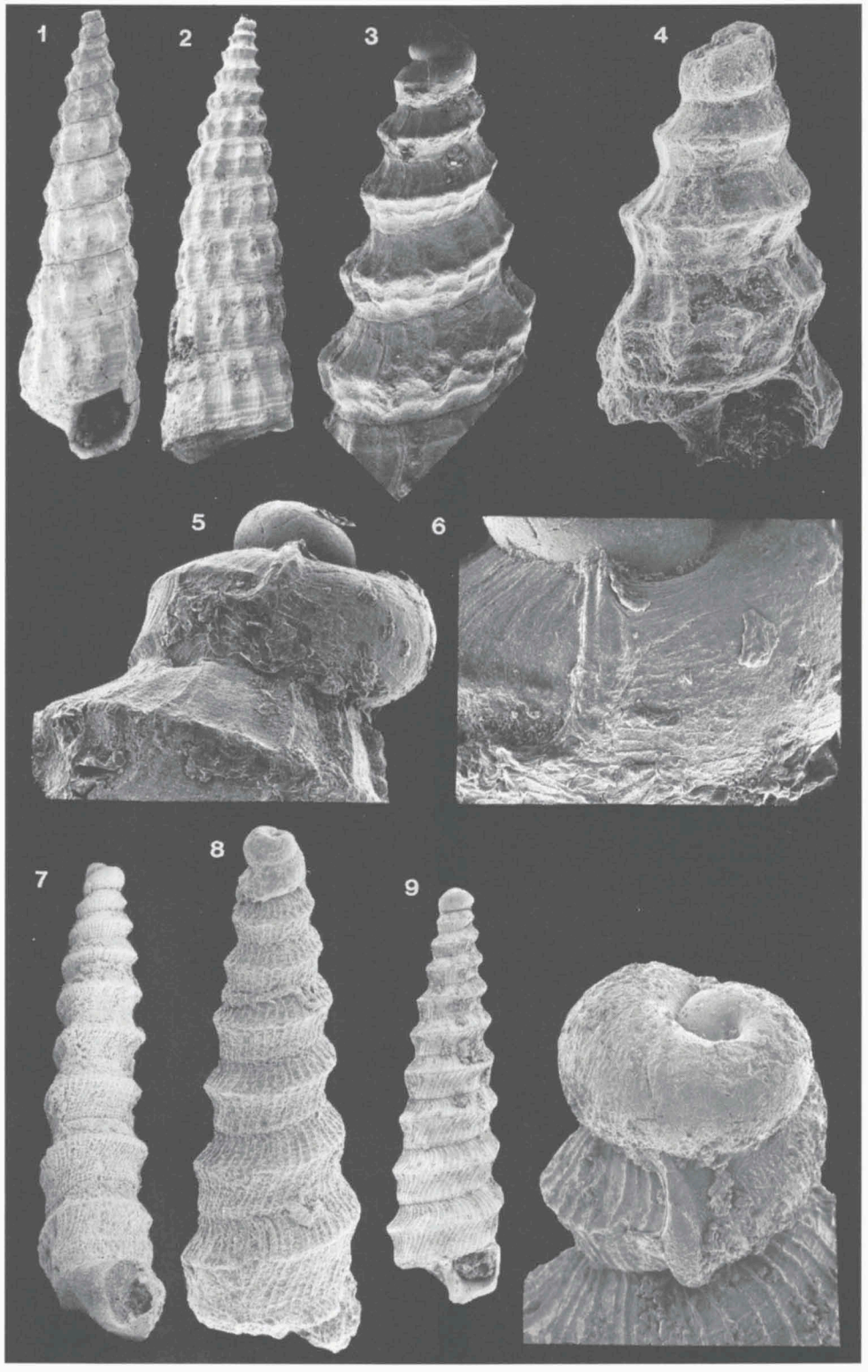

1
2
3
4
5
6
7
8
9

Plate 11

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Cristalloella cassiana sp. nov.
Fig. 1. Shell from Campo (detail of Pl. 10, fig. 7) with the apex showing the ornament of the protoconch that consists of fine wrinkles quite different from that of the teleoconch (RGM 219 034).
Fig. 2. Apex of the shell shown in Pl. 10, fig. 7 with 0.3 mm high protoconch (RGM 219 034.
Fig. 3. Apical view of the protoconch shown in Pl. 10, fig. 8 that is 0.3 mm wide and has a sinistral initial whorl (RGM 219 034).

Tofanella cancellata sp. nov.
Fig. 4. Holotype from Campo, with 3.5 mm high shell (NHM 1994/167).
Fig. 5. Shell from Alpe di Specie, 1.3 mm high (RGM 219 031).
Fig. 6. Juvenile shell from Misurina. 1.1 mm high (RGM 219 030).
Fig. 7. Shell from Campo, 2.4 mm high (RGM 219 032).
Fig. 8. Detail of fig. 4, with apex of 0.2 mm width and fine lirae on the larval whorl.
Fig. 9. Protoconch from Misurina (detail of fig 6), provided with a larval projection and measuring 0.2 mm in diameter.

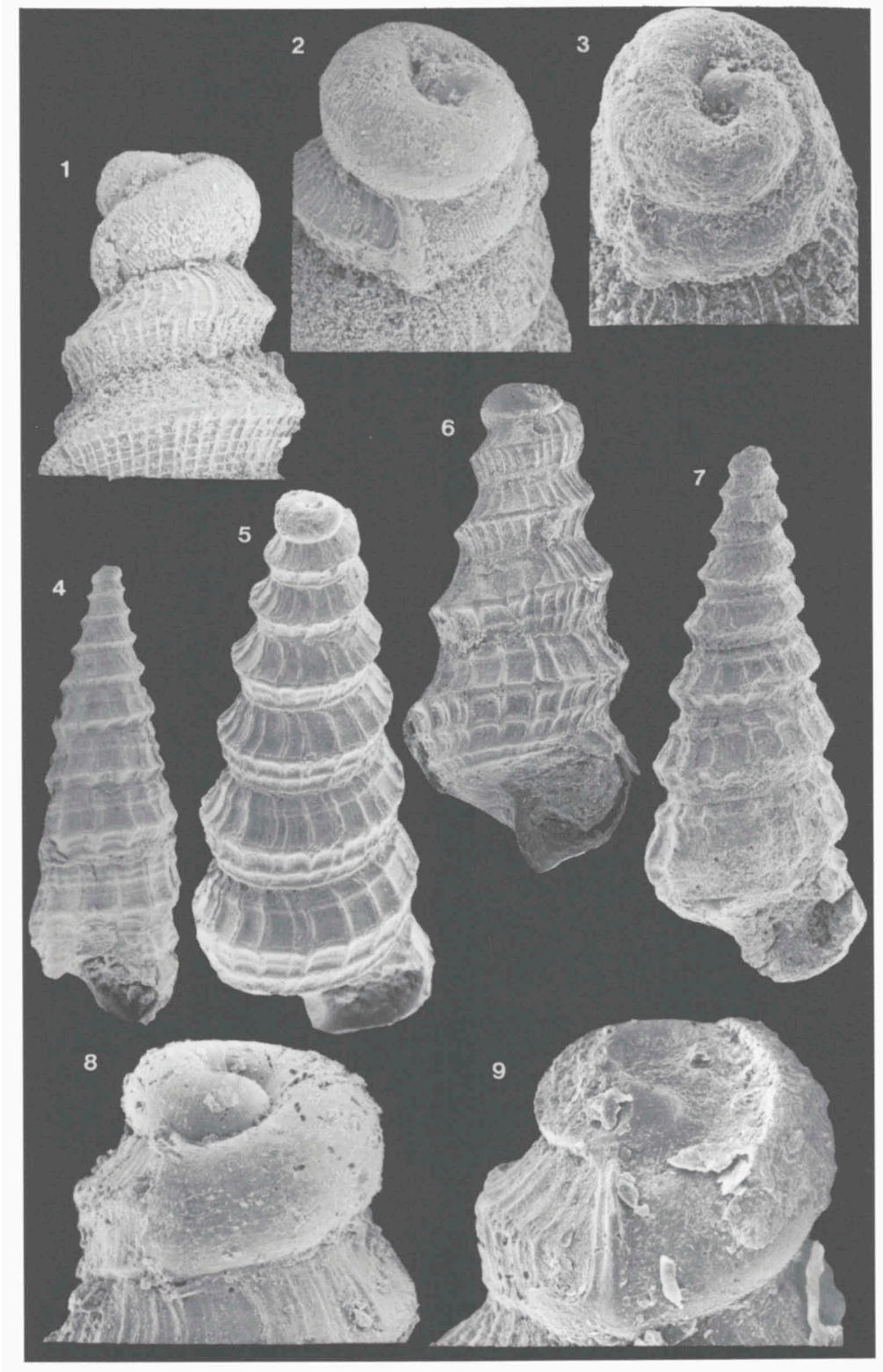

1
2
3
4
5
6
7
8
9

Plate 12

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Tofanella cancellata sp. nov.
Fig. 1. Shell from Alpe di Specie (detail of Pl. 11, fig. 5) with protoconch of 0.2 mm width that ends with an apertural rim (RGM 219 031).

Cristalloella sinuata sp. nov.
Fig. 2. Apex from Misurina (detail of Pl. 13, fig. 1) with a smooth protoconch that measures 0.21 mm in diameter.
Fig. 3. Juvenile shell from Misurina that is 0.65 mm high (GPIH).
Fig. 4. Holotype (juvenile) from Misurina, with a 0.6 mm high shell (NHM 1994/169).
Fig. 5. Juvenile shell from Misurina with 0.8 mm height (GPIH).
Fig. 6. Apex (detail of Pl. 13, fig. 1) from Misurina with smooth protoconch, 0.21 mm in diameter.
Fig. 7. Protoconch from Alpe di Specie (detail of fig. 4) with sinistral initial whorl measuring c. 0.2 mm across.
Fig. 8. Detail of Pl. 13, fig. 1, with the protoconch ending in a smooth simple apertural lip.

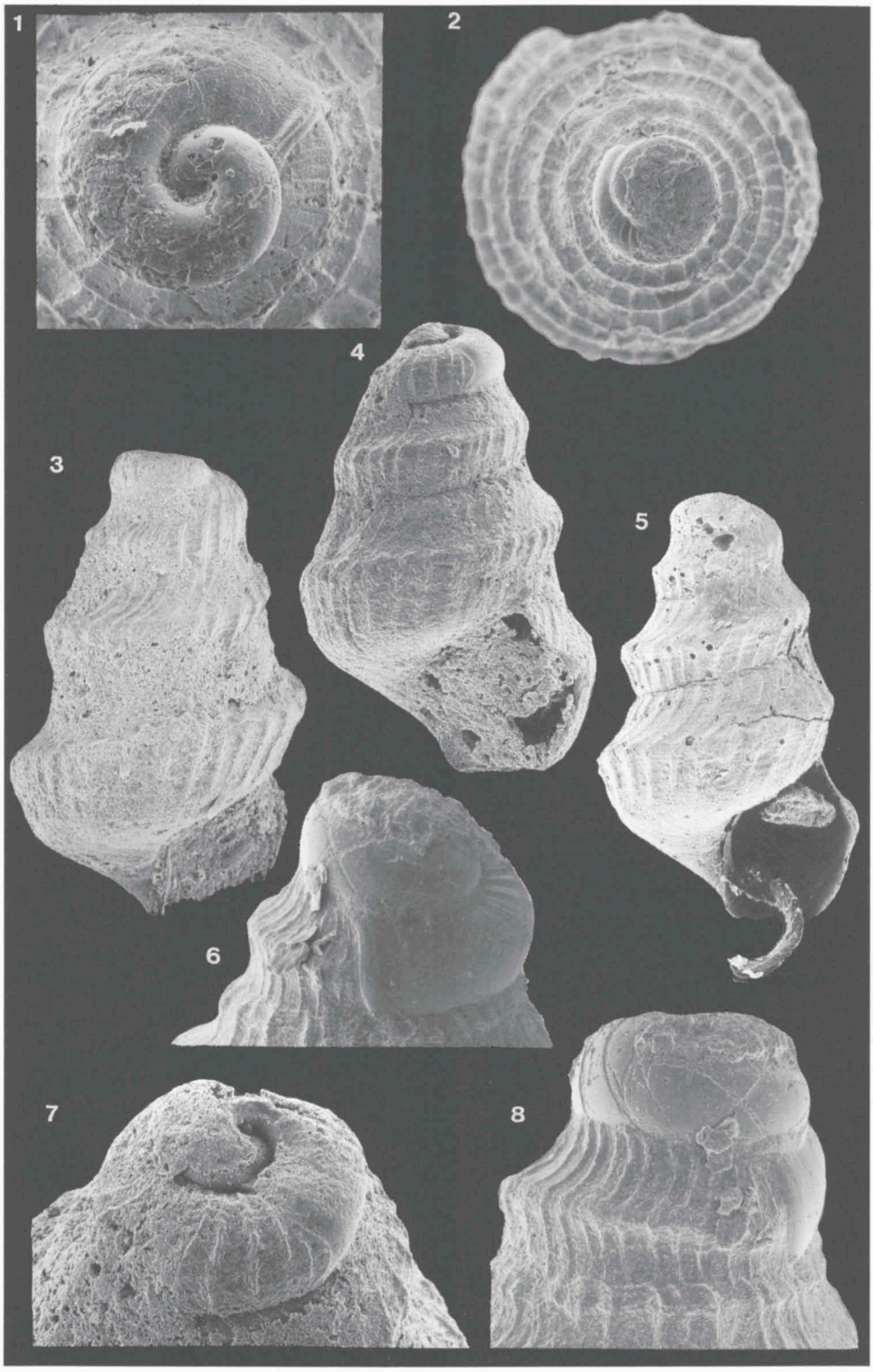

1
2
3
4
5
6
7
8

Plate 13

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Cristalloella sinuata sp. nov.
Fig. 1. Shell from Misurina, 1.4 mm high (GPIH).

Cristalloella delicata sp. nov.
Fig. 2. Shell from Alpe di Specie, 0.9 mm high (GPIH).
Fig. 3. Shell from Alpe di Specie, 1 mm high (GPIH).
Fig. 4. Shell from Alpe di Specie, 0.6 mm high (GPIH).
Fig. 5. Shell from Alpe di Specie (detail of fig. 2) with simple, almost smooth protoconch of 0.23 mm width.
Fig. 6. Holotype from Alpe di Specie, with 0.9 mm high shell (NHM 1994/170).
Fig. 7. Shell from Alpe di Specie (detail of fig. 4) with simple almost smooth protoconch of 0.23 mm width and sinistral initial whorl.
Fig. 8. Apical view (detail of fig. 2) of protoconch with sinistral embryonic shell and some axial folds in the larval shell.

Camponaxis lateplicata (Klipstein, 1843)
Fig. 9. Apical view of shell from Misurina (detail of Pl. 14, fig. 4), 0.7 mm wide, smooth protoconch.

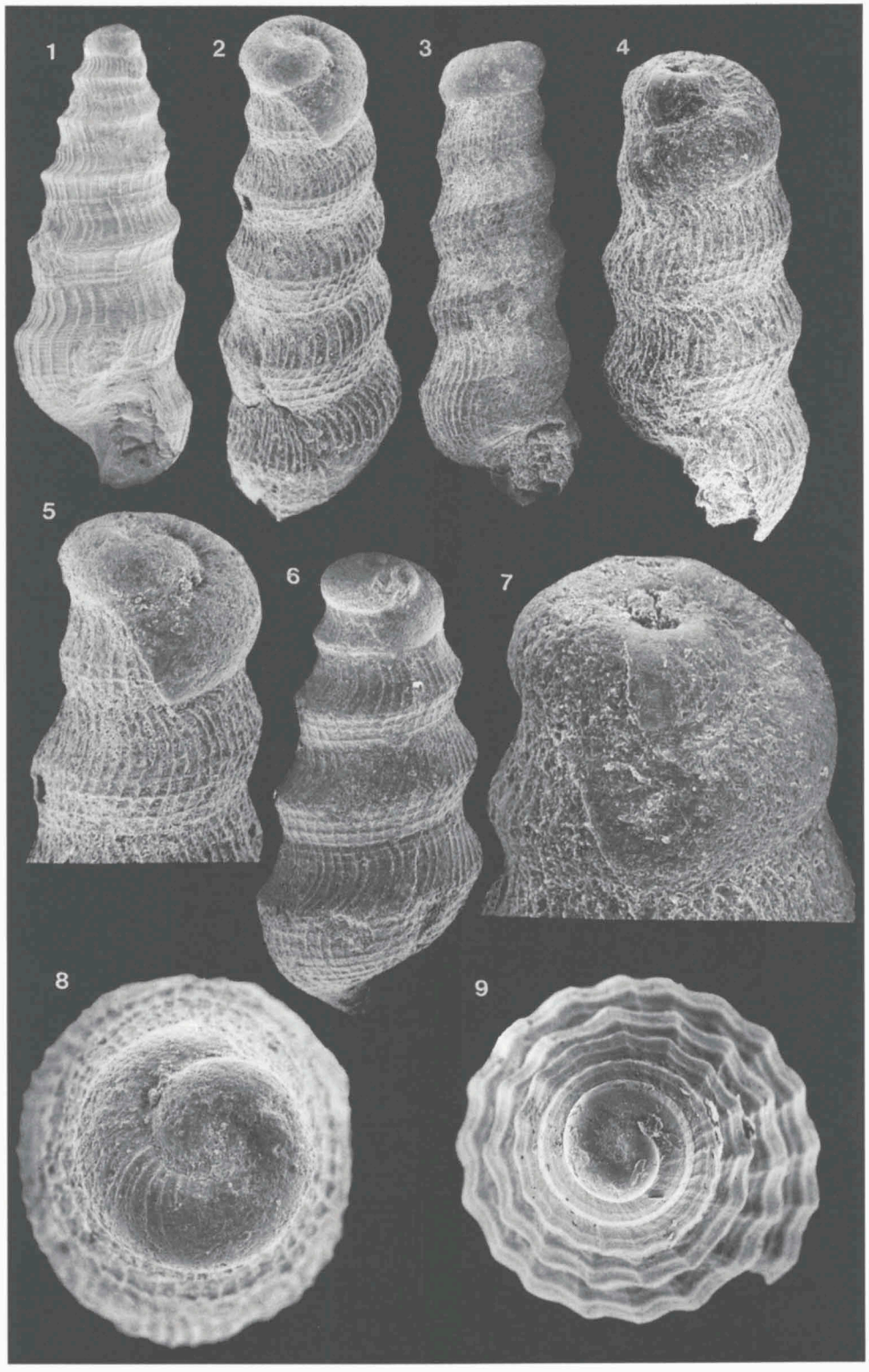

1
2
3
4
5
6
7
8
9

Plate 14

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Camponaxis lateplicata (Klipstein, 1843)
Figs. 1-2. Apical part of the shell (detail of fig. 4), with 0.2 mm wide protoconch forming a sinistral and slightly deviating point of the teleoconch.
Fig. 3. Frontal view of juvenile shell from Misurina, 1.4 mm high (GPIH).
Fig. 4. Same shell as in fig. 3 seen from the back (details in Pl. 13, fig. 9 and Pl. 14, fig. 1-2) (GPIH).
Fig. 5. Shell from Dibona with 2.5 mm height (RGM 219 039).

Camponaxis subcompressa (Kittl, 1894)
Fig. 6. Juvenile shell of 0.55 mm height from Misurina (RGM 219 041).
Fig. 7. Protoconch (detail of fig. 6), 0.18 mm wide.
Fig. 8. Apical view (detail of fig. 6), 0.18 mm wide protoconch.

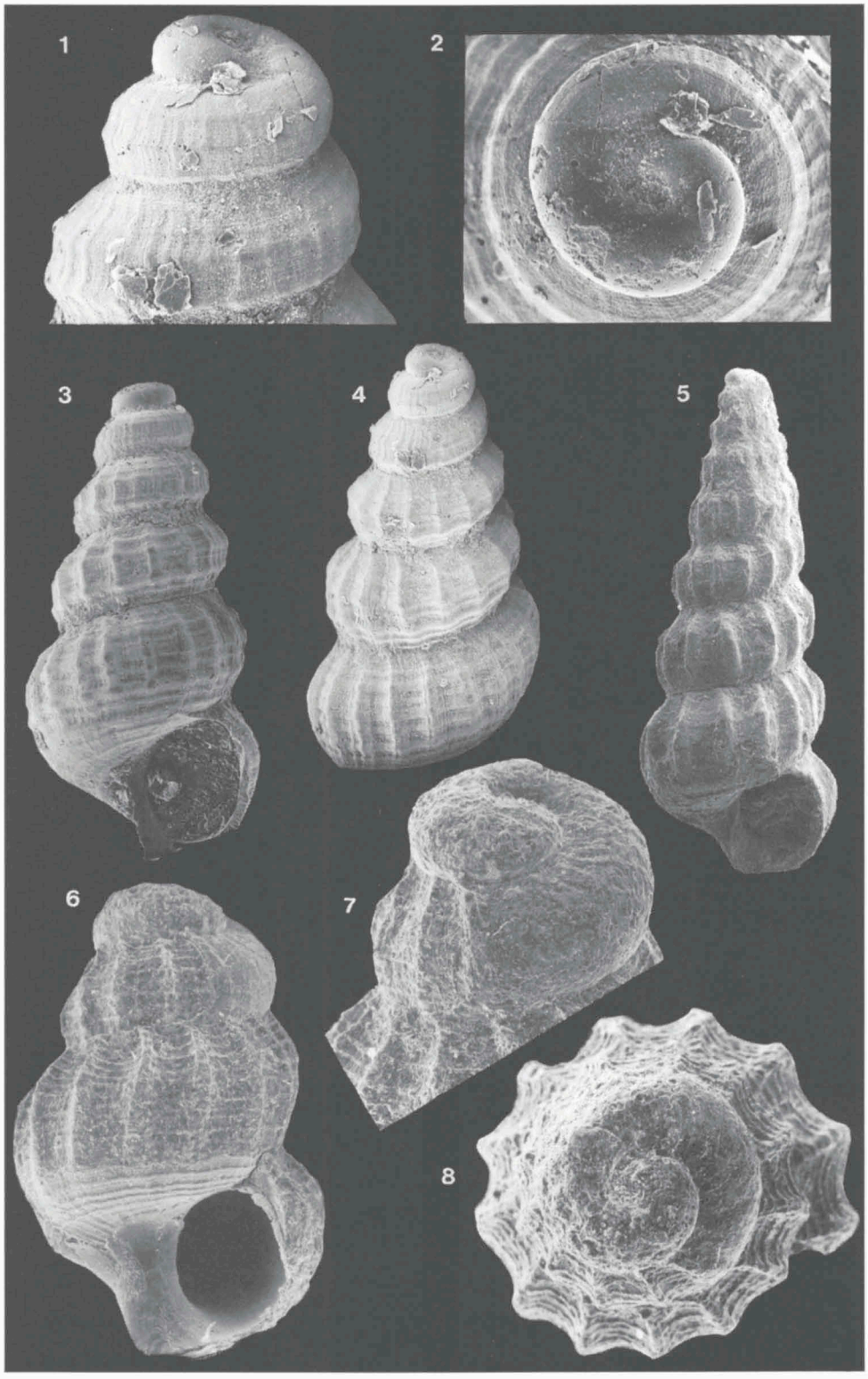

1
2
3
4
5
6
7
8

Plate 15

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Camponaxis subcompressa (Kittl, 1894)
Fig. 1. Shell from Dibona, 4.4 mm high (RGM 219 042).

Camponaxis beneckei (Kittl, 1894)
Fig. 2. Shell from Misurina, 0.8 mm high (GPIH).
Fig. 3. Apical view (detail of fig. 2) with 0.25 mm wide protoconch.
Fig. 4. Shell from Alpe die Specie, 1.1 mm high (RGM 219 044).
Fig. 5. Shell from Campo, 0.56 mm high (RGM 219 043).
Fig. 6. Shell from Campo, 0.7 mm high (GPIH).
Fig. 7. Apical view (detail of fig. 5) of the 0.25 mm wide and smooth protoconch (RGM 219 043).

Trachoecus gemmellaroi Kittl, 1894
Fig. 8. Juvenile shell from Misurina, 1.5 mm high (RGM 219 045).

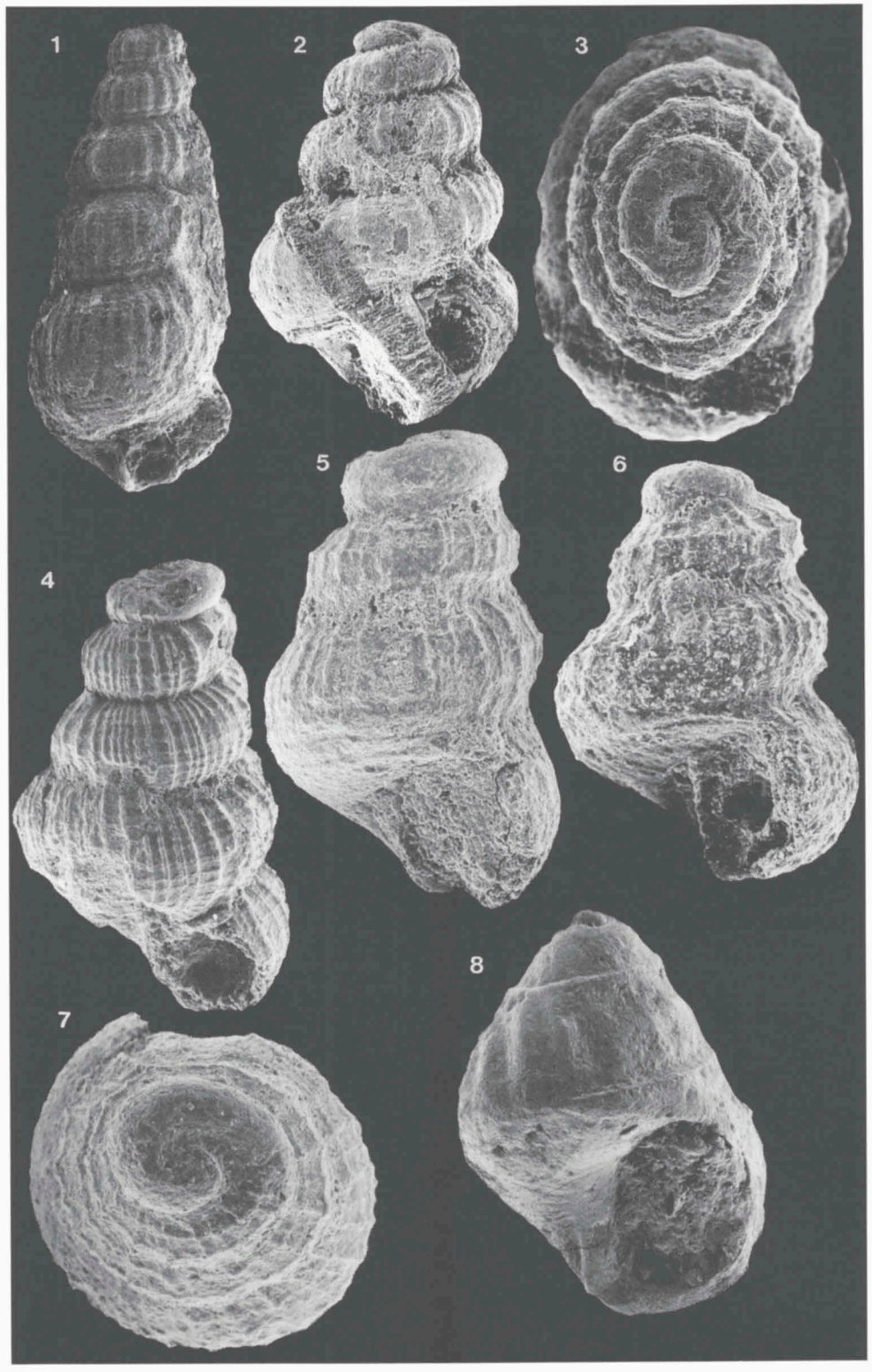

1
2
3
5
6
4
8
7

Plate 16.

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Trachoecus gemmellaroi Kittl, 1894
Fig. 1. Apical view of shell from Misurina (detail of Pl. 15, fig. 8), sinistral initial whorl in a 0.25 mm large protoconch that ends with a thickened apertural rim (RGM 219 045).
Fig. 3. Apical view of the shell in fig. 4.
Fig. 4. Juvenile shell from Misurina, 3.3 mm high (RGM 219 045).

Vallandroella seelandica (Kittl, 1894)
Fig. 2. Initial whorl of protoconch from Alpe di Specie (detail of Pl. 17, fig. 6), with 0.13 mm wide first whorl (RGM 219 049).
Fig. 6. Apical view of shell from Alpe di Specie (detail of Pl. 17, fig. 2), 0.75 mm wide (RGM 219 049).
Fig. 9. Fragment c. 5 mm long from Alpe di Specie with an intact aperture (RGM 219 049).

Vallandroella antorni (Zardini, 1985)
Fig. 5. Juvenile shell from Alpe di Specie, 1.2 mm high (RGM 219 048).
Fig. 7. Apical view of the shell in fig. 5 that shows the 0.28 mm wide protoconch ending with a long larval hook.
Fig. 8. Apical view of shell from Alpe di Specie that shows a smooth protoconch and height of 1 mm (GPIH).

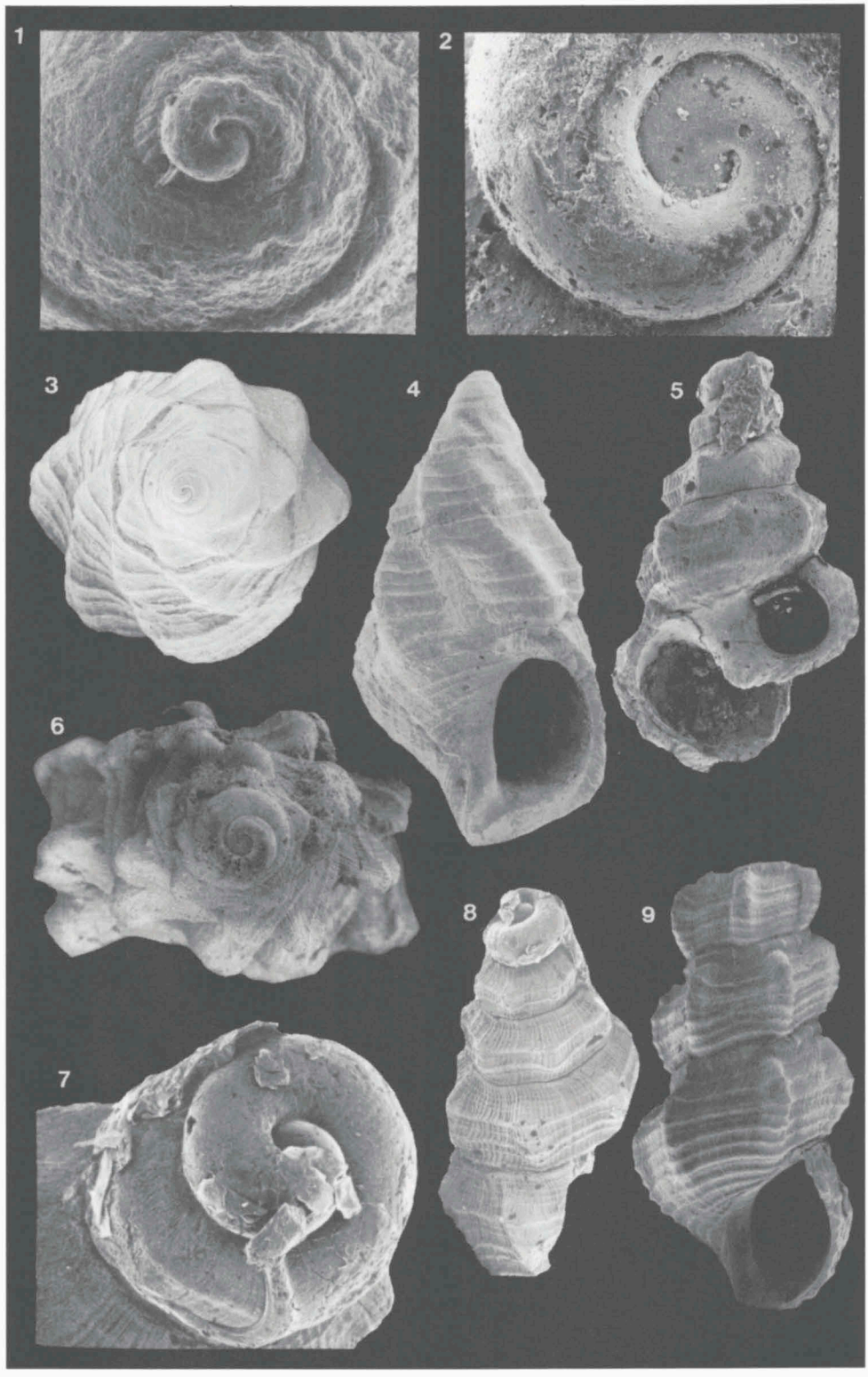

1
2
3
4
5
6
7
8
9

Plate 17.

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aon* Zone (figs. 7-8, 10), *Trachyceras aonoides* Zone (other figures) (Late Triassic, Early Carnian).

Vallandroella seelandica (Kittl, 1894)

Fig. 1. Shell from Misurina, 5.5 mm high (RGM 219 050).
Fig. 2. Shell from Alpe di Specie, 8.5 mm high (RGM 219 049).
Figs. 4-5. Apex (detail of fig. 2) that shows the 0.5 mm wide protoconch with sinistral initial whorl.
Fig. 6. Apical view of shell from Alpe di Specie, 1.6 mm wide (RGM 219 049).

Ampezzanilda aialensis (Zardini, 1985)
Fig. 3. Shell from Campo, 6 mm high (RGM 219 051).
Fig. 7. Shell from Pralongia (St Cassiano), 2.1 mm high (RGM 219 053).
Fig. 8. Juvenile shell from Pralongia, 0.9 mm high (RGM 219 053).
Fig. 10. Apical view of shell from Pralongia (detail of fig. 8) that shows an ornamented and 0.35 mm wide protoconch.

Vallandroella antorni (Zardini, 1985)
Fig. 9. Apical view of shell from Alpe di Specie, shown in Pl. 16, fig. 5, 0.6 mm wide (RGM 219 048).

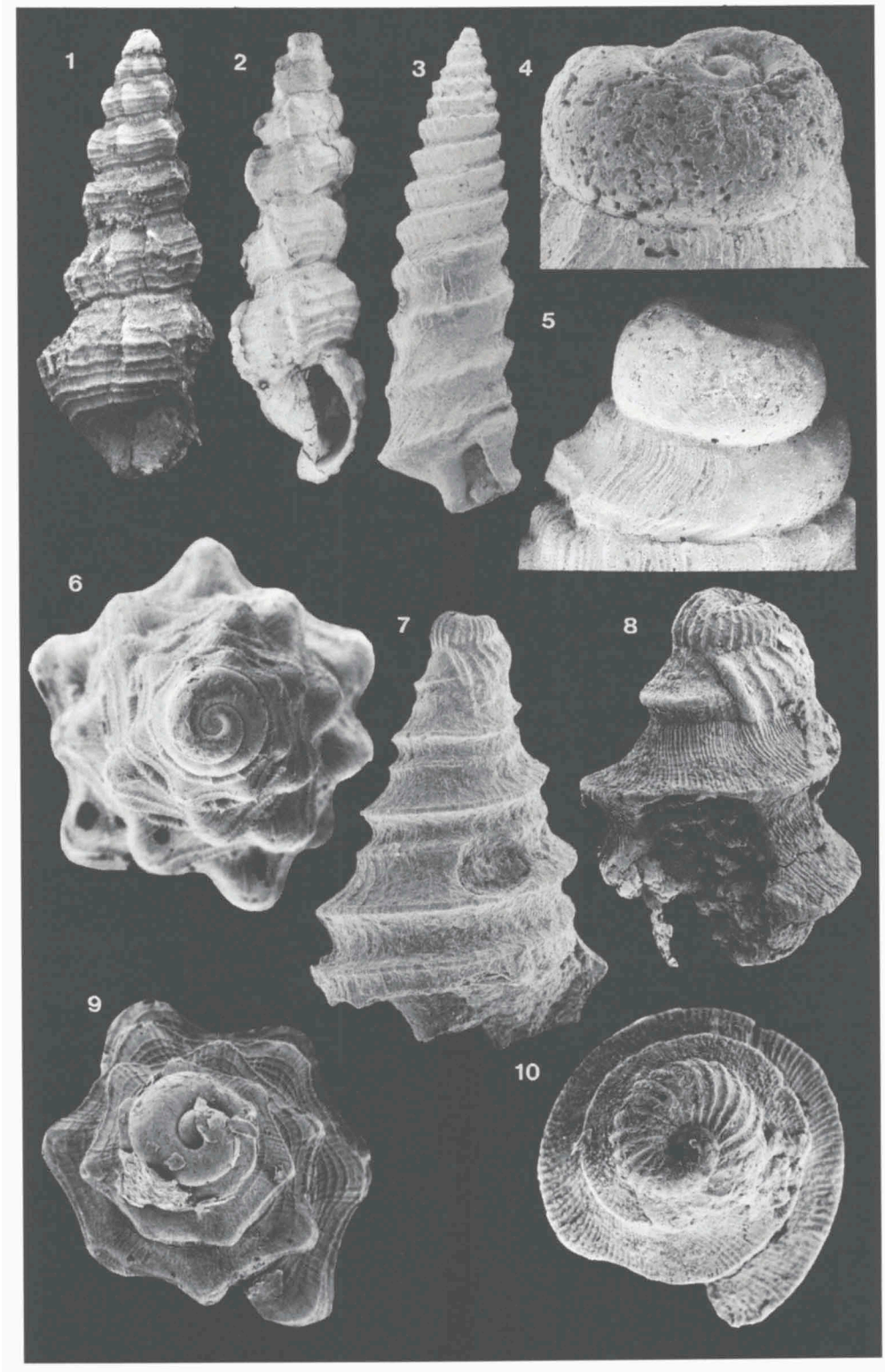

1
2
3
4
5
6
7
8
9
10

Plate 18

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aon* Zone (figs. 1, 3, 5-7), *Trachyceras aonoides* Zone (other figures) (Late Triassic, Early Carnian).

Cassianilda margaritifera (von Münster, 1841)
Fig. 1. Juvenile shell from Pralongia (St Cassiano), 0.75 mm high (RGM 219 054).
Fig. 3. Protoconch from Pralongia, axial ornament with fine spiral lirae, with a thickened margin, and measures 0.25 mm in width (GPIH).
Fig. 6. Shell from Pralongia, with sinistral initial whorl and a 0.25 mm wide protoconch, same axis of coiling as the teleoconch (RGM 219 054).
Fig. 7. Apex of the same shell as in fig. 1, the ornamented protoconch bordering against the teleoconch with a thickened apertural rim.

Ampezzanilda aialensis (Zardini, 1985)
Figs. 2, 4. Protoconch from Alpe di Specie, 0.6 mm high. The beginning of the teleoconch is present (RGM 219 052).
Fig. 5. Protoconch from Pralongia (detail of Pl. 17, fig. 7), 0.4 mm high and ending with an apertural thickened rim (RGM 219 053).

Stuorilda cassiana sp. nov.
Fig. 8. Holotype from Stuores, 2.6 mm high (NHM 1994/171).

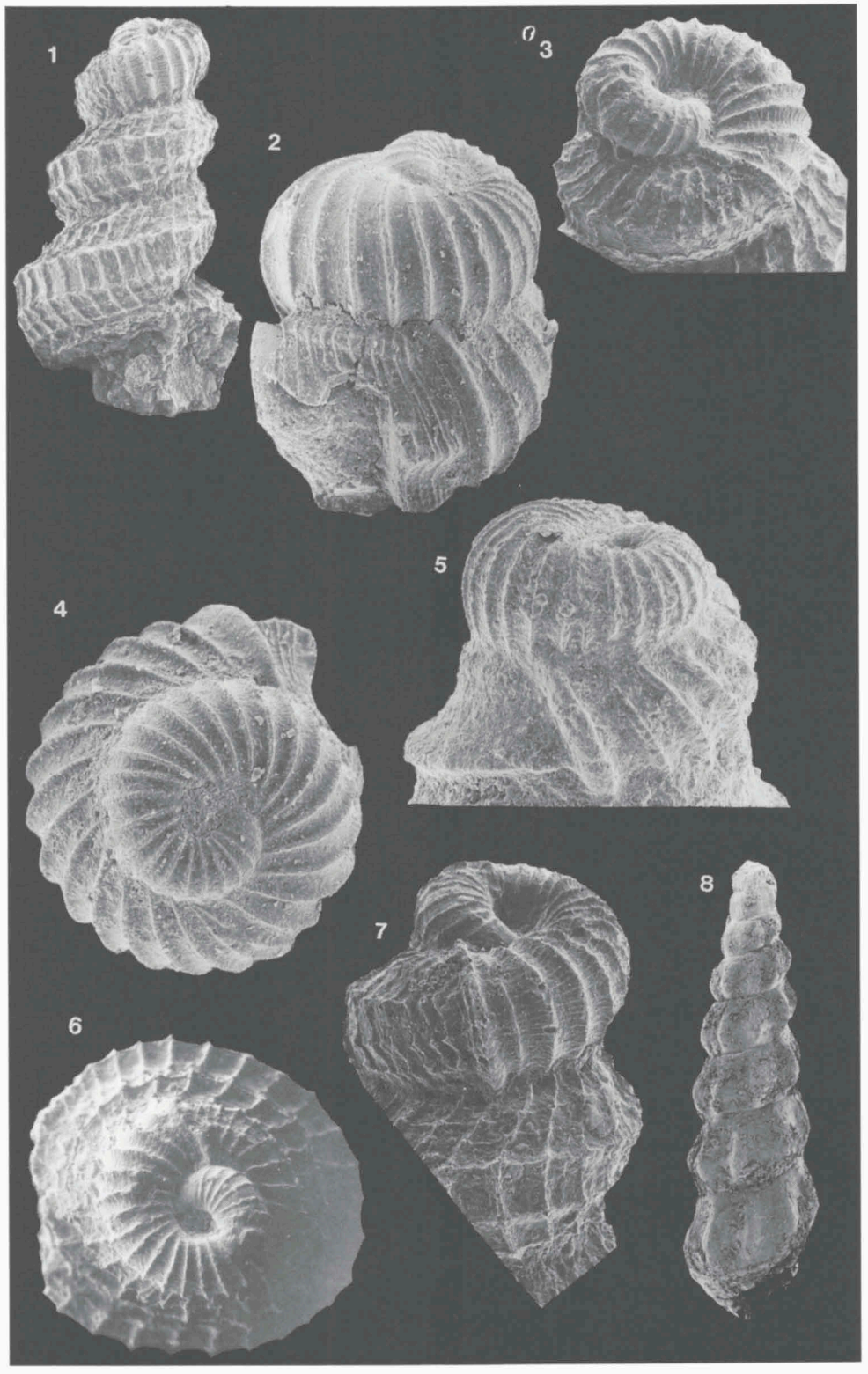
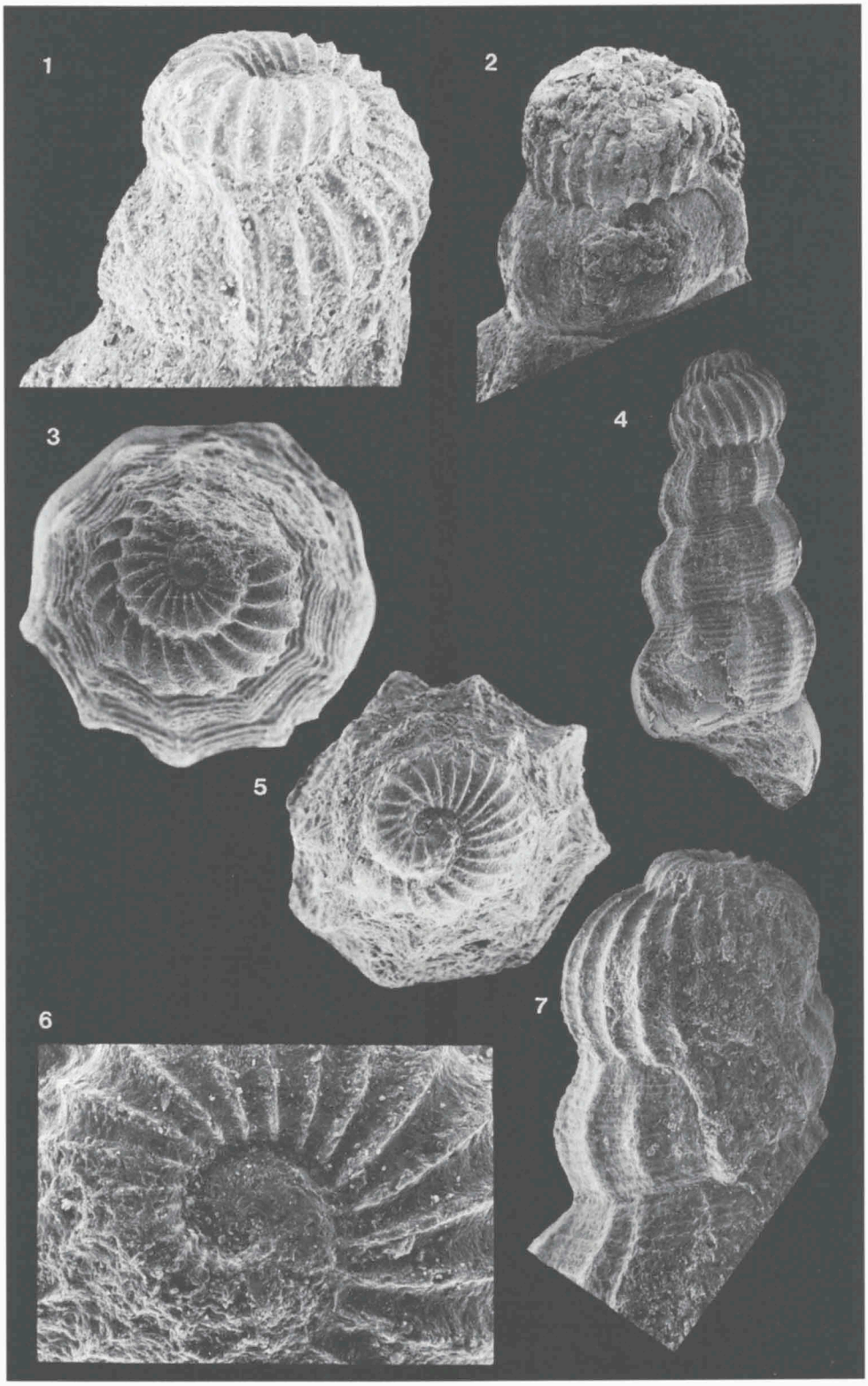

1
2
3
4
5
6
7
8

Plate 19

All specimens from the Cordevol Member, St Cassian Formation, *Trachyceras aonoides* Zone (Late Triassic, Early Carnian).

Stuorilda cassiana sp. nov.
Fig. 1. Shell from Campo showing apical shell portion, with 0.26 mm wide protoconch (GPIH).
Fig. 2. Holotype (detail of Pl. 18, fig. 8) from Stuores, apex with ornamented protoconch that ends in a thickened apertural rim at the onset of the teleoconch (NHM 1994/171).
Fig. 5. Apical view of shell from Campo, with 0.26 mm wide protoconch (RGM 219 056).

Stuorilda tichyi sp. nov.
Fig. 3-4. Holotype, apical view, from Misurina (detail of fig. 4), with 0.33 mm wide protoconch (NHM 1994/172).
Fig. 6. Holotype, from Misurina, showing a sinistral, smooth embryonic shell while the larval shell is ornamented by axial ribs (detail of fig. 3).
Fig. 7. Protoconch of holotype, from Misurina, showing barrel-shape, 0.33 mm high (detail of fig. 4).


1
2
3
4
5
6
7