Journal of Foraminiferal Research, v. 43, no. 4, p. 317–339, October 2013

TAXONOMY AND PHYLOGENY OF THE TROCHOLINIDAE (INVOLUTININA)

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ABSTRACT

Exceptionally well-preserved trochospirally coiled Involutinina have been found in Late Triassic (Wallowa Mountains, Oregon, U.S.A.) and Early Jurassic (northern Calcareous Alps, Austria) carbonate rocks. Their remarkable preservation, related to impregnation of the test prior to recrystallization, allowed us to observe features usually obliterated by diagenetic and metamorphic processes. This paper provides a revision of the morphology, structure, systematic position, phylogeny, and stratigraphic range of the family Trocholinidae Kristan-Tollmann. New criteria permitting the distinction between trocholinid genera, even in cases of intense recrystallization, are presented. An identification key and a new, monophyletic tree are proposed for the whole family. The main outcomes of this work are that 1) *Neotrocholina* Reichel is definitively excluded from the Involutinina; 2) the genera *Andersenolina* Neagu, *Hottingerella* Piller, and *Septatrocholina* BouDagher-Fadel and Banner are placed in synonymy with *Coscinoconus* Leupold; 3) the genus *Ornatoconus* di Bari is considered a synonym of *Trocholina* Schlumberger; 4) the distinction between the genera *Auloconus* Piller and *Lamelliconus* Piller is abandoned; 5) five new genera (*Coronaserra* n. gen., *Frentzenella* n. gen., *Kristantollmanna* n. gen., *Papillaconus* n. gen., and *Wallowaconus* n. gen.) and three new species (*Frentzenella frentzeni* n. gen., n. sp., *Frentzenella perforata* n. gen., n. sp., and *Wallowaconus oregonensis* n. gen., n. sp.) are introduced; 6) the species "*Trocholina intermedia*" Henson is reinstituted; 7) "*Trocholina gigantea*" Pelissié and Peybernès, and "*Semiinvoluta verrucosa*" Tollmann and Kristan-Tollmann are renamed *Coscinoconus limognensis* nom. nov. and *Papillaconus kristani* nom. nov., respectively; and 8) new combinations for several species of Trocholinidae are provided.

The recognition of two subfamilies (Lamelliconinae and Trocholininae) and twelve genera within the Trocholinidae underlines the high diversity of the family. The rapid diversification and widespread distribution characterizing the group suggest that the potential of trochospirally coiled Involutinina in stratigraphic and paleoenvironmental studies is greatly undervalued.

INTRODUCTION

Representatives of the Suborder Involutinina Hohenegger and Piller are an important constituent of Mesozoic rocks. Globally distributed, they showed a rapid diversification during the Late Triassic and Early Jurassic. First suggested by Reichel (1955), the aragonitic composition of the involutinins has been recognized later by Hohenegger and Piller (1975) and Zaninetti and Brönnimann (1977). While some authors have included calcitic taxa within the group (Hohenegger and Piller, 1977; Piller, 1983), it is generally accepted that the suborder only comprises aragonitic forms (Zaninetti and Brönnimann, 1977; Loeblich and Tappan, 1981). The early, intense recrystallization usually affecting their aragonitic test commonly obstructs primary structures, hampering their specific and generic identification and use for paleoecologic and stratigraphic purposes. Their classification remains superficial. Taxonomic works rarely integrate their whole complexity, and they are commonly confused with their coeval calcitic homeomorphs.

Under exceptional diagenetic settings, the aragonite may be partially preserved. Based on very few but well-preserved specimens, Piller (1978) and di Bari and Laghi (1994) proposed two major models for the Involutinina structure. In the first one ("*Triadodiscus* model"), the lateral laminar extensions of the tube wall (L2 lamellae sensu Piller, 1978), are added to every whorl, following the tubular chamber formation. In the second ("*Aulotortus* model"), the lateral laminar extensions also appear subsequent to the tubular chamber formation, but are added every half whorl and only partially cover the test surface. From these authors' observations, high-rank taxonomy in the Involutinina is based on fine details of the lamellae arrangement. The latter, however, are generally erased by diagenetic and metamorphic processes so that the systematic position of involutinins is a matter of conjecture.

The latest Involutinina taxonomic subdivision (Zaninetti, 1984; Zaninetti and others, 1987; Loeblich and Tappan, 1987) classified trochospiral forms into three different lineages (i.e., families Aulotortidae, Involutinidae, and Triadodiscidae sensu Zaninetti and others, 1987), together with planispiral forms. Based on a thorough morphological study of trochospirally coiled Involutinina, this paper aims to demonstrate that they all derive from a single trochospiral ancestor and, thus, should be included in a single group.

CURRENT KNOWLEDGE ON TROCHOSPIRALLY COILED INVOLUTININA

The earliest trochospirally coiled Involutinina, grouped into the subfamily Lamelliconinae, have been first recorded in an Early Triassic (late Olenekian–Anisian) non-carbonate borehole succession of Western Australia (Apthorpe, 2003). These forms showed a rapid radiation during the Middle Triassic (Ladinian–Carnian; Oberhauser, 1957; di Bari and Laghi, 1994; Rettori and others, 1998). Characterized by straight, outwardly continuous lamellae, the lamelliconins show high variability in size and shape, and have been classified within the Triadodiscidae ("*Triadodiscus* model").

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The first trochospirally coiled taxa possessing small papillae (sensu Piller, 1983) are known from the late Ladinian–Carnian as "*Trocholina*" *cordevolica* Oberhauser and "*Ornatoconus*" *francorussoi* di Bari (Oberhauser, 1964; di Bari, 1998). The lamellae arrangement of these species has never been observed and their systematic position is still indefinite. Most authors have considered them to be Lamelliconinae, notably because the tubular chamber is close to the spiral surface (a feature considered more characteristic of *Lamelliconus* than "*Trocholina*" in the Triassic). However, the presence of small papillae in the umbilical region indicates a lamellae arrangement closer to that of the Trocholininae.

Forms presenting clear, protuberant papillae are only encountered from the Late Triassic (Norian–Rhaetian) with the genera *Trocholina* and *Semiinvoluta*, when a significant diversification of trochospirally coiled Involutinina occurred. New, non-papillose forms also appeared at that time with representatives of the genera *Auloconus* and *Coronipora*. According to Piller (1978), *Auloconus* and *Trocholina* would show different lamellae arrangements, with the former, classified in the Aulotortidae, adding lamellae every half whorl ("*Aulotortus* model": Piller, 1978; di Bari and Laghi, 1994) and the latter, classified in the Involutinidae, adding lamellae every whorl ("*Triadodiscus* model": di Bari and Laghi, 1994). Although their mode of test construction was unknown, the genera *Coronipora* and *Semiinvoluta* were placed into the Involutinidae (Zaninetti, 1984; Loeblich and Tappan, 1987). Later, Blau and Grün (1997) from Early Jurassic material of Adnet, Austria, however, documented interfingered lamellae in the umbilical region of *Coronipora*, a feature characteristic of the "*Aulotortus* model." The lamellae arrangement in *Semiinvoluta* remains undefined.

During the Early Jurassic, another rapid diversification of trochospirally coiled Involutinina occurred, together with a Spirillinina radiation. Much morphologic confusion exists between the aragonitic Involutinina and their calcitic, monocrystalline homeomorphs, the Spirillinina. Blau and Wernli (1999) clearly demonstrated the differences between the two groups. According to the apparently high level of recrystallization of their walls, the Early and Middle Jurassic genera *Babelispirillina* Ruggieri and Giunta, *Cylindrotrocholina* Loeblich and Tappan, *Licispirella* Blau and Grün, and *Piriniella* Blau might be originally aragonitic. However, the lamellae arrangement of these genera is either unknown (in *Babelispirillina*, *Cylindrotrocholina*, and *Piriniella*) or does not fit with any pre-existing model (in *Licispirella*), rendering their exact taxonomic position unclear.

In the Middle–Late Jurassic to Early Cretaceous, most trochospirally coiled genera disappeared, and although the few described forms are morphologically close to *Trocholina,* they present more complex morphologies. For example, the primary aperture in *Andersenolina* Neagu would be replaced by umbilical pores (Neagu, 1994); *Hottingerella* Piller shows a relatively complex canal system (Hottinger, 1976; Piller, 1983); and *Coscinoconus* Leupold displays a structured umbilical region (Leupold and Bigler, 1936).

Among the Involutinina, "*Trocholina*" is the genus considered to have the longest stratigraphic range (Norian–Cenomanian). The first, very broad diagnosis of the genus (Paalzow, 1922) has been emended in several works. Opinions are varied on the morphology of the spiral side: evolute according to Dessauvagie (1968), involute as determined by Koehn-Zaninetti (1969), Piller (1978), and Neagu (1995), and evolute to involute according to Henson (1947). Calcitic homeomorphs of *Trocholina* are numerous. *Neotrocholina*, a probable tubular ancestor of some multichambered Rotaliidae, is one of the most famous examples (Reichel, 1955; Dessauvagie, 1963). With a wall clearly hyaline-radial, it occurs in the Tithonian–Cenomanian and has erroneously been considered a synonym for *Trocholina* (e.g., Gorbatchik, 1959; Dessauvagie, 1968; Koehn-Zaninetti, 1969; Piller, 1978; Blau, 1987a; Loeblich and Tappan, 1987).

No trochospirally coiled Involutinina had been reported after their hypothesized Cenomanian extinction until discovery of *Trocholinopsis* Piller in the Holocene. Piller (1983) described that genus' wall ultrastructure and mode of test construction, in which one papillose L2 lamella would be developed on one side of the tubular chamber for each whorl added, covering the umbilical side only.

STUDIED MATERIAL

Our study focuses on diversified and very well-preserved, trochospirally coiled Involutinina assemblages. Not all trochospiral Involutinina discussed in the text occur in our material, and we either referred to the literature or restudied type material to comprehend the structure of those that are not at hand.

The Late Triassic material mainly comes from the Black Marble Quarry (BMQ), a locality first investigated for its foraminiferal content by Kristan-Tollmann and Tollmann (1983). It is located in the northern Wallowa Mountains (Blue Mountains Province, Oregon, U.S.A.; Fig. 1). The BMQ is a structurally isolated carbonate block, part of the late Carnian–middle/late? Norian Martin Bridge Formation of the Wallowa terrane (Rigaud, 2012). From this locality, about 200 thin sections have been made from 130 samples collected between 2007–2009. Trochospirally coiled Involutinina occur within the first 46 m of the BMQ succession and are particularly abundant in muddy lagoonal deposits. A pervasive hydrocarbon impregnation of their test microporosity has allowed the ghost preservation of their innermost structure and lamellae arrangement.

The Early Jurassic material mainly comes from the Adnet area (northern Calcareous Alps, Austria; Fig. 2) and subordinately, from the Lienz Dolomites, Austria (see Blau, 1987a, for details). Several quarries, some still active, can be found in the Adnet area. Over the years, quarrymen have collected numerous ammonites that have been the basis for several classic works dealing with Early Jurassic faunas (e.g., Quenstedt, 1845–1849; von Hauer, 1856), and studies continue up to today (e.g., Meister and Böhm, 1993; Böhm and others, 1999). The quarries also became the subject of detailed geological and sedimentological studies (see overview in Böhm, 2003). A spectacular bed and notable lithological guide horizon is the marmorea crust.

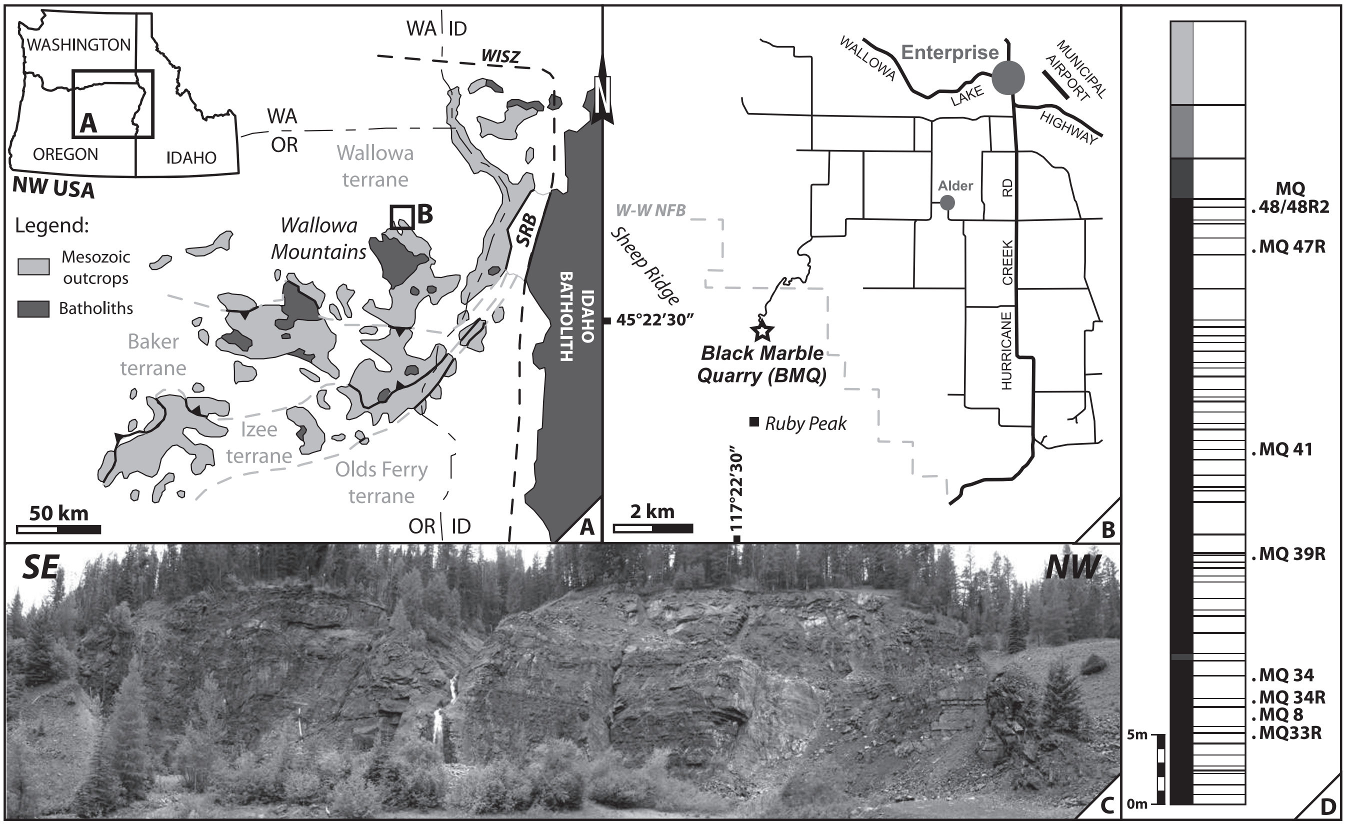

FIGURE 1. A Geological map of the Blue Mountains Province (northwest U.S.A., location map in the upper left corner) modified from Dorsey and LaMaskin (2007). **B** Map view of the northern end of the Wallowa Mountains (square labeled "B" in Figure 1A) showing the location of the Black Marble Quarry (BMQ; N45°22′24″, W117°21′14″, 1780 m elevation) and the road access from Enterprise, Oregon. **C** Panorama of the BMQ which is approximately 60-m high. **D** Columnar section of part of the limestone succession of the Martin Bridge Formation at the BMQ showing position of samples (MQ) which contain type specimens illustrated in Figures 5 and 6.

According to Böhm (2003, p. 241) and Böhm and others (1999), this crust forms the uppermost part of the Schnöll Formation and is latest Hettangian–earliest Sinemurian in age. This multiphased ferromanganese crust rests in part directly on the underlying Late Triassic reefal limestones. Our material, finely impregnated by ferromanganese solutions, comes from Quarry XXXI (see Fig. 2). There the marmorea crust forms the boundary bed between the Schnöll Formation (= "Enzesfelder Kalk" in Blau and Grün, 1996, 1997) and the Adnet Formation.

In spite of the large number of studied specimens and the outstanding preservation of our material, some of the most fragile elements of the foraminiferal tests are not visible. For example, the hydrocarbon and Fe-Mn impregnation only rarely preserved the finest laminar deposits (L1 lamellae sensu Piller, 1978). That might explain why we, as well as di Bari and Laghi (1994), did not observe Piller's Dh lamellae (see Piller, 1978 for definition). Furthermore, early diagenesis may have slightly modified the foraminiferal test structure prior to its impregnation.

NEW OBSERVATIONS

Triassic researchers usually limit the Involutinina only to involute forms. The recent observation that Aulotortidae may possess reduced lamellae during their ontogeny (Rigaud and others, 2012) questions this assertion. It leads us to reconsider the systematic position of many tubular, trochospirally coiled forms, including those that are evolute. The existence of coeval, non-aragonitic, homeomorphs (e.g., *Hungarillina*, *Neotrocholina*, *Spirilliconus*) necessitated a comparative study of well-known aragonitic organisms [i.e., gastropods, scleractinian corals, ammonites, dasycladacean green algae, aragonitic foraminifers (duostominids, epistominids, oberhauserellids, among others)] in order to select only potentially aragonitic forms. Results confirm that trochospirally coiled Involutinina are highly diversified and, when preserved, show interfingered lamellae, a distinctive characteristic of the "*Aulotortus* model" (Fig. 3; Figs. 4.1c?, 4.12–4.14?; Figs. 5.1–5.3?, 5.6, 5.9, 5.11?; Figs. 6.2, 6.12). This observation challenges the latest Involutinina classifications (Zaninetti and others, 1987; Loeblich and Tappan, 1987) and the phyletic tree proposed by di Bari and Laghi (1994), in which all trochospirally coiled Involutinina, except *Auloconus*, are classified in the family Triadodiscidae ("*Triadodiscus*" model).

The restudy of *Involutina conica* Schlumberger, type-species of *Trocholina*, and subsequent comparison with Triassic and Early Jurassic "*Trocholina*" has underlined the need for a thorough revision of the genus. While *T. conica* (Schlumberger) and some other representatives of the genus (e.g., *T. acuta* Oberhauser, *T. ultraspirata* Blau, *T. piriniae* Blau) show an evolute spiral side with reduced lateral laminar deposits, numerous other forms display a thick,

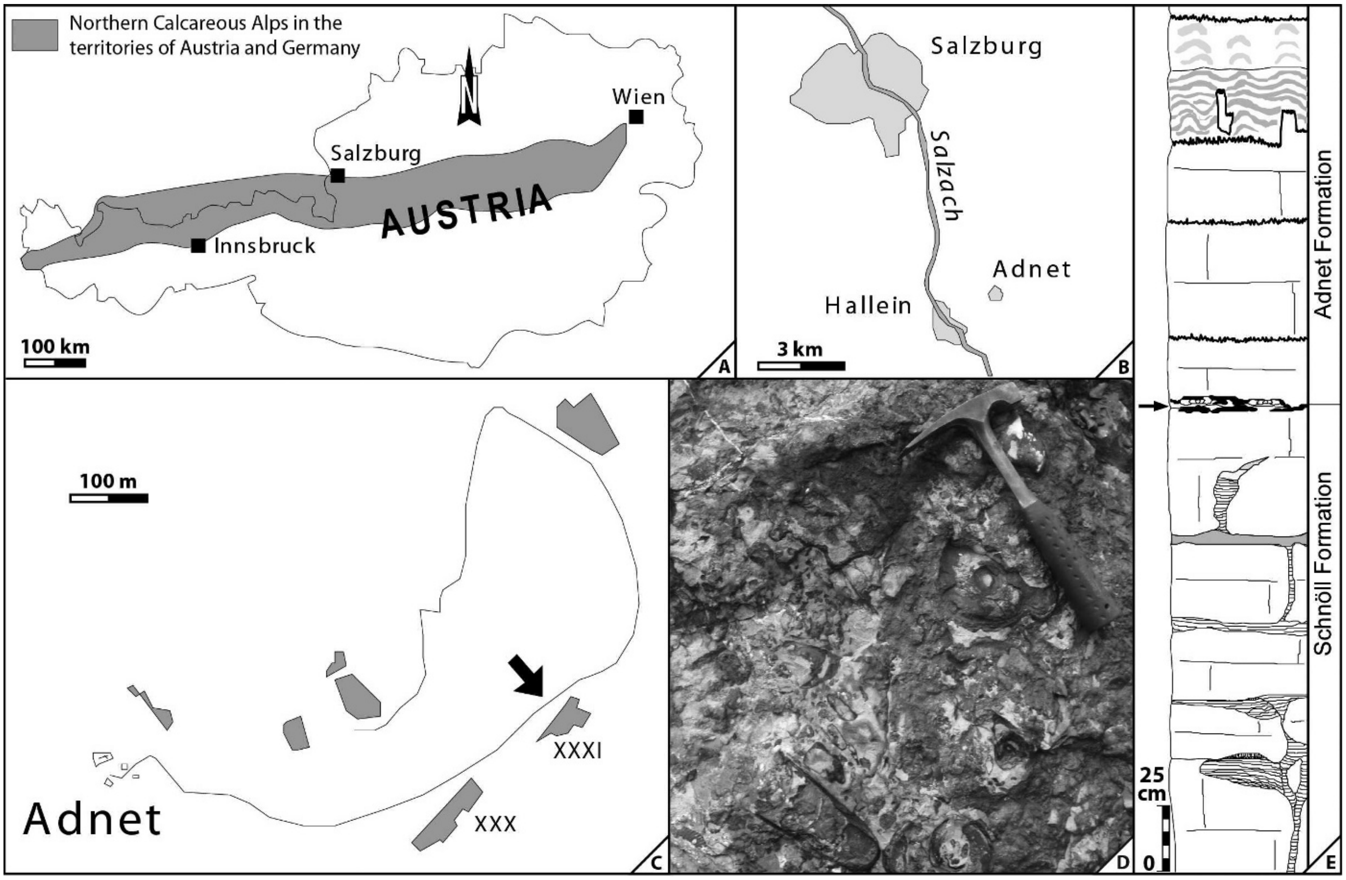

FIGURE 2. **A** Map of Austria showing the location of the northern Calcareous Alps. **B** Enlargement of the Salzburg area showing the Adnet locality. **C** Location of the sampled quarry (XXXI); the quarry numbering follows that of Kieslinger (1964). **D** Picture of the marmorea crust. **E** Columnar section at Quarry XXXI, showing the stratigraphic position of the marmorea crust (arrow), which contains the Adnet specimens.

involute spiral side endowed with well-developed lamellae (e.g., *T. granosa* Frentzen, *T. crassa* Kristan, *T. laevis* Kristan) and potentially covered by papillose lamellae (e.g., *T. verrucosa* Kristan). On the spiral side of involute "*Trocholina*," the lamellae are interfingered (Figs. 5.6, 5.9). On the umbilical side, the lamellae show local thickening, responsible for the papillae, which complicates the examination of the lamellae arrangement. However, in section, the presence of lamellae, regularly interrupted in the middle part of the umbilical mass (Figs. 5.3, 5.9), strongly suggests that, as in *Auloconus*, lamellae are interfingered on both sides of the test. It is noteworthy that interrupted lamellae are also observable on the umbilical side of evolute trochospirally coiled forms (e.g., in the type species of *Trocholina*, Fig. 4.1c). These observations contradict the model proposed by Piller (1978).

Comparison of *Trocholina conica* (Schlumberger) with Late Jurassic-Cretaceous Trocholininae has also highlighted a striking dissimilarity in the pores/perforations size. While *Trocholina* lacks perforation in the umbilical mass, Cretaceous forms show large pores (Hottinger, 1976), a characteristic easily visible thanks to the presence of micritic cements or fine sediments commonly infilling the pores (Figs. 4.4, 4.5, 4.7–4.10). Moreover, *T. conica* shows an umbilical mass covered by rounded–elongated papillae (Fig. 4.2), whereas polygonal nodes are observed in most Late Jurassic-Cretaceous forms (Figs. 4.3, 4.11).

Representatives of Involutinina are finely perforate on one or both sides of the test, where the perforations may riddle the tube wall and the lamellae. At the tubular-chamber lumen contact, the perforations are generally very small, <3–4 μm in diameter.

Larger perforations have been observed in several trochospiral taxa. When present, these large perforations are well-distributed on the spiral side of forms with laterally restricted lamellae (Figs. 6.7–6.11, 6.13), limited to the suture area of the spiral side in forms possessing erect lamellae (Figs. 6.2–6.6), and structured as simple canals or relatively complex canal systems in forms presenting well-developed lamellae (Figs. 4.4, 4.5, 4.7–4.10, 4.12–4.15). These large perforations, at the tubular chamber lumen contact, are comparable in size to the juvenile part of the tubular chamber (4–7 μm in diameter), and possibly were used as secondary apertures. If confirmed by further study, the absence of a primary aperture in "*Andersenolina*" (replaced by umbilical pores) would corroborate this assumption. Besides, the perforations observed on the spiral-side suture of the genus *Coronipora*, for example, are morphologically close to those observed in *Lasiodiscus*, which are considered as secondary apertures (Martini and Zaninetti, 1988).

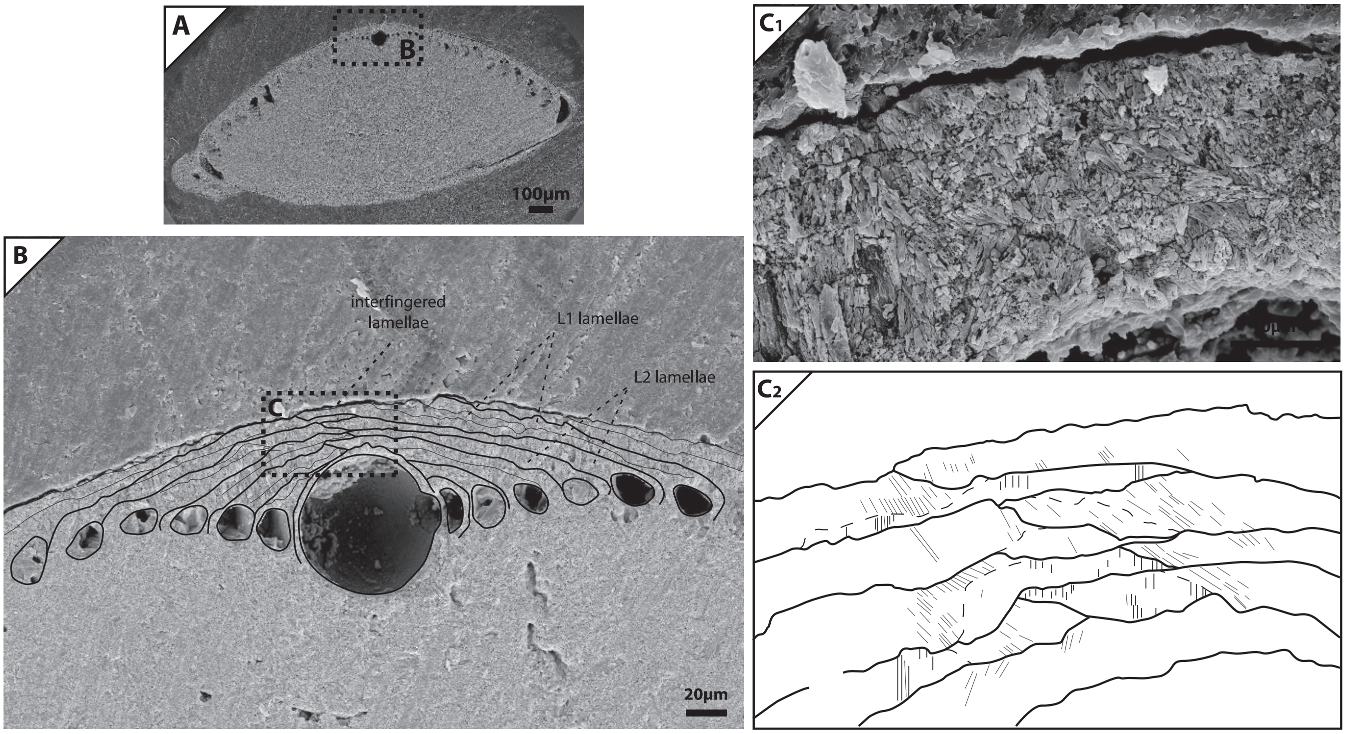

FIGURE 3. *Lamelliconus biconvexus* (Oberhauser), SEM images of the spiral side. Axial section made from di Bari and Laghi's (1994) material (MHNG 2011-1-90; late Carnian, Italy). **A** General view of a sectioned, isolated specimen after etching with diNaEDTA (1% by volume). **B** Reconstitution of the lamellae outline, clearly showing interfingering in the apical region. **C_1** Enlarged view of the lamellae interfingering area; note the good preservation of the aragonite needles. **C_2** Drawing of the interfingered L2 lamellae figured in C_1; note that the orientation of aragonite needles (thin gray lines) helps to differentiate successive lamellae; dashed lines represent possible L1 lamellae.

SYSTEMATICS

The following taxonomic revision is based on the study of well-preserved trochospirally coiled Involutinina from Austria, Italy [di Bari and Laghi's (1994) material], and Oregon and on the revision of the original material of *Hottingerella* (*Trocholina chouberti* Hottinger), *Licispirella* (*Semiinvoluta violae* Blau), *Neotrocholina* (*N. valdensis* Reichel), *Piriniella* (*P. blindi* Blau), and *Trocholina* (*Involutina conica* Schlumberger). Unfortunately, all attempts to find type specimens of the type species of *Coscinoconus* Leupold failed.

On account of the uncertain wall composition and lamellae arrangement of the trochospiral foraminifers *Babelispirillina* Ruggieri and Giunta, *Cylindrotrocholina* Loeblich and Tappan, and *Turrispirillina* Cushman, their assignment to the Involutinina was not attempted here.

Genera are erected or emended here based on organization of the lamellae and perforations, criteria consistent with previous works on the Trocholinidae. The laminar lateral extensions of the tube wall (L2 lamellae sensu Piller, 1978) are highly variable. During ontogeny, the L2 lamellae may be reduced (if the lateral thickening of the tube is limited to its base), well-developed (if interfingered), or shortened (in intermediate cases). The presence and position of the perforations are decisive criteria for taxonomic determination. In Involutinina, perforations are either radially oriented or positioned perpendicularly to the laminar deposits, crossing the lamellae throughout their height. The latter characteristic allows the distinction between foraminifers with lamellae (e.g., Involutinina) and those without lamellae (Rigaud and others, 2012).

Although species names are listed, the aim of this systematic review is to describe genera of the Trocholinidae, not to provide detailed species synonymies or descriptions for previously established species. Descriptions, however, are provided for the three new species discussed later in the systematics. All figured specimens from Oregon (BMQ) and Austria (Adnet and Lienz Dolomites) are reposited in the Museum of Natural History of Geneva, Switzerland, in collections MHNG 2011-1 and MHNG 75631, respectively.

Order INVOLUTINIDA Hohenegger and Piller, 1977,
name translat. herein
Suborder INVOLUTININA Hohenegger and Piller, 1977
Superfamily INVOLUTINOIDEA Bütschli, 1880
Family TROCHOLINIDAE Kristan-Tollmann, 1963,
emend. herein

Emended description. Test flat trapezoid to conical, evolute to involute, formed by a proloculus and a trochospirally enrolled, undivided tubular chamber. Tube wall composed of thin laminar deposits (L1 lamellae). In each whorl, the L1 lamellae stacking forms at least two laminar extensions of the tubular chamber wall (L2 lamella). These laminar extensions are laterally restricted on both sides of the tubular chamber and only partially cover the test surface. Wall hyaline, fibrous aragonitic, and perforate.

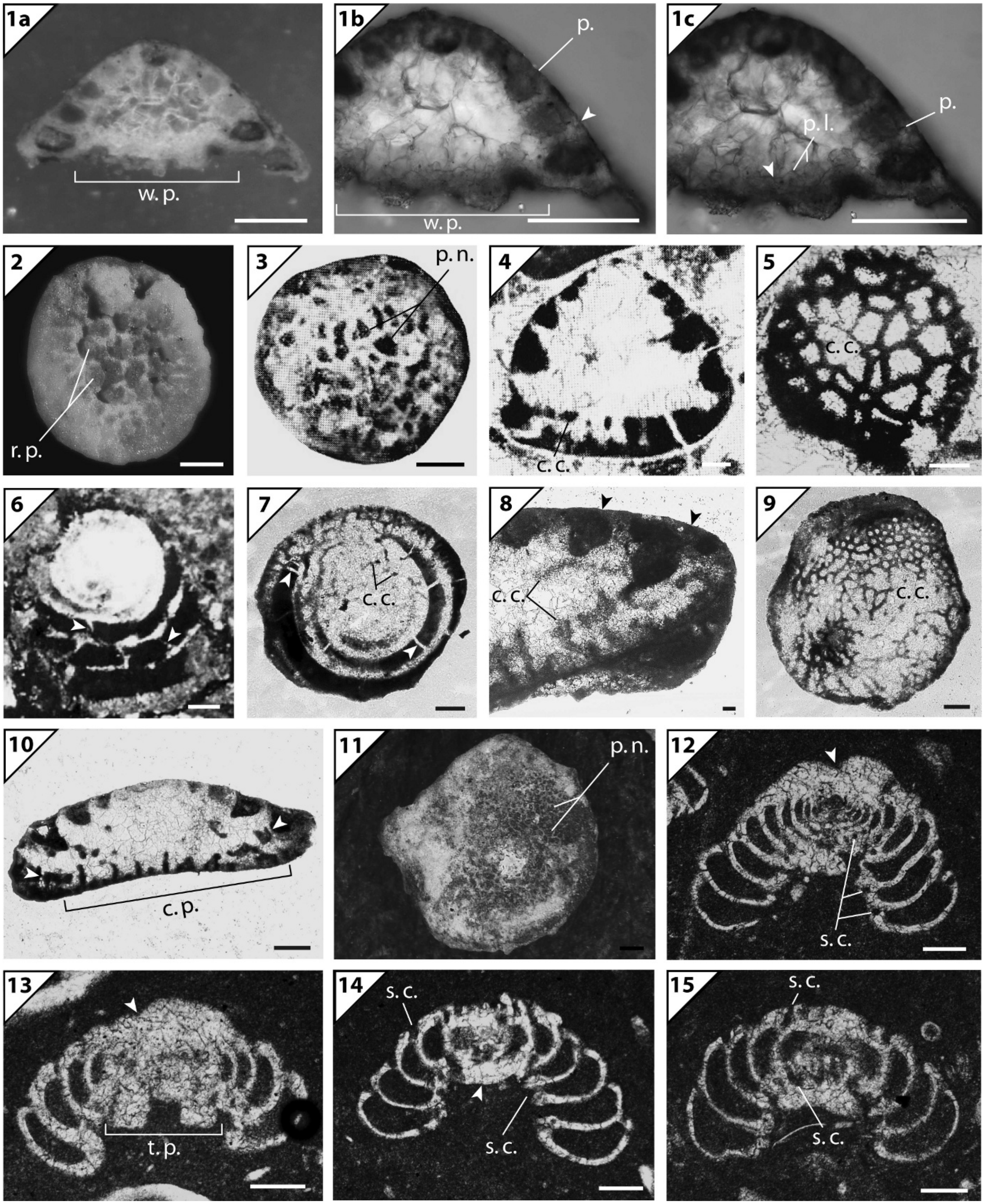

FIGURE 4. Views of the genera *Trocholina*, *Coscinoconus*, and *Piriniella*. **1, 2** New illustrations of *Trocholina conica* (Schlumberger): 1a–c, lectotype (''holotype'' sensu Reichel, 1955), Muséum national d'Histoire Naturelle, Paris, specimen No. MNHN.FS.157; 1a, thick axial section; 1b, the white arrow points to the reduced lamellae lateral extension; 1c, probable interfingering lamellae indicated by interrupted lamellae in the middle part of the umbilical mass (arrow). 2, paralectotype (''paratype'' sensu Reichel, 1955) of an isolated specimen, Basel Museum collection MHNB C39353; note the rounded shape of the papillae. **3–5** Reillustration of syntypes of *Coscinoconus alpinus* Leupold (from Leupold and Bigler, 1936, pl.

Composition. The family includes the subfamily Lamelliconinae Zaninetti and others, 1987, and the subfamily Trocholininae Kristan-Tollmann, 1963.

Stratigraphic distribution. Early Triassic? (Olenekian)/ Middle Triassic–Late Cretaceous (Cenomanian).

Comparison and remarks. We here reintroduce the family Trocholinidae of Kristan-Tollmann (1963), improving its definition, especially regarding its external morphology and lamellar architecture.

Piller (1983) described the Holocene genus *Trocholinopsis* as a form lacking lamellae on its spiral side and displaying only one L2 lamella/whorl on its umbilical side. These characteristics exclude this trochospiral aragonitic form from the Trocholinidae. Unlike Hohenegger and Piller (1977) and Piller (1983), we follow Zaninetti and Brönnimann (1977) and Loeblich and Tappan (1981, 1987), who excluded the Lasiodiscidae Reytlinger from the Involutinina. These calcitic, double-layered, Paleozoic trochospiral foraminifers show a strong homeomorphism with the Trocholinidae. Representatives of the family Spirillinidae Reuss possess a calcitic monocrystalline wall and differ from the Trocholinidae (aragonitic) in wall composition.

Subfamily LAMELLICONINAE Zaninetti and others, 1987, emend. herein

Type genus: *Lamelliconus* Piller, 1978

Emended description. The test is free, flat trapezoid to conical. Proloculus followed by a trochospirally enrolled, undivided tubular chamber. Reduced, shortened to well-developed on one or both sides of the tubular chamber, the lateral laminar extensions of the tube wall (L2 lamellae) are straight, uniform to slightly uneven. Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Composition. The subfamily includes the genera *Coronipora* Kristan, 1958, *Lamelliconus* Piller, 1978, *Licispirella* Blau and Grün, 1997, *Piriniella* Blau, 1987a, and the newly erected genera *Coronaserra*, *Kristantollmanna*, and *Wallowaconus*.

Stratigraphic distribution. Early Triassic? (Olenekian)/ Middle Triassic–Middle Jurassic.

Comparison and remarks. The definition of the Lamelliconinae is here expanded to include all trochospiral involutinins lacking papillose lamellae. Special attention is given to the test architecture.

The lamellae arrangement of *Lamelliconus*, *Coronipora*, and *Wallowaconus* n. gen. shows affinities with the "*Aulotortus* model" (interfingering lamellae). *Licispirella*, *Coronaserra* n. gen., and *Kristantollmanna* n. gen. possess only reduced to shortened lamellae. It is thus difficult to decipher how many lamellae are added per whorl and hence to compare their lamellae arrangement with preexisting models. However, representatives of *Coronipora*, *Coronaserra* n. gen., *Wallowaconus* n. gen., *Licispirella*, and *Kristantollmanna* n. gen. have a strongly similar arrangement of spiral-side lamellae, leading us to place these genera in the same subfamily. While the lamellae arrangement of *Piriniella* has never been observed, the smooth periphery of its umbilical side (Fig. 4.14) indicates a structure closer to that of the Lamelliconinae (straight lamellae) than the Trocholininae (papillose lamellae).

Within the Involutinina, the Lamelliconinae show a trochospiral coiling mode that differentiate them from the Aulotortinae Zaninetti and the Parvalamellinae Rigaud, Martini, and Rettori, which are planispirally and glomospirally coiled, respectively. Likewise, the Lamelliconinae do not possess internal tubular structures (pillars or strengthenings) typical of the Triasininae Loeblich and Tappan (see Rigaud and others, 2013).

Genus *Coronipora* Kristan, 1958, emend. herein

Type species: *Coronella austriaca* Kristan, 1957
Figs. 6.2–6.4

Diagnosis. A Trocholinidae with erect, ridge-like lamellae on the spiral side and, straight, uniform to slightly uneven, interfingered lamellae on the umbilical side.

Emended description. The test is free, flat trapezoid to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. Erect on the spiral side (Fig. 6.3), the lateral laminar extensions of the tube wall (L2 lamellae) are straight, uniform to slightly uneven (Fig. 6.2) on the umbilical side and, at least in the juvenile part, well-developed and interfingering in the umbilical region (Fig. 6.2). Wall hyaline, fibrous aragonitic, and perforate. Large perforations or short canals, probable secondary apertures, are limited to the vicinity of the spiral-side suture (Figs. 6.2–6.4). Primary aperture simple, terminal.

Stratigraphic and geographic distribution. Norian–Rhaetian and Early Jurassic of Tethys.

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XVIII, figs. 3, 7, 9). 3, umbilical side of an isolated specimen; the polygonal nodes display a typical angular periphery that distinguishes them from *Trocholina*'s papillae. 4, oblique section of a recrystallized specimen showing a crenellated periphery. 5, basal section of a recrystallized specimen; the canal network is outlined by infiltrated, dark, micritic material. **6** Reillustration of *Coscinoconus banneri* (BouDagher-Fadel) n. comb. (from BouDagher-Fadel, 2008, pl. 4.2., fig. 2); oblique section of a poorly preserved specimen; arrows point to endoskeletal structures (rudimentary septa sensu BouDagher-Fadel, 2008). **7–11** New illustrations of syntypes of *Coscinoconus chouberti* n. comb. (Hottinger), Basel Museum collection MHNB TSL203. All specimens are recrystallized and have been eroded by transport prior to deposition; note the presence of endoskeletal structures (7, 10, white arrows), reduced lamellae (8, black arrows), and a relatively complex canal system, only preserved in areas infiltrated by micrite (7–10). 11, umbilical side of isolated specimen showing partly preserved polygonal nodes. **12–15** *Piriniella blindi* Blau. 12, reillustration of the holotype (from Blau, 1987a, pl. 3, fig. 1, Lienz Dolomites, No. 75631-948a); the white arrow points to a depressed apical thickening, indicative of slight lamellae interfingering in the last whorl. 13, reillustration of a paratype from Blau (1987a: pl. 3, fig. 2, Lienz Dolomites, No. 75631-948b) showing a toothed periphery; the white arrow points to the end of the last-formed L2 lamella. 14, specimen showing sutural canals on both sides of the test; note the smooth periphery on the umbilical side; the white arrow possibly indicates the end position of the lastly formed L2 lamella (Lienz Dolomites, No. 75631-89405). 15, specimen with sutural canals on both sides of the test (Lienz Dolomites, No. 75631-94812). White scale bars = 100 μm; black scale bars = 200 μm. Abbreviations: c. c. = complex canal (system); c. p. = crenellated periphery; p. = perforation; p. n. = polygonal nodes; r. p. = rounded papillae; s. c. = sutural canal; t. p. = toothed periphery; p. l. = papillose lamella; w. p. = wavy periphery.

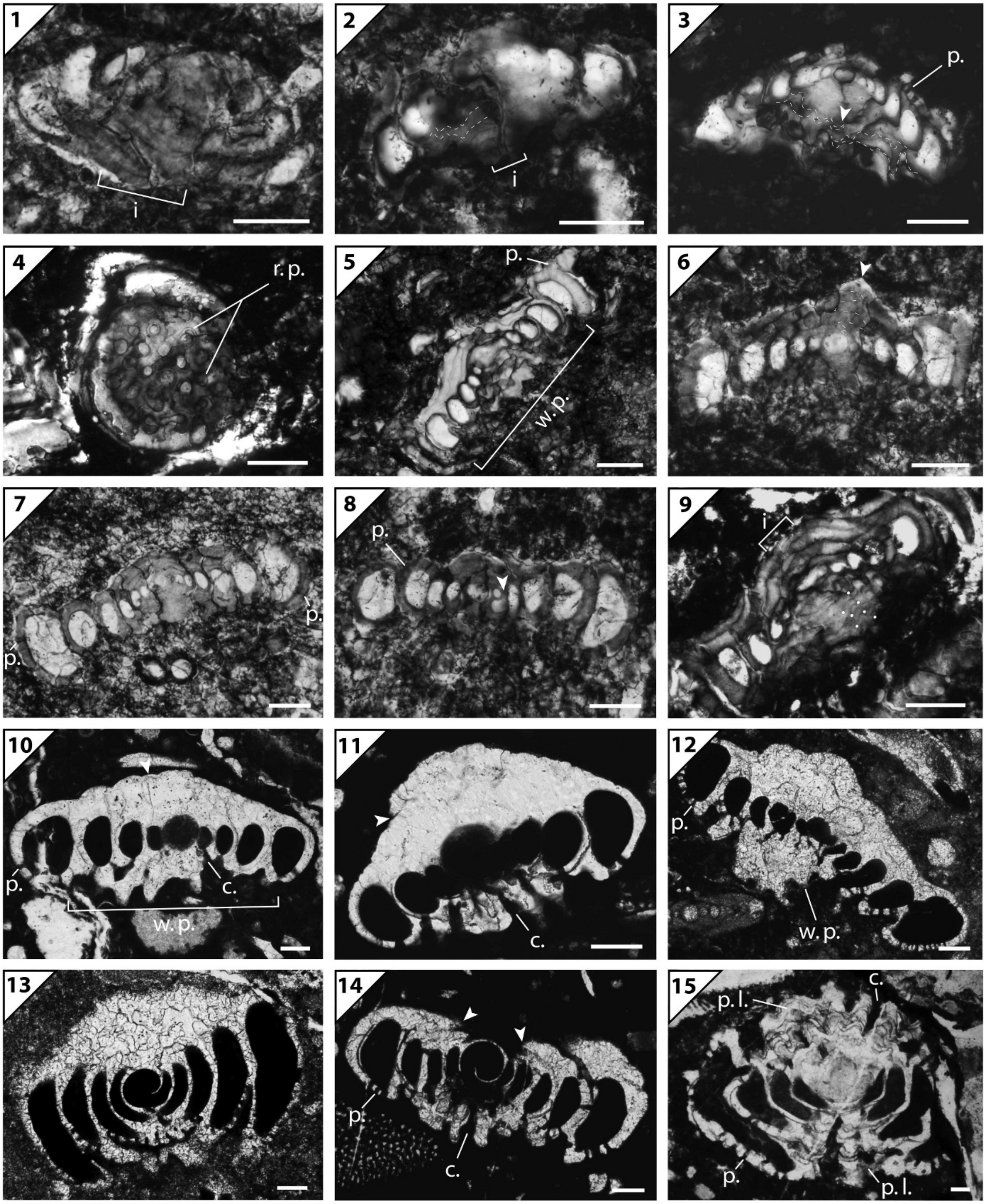

FIGURE 5. Thin-section views of the genera *Lamelliconus*, *Frentzenella*, *Semiinvoluta*, and *Papillaconus*. **1–4** Gradual evolution of papillose lamellae from *Lamelliconus* Piller to *Frentzenella* n. gen. 1, *Lamelliconus* sp., oblique section (BMQ, No. 2011-1-331, spl. MQ33R); note the interfingering lamellae. 2, intermediate form, centered-oblique section (BMQ, No. 2011-1-880a, spl. MQ8); dashed lines outline one L2 lamella, which is slightly deformed. 3, *Frentzenella laevis* (Kristan) n. comb., centered, subaxial section (BMQ, No. 2011-1-340a, spl. MQ34); arrow points to interrupted lamellae in the middle part of the umbilical mass (= interfingered lamellae?); dashed lines outline the papillose lamellae. 4, *Frentzenella*

Included species. Coronipora austriaca (Kristan, 1957), Rhaetian–Early Jurassic; *C. convergens* Blau, 1987a, Early Jurassic; *C. etrusca* (Pirini, 1965), Rhaetian?–Early Jurassic; *C. gusici* Blau, 1987b, Early Jurassic; *C. kristantollmannae* Blau and Grün, 1997, Early Jurassic; *C. serraforma* Senowbari-Daryan and others, 2010, Rhaetian?; and *C. yushuensis* He and Wang, 1990, Norian.

Comparison and remarks. Our emendation provides precise details about the test shape, perforation arrangement, and lamellar structure of *Coronipora* that were not defined by Kristan (1958). The genus is the only Trocholinidae displaying erect lamellae or spiral ridges/flanges on the spiral side and interfingered lamellae on the umbilical side. In isolated specimens, small bumps (bosses sensu di Bari and Laghi, 1994) are observed on the umbilical side (see Piller, 1978, pl. 21, fig. 1). This feature is related to the discontinuity of the thinnest laminar deposits (L1 lamellae) and is responsible for the unevenness (Fig. 6.2) that characterizes the lateral laminar extensions (L2 lamellae).

Coronipora shows morphological similarities with Paleozoic representatives of the double-layered wall genera *Lasiodiscus* Reichel and *Lasiotrochus* Reichel. The wall and exoskeletal structures are, however, less complex in *Coronipora*. From *Conicospirillinoides* Cheng and Zheng, 1978, it differs in the absence both of papillae-like structures on the umbilical side and of radial elements connecting the spiral-side flanges. Since *Conicospirillinoides* has been placed in the monocrystalline Spirillinida, its wall composition should also differ from that of *Coronipora*.

Genus *Lamelliconus* Piller, 1978, emend. herein
Type species: *Trocholina biconvexa* Oberhauser, 1957
Figs. 5.1, 5.2?

Auloconus Piller, 1978, p. 74 (type species = *Trocholina permodiscoides* Oberhauser, 1964, p. 207, pl. 2, figs. 13–15, 18, 20, 22, pl. 3, fig. 1).

Diagnosis. A Trocholinidae with straight lamellae interfingering on both sides of the test.

Emended description. The test is free, sublenticular to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. Well-developed on both sides of the tubular chamber, at least in the juvenile part, the lateral laminar extensions of the tube wall (L2 lamellae) are straight and interfingered, building an apical thickening and an umbilical mass. Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Stratigraphic and geographic distribution. Olenekian?/Anisian–Rhaetian of Tethys and Late Triassic of Panthalassa (Oregon and Japan).

Included species. Lamelliconus alticonus (He and Wang, 1990) n. comb., Norian; *L. artiskomorphos* di Bari and Laghi, 1994, late Carnian; *L. biconvexus* (Oberhauser, 1957), Ladinian?–Carnian; *L. cucullatus* di Bari and Laghi, 1994, late Carnian; *L. depressus* di Bari and Laghi, 1994, late Carnian; *L. minor* (Oberhauser, 1957), Ladinian?–Carnian; ?*L. multispirus* (Oberhauser, 1957), late Ladinian–Carnian/Norian?; *L. permodiscoides* (Oberhauser, 1964) n. comb., Norian–Rhaetian; *L. planoconvexus* (Apthorpe, 2003) n. comb., Olenekian?–Anisian; ?*L. procerus* (Liebus, 1942), Ladinian–Carnian/Norian?; *L. semivacuus* (He and Yue, 1987) n. comb., Norian; and *L. ventroplanus* (Oberhauser, 1957), Ladinian?–Carnian.

The taxonomic position of the species *Trocholina multispirus* Oberhauser, 1957, and *T. procerus* Liebus, 1942, is problematic, because illustrated specimens, although resembling *Lamelliconus*, have never shown any apical thickening, hampering their confident attribution to that genus. These two species, however, should not be maintained in the genus *Trocholina* as they do not display papillose lamellae.

Comparison and remarks. The recognition of interfingered lamellae in the type species of *Lamelliconus* compelled us to emend Piller's generic diagnosis (1978). *Lamelliconus* differs from *Aulotortus* in its conical shape and trochospiral coiling. It is the only Trocholinidae possessing straight, well-developed lamellae on both sides of the tubular chamber. The genus is partially homeomorphic with Carboniferous *Howchinia* Cushman, which differs in its calcitic, double-layered wall.

The genus *Auloconus* Piller is here placed in synonymy with *Lamelliconus* Piller. Piller (1978) erected the former genus for trochospiral forms displaying the same test architecture as *Aulotortus*. As interfingered lamellae are also observed on the spiral side (Fig. 3) and on the umbilical side (see the tapered, interfingered L2 lamellae in Oberhauser, 1964, pl. 4, fig. 6) of the type species *L. biconvexus*, no other known criteria of generic value allow distinction between the two forms. Oberhauser (1964, pl. 3, fig. 1) and Koehn-Zaninetti (1969, figs. 28D, F, J, M) illustrated supposed intermediate forms between planispiral Aulotortidae and trochospiral Lamelliconinae, leading to the widely accepted hypothesis that "*Auloconus*" originated from *Aulotortus*. These illustrated forms, however, had

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laevis (Kristan) n. comb., basal section showing rounded papillae (BMQ, No. 2011-1-341, spl. MQ34R). **5–9** *Frentzenella frentzeni* n. gen., n. sp. 5, holotype (BMQ, No. 2011-1-48, spl. MQ48R2), oblique, sub-centered section. 6–8, paratypes (BMQ, No. 2011-1-471a, b, c; spl. MQ47R), oblique, centered to axial sections with 6 showing well-interfingered (dashed lines), spiral-side lamellae, forming a bulge (arrow), and 8 showing coiling irregularity (arrow). 9, paratype (BMQ, No. 2011-1-480, spl. MQ48) transverse section; dorsal-side lamellae are clearly interfingered; umbilical-side lamellae, most likely interfingered, are all interrupted in the middle part of the umbilical mass (white dots). **10–13** *Frentzenella perforata* n. gen., n. sp. 10, holotype (Adnet, No. 75631-424a; axial section); dorsal-side lamellae are slightly undulated (arrow), following the tubular chamber morphology; note the presence of large canals in the umbilical mass. 11, paratype (Adnet, No. 75631-423a), subaxial section; the white arrow points to the end of the last-formed L2 lamella. 12, paratype (Adnet, No. 75631-428a), subaxial section in which randomly distributed umbilical canals are joined together. 13, paratype (Adnet, No. 75631-1622a), oblique-centered section. **14** *Semiinvoluta* sp., axial section (Adnet, No. 75631-428b); note the shortened lateral extension of the dorsal-side L2 lamellae (arrows); the proloculus is not covered by laminar deposits. **15** *Papillaconus* sp., oblique, subcentered section (Adnet, No. 75631-415), showing a wavy periphery interrupted by large canals. All scale bars = 50 μm. Abbreviations: c = canal; i = interfingered (lamellae); p = perforation; r. p. = rounded papillae; p. l. = papillose lamella; w. p. = wavy periphery.

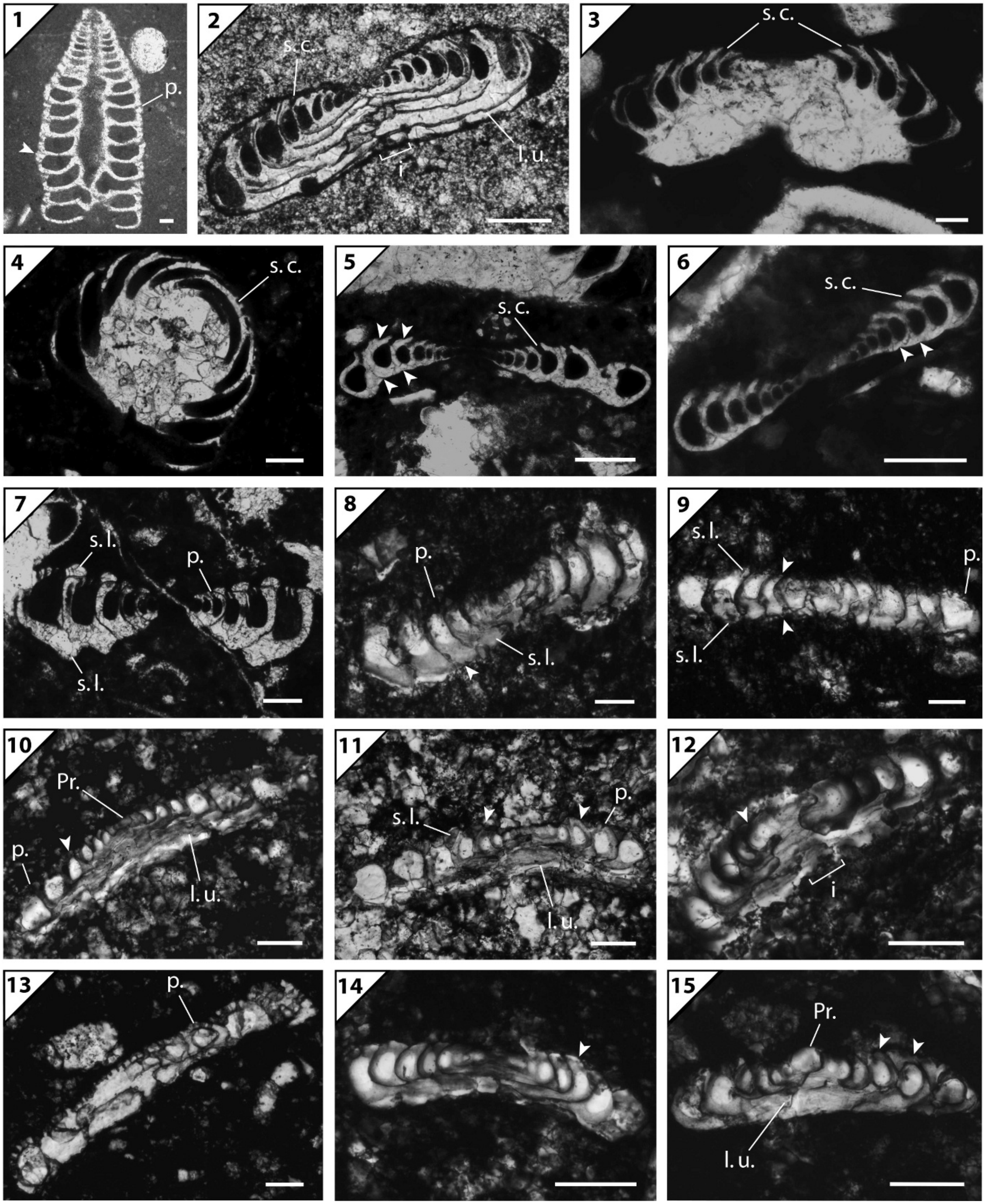

FIGURE 6. Thin-section views of the genera *Kristantollmanna*, *Coronipora*, *Coronaserra*, *Licispirella*, and *Wallowaconus*. **1** New illustration of the holotype of *Kristantollmanna lavanta* (Blau) n. gen., n. comb. from Blau (1987a, pl. 5, fig. 2; Lienz Dolomites, No. 75631-8943), oblique subcentered section; note that the tube base is thickened (arrow). **2–4** *Coronipora* Kristan, in which perforations are limited to the vicinity of the spiral-side suture. 2, *Coronipora austriaca* Kristan, oblique section (Adnet, No. 75631-41) showing the well-developed, interfingered umbilical-side lamellae and shortened spiral-side lamellae, perforated by sutural canals. 3, *Coronipora* sp., transverse section (Adnet, No. 75631-42a) showing erect lamellae and

been selected from populations of oscillatory specimens, which are recrystallized in their central, inner part, and may, according to the section, roughly appear trochospirally coiled. Conversely, some trochospiral forms such as *Lamelliconus semivacuus* (He and Yue, 1987) incontestably represent intermediate forms between *L. biconvexus* (=*Lamelliconus*) and *L. permodiscoides* (=*"Auloconus"*).

Genus *Licispirella* Blau and Grün, 1997, emend. herein
Type species: *Semiinvoluta violae* Blau, 1987b
Figs. 6.7–6.9

Diagnosis. A Trocholinidae with shortened lamellae developed on both sides of the tubular chamber.

Emended description. The test is free, flat trapezoid to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. The lateral laminar extensions of the tube wall (L2 lamellae) are, at least in the juvenile part, shortened on both sides of the tubular chamber (Figs. 6.7–6.9). Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Stratigraphic and geographic distribution. Rhaetian of Iran, Early Jurassic of Austria, Middle Jurassic of Hungary, and late Carnian?–early/middle? Norian of the Martin Bridge Formation (BMQ, Wallowa terrane, Oregon, U.S.A.; Figs. 6.8, 6.9).

Included species. Licispirella bakonyensis (Blau, 1989), Middle Jurassic; *L. iranica* (Senowbari-Daryan and others, 2010) n. comb., late Carnian?/Norian–Early Jurassic; *L. tricarinata* Blau and Grün, 1997, Early Jurassic; and *L. violae* (Blau, 1987b), Early Jurassic.

The indeterminate Early Jurassic specimens illustrated by Blau (1987a, pl. 7, figs. 4–8) belong to *L. iranica*.

Remarks. Licispirella is the only Trocholinidae possessing shortened lamellae on both sides of the tubular chamber. That distinctive feature was not mentioned in the original description of the taxon.

Genus *Piriniella* Blau, 1987a, emend. herein
Type species: *Piriniella blindi* Blau, 1987a
Figs. 4.12–4.15

Diagnosis. A Trocholinidae with simple canals developed from the sutural perforations on one or both sides of the tubular chamber.

Emended description. The test is free, sublenticular to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. The lateral laminar extensions of the tube wall (L2 lamellae) are, at least in the juvenile part, well-developed on both sides of the test, building an apical thickening and an umbilical mass. Wall hyaline, fibrous aragonitic, and perforate. Large perforations, probable secondary apertures, are developed from the spiral sutures on one or both sides of the tubular chamber, forming simple canals through the lamellae (Figs. 4.12–4.15). Aperture not observed, probably simple, terminal.

Stratigraphic and geographic distribution. Early Jurassic of Austria, Middle Jurassic? of Italy (Sicily).

Included species. Piriniella blindi Blau, 1987a, Early Jurassic, and ?*P. involutinoides* (Ruggieri and Giunta, 1965) n. comb., Middle Jurassic.

Comparison and remarks. According to Blau (1987a), *Piriniella* mainly differs from *Trocholina* by the presence of a deep umbilicus (lamellae being reduced in the last volutions of the type species). We now regard this characteristic of specific value and consider the main difference to be the presence in *Piriniella* of simple sutural canals developed from the sutural perforations, as stated in the emended diagnosis of the genus. Because the lamellae arrangement of *Piriniella* remains unknown, its assignment to the Lamelliconinae rather than to the Trocholininae is uncertain. However, as its umbilical mass shows either a toothed (Fig. 4.13) or smooth (Fig. 4.14) periphery in section, we presume that the form possesses straight, non-papillose lamellae. The canal system observed in *Piriniella* is different from that of *Coscinoconus*, which is, by far, more complex.

The specimens illustrated by Ruggieri and Giunta (1965, pl. II, figs. 20–22) as *Pachyspirillina*? *involutinoides* show a comparable kind of sutural canals. However, the wall composition of the species needs clarification before its definitive assignment to *Piriniella*.

Genus *Coronaserra* n. gen.
Type species: *Coronipora deminuta* Blau, 1987a
Figs. 6.5, 6.6

Derivatio nominis. From the Latin "corona" (= crown) and "serra" (= saw). The new genus is named after the crown-like shape of its spiral side (as in *Coronipora*) and its saw-like shape in axial section.

Diagnosis. A Trocholinidae with erect, ridge-like lamellae on the spiral side and shortened lamellae on the umbilical side.

Description. The test is free, flat trapezoid to conical. Globular proloculus followed by a trochospirally enrolled,

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sutural canals. 4, *Coronipora kristantollmannae* Blau, oblique section (Adnet, No. 75631-42b) with transversally sectioned sutural canals. **5, 6** *Coronaserra* n. gen., Adnet sample 4a2. 5, new illustration of the holotype of *Coronaserra marmorensis* (Blau and Grün) n. comb from Blau and Grün (1997, pl. 5, fig. L; Adnet, No. 75631-423b), oblique section; arrows point to the lamellae lateral extension; note that the spiral-side canals are separated from the spiral suture by a thin laminar deposit. 6, *Coronaserra* sp., oblique section (Adnet, No. 75631-424b); the lamellae lateral extension is indicated by white arrows. **7–9** *Licispirella* Blau and Grün; the lamellae are shortened on both sides of the test and the perforations limited to the spiral side and the tubular-chamber periphery. 7, *Licispirella violae* (Blau), transverse section (Adnet, No. 75631-1622b). 8, 9, *Licispirella iranica* (Senowbari-Daryan and others, 2010; BMQ, No. 2011-1-880b, c; sample MQ8). 8, oblique section. 9, subaxial section; arrows indicate the shortened-lamellae lateral extension. **10–15** *Wallowaconus oregonensis* n. gen., n. sp. 10, holotype (BMQ, No. 2011-1-39; spl. MQ39R), subaxial section; note the spiral side perforations (arrow) and the presence of slightly uneven lamellae. 11, paratype (BMQ, No. 2011-1-391, spl. MQ39R), oblique section, arrows point the spiral-side lamellae extension. 12, paratype (BMQ, No. 2011-1-880d, spl. MQ8), subcentered oblique section; the white arrow points to the end of one shortened L2 lamella. 13, paratype (BMQ, No. 2011-1-410; spl. MQ41), last whorls of an obliquely sectioned adult specimen showing large perforations, 14, paratype (BMQ, No. 2011-1-340b; spl. MQ34), subcentered oblique section, with well-preserved spiral-side lamellae (arrow). 15, paratype (BMQ, No. 2011-1-340c; spl. MQ34), centered, subaxial section, arrows point to the shortened lamellae extension. All scale bars = 50 μm. Abbreviations: i = interfingered (lamellae); l. u. = lamellae unevenness; p = perforation; Pr. = proloculus; s. c. = sutural canal; s. l. = shortened lamellae.

undivided tubular chamber. Erect on the spiral side, the lateral laminar extensions of the tube wall (L2 lamellae) are only slightly developed on the umbilical side (Figs. 6.5, 6.6). Wall hyaline, fibrous aragonitic, and perforate. Large perforations or short canals, probable secondary apertures, are limited to the vicinity of the spiral-side suture. Primary aperture not observed, most likely simple, terminal.

Stratigraphic and geographic distribution. Early Jurassic of Austria.

Included species. Coronaserra deminuta (Blau, 1987a) n. comb., Early Jurassic, and *C. marmorensis* (Blau and Grün, 1997) n. comb., Early Jurassic.

Comparison and remarks. Coronaserra is the only Trocholinidae displaying erect lamellae on the spiral side and non-interfingered lamellae on the umbilical side, even in its juvenile part. It differs from *Coronipora* in the poor extension of its umbilical-side lamellae throughout its ontogeny.

Genus *Kristantollmanna* n. gen.
Type species: *Turrispirillina*? *lavanta* Blau, 1987a
Fig. 6.1

Derivatio nominis. The name of this genus is dedicated to Dr. Edith Kristan-Tollmann for the valuable work she accomplished on Triassic foraminifers.

Diagnosis. A Trocholinidae with reduced lamellae on both sides of the tubular chamber.

Description. The test is free, conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. Reduced on both sides of the tubular chamber, the lateral laminar extensions of the tube wall (L2 lamellae) only slightly cover the suture area (Fig. 6.1). Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Stratigraphic and geographic distribution. Norian–Early Jurassic of Tethys.

Included species. Kristantollmanna altissima (Pirini, 1965) n. comb., Early Jurassic; *K. bicarinata* (Blau, 1987b) n. comb., Early Jurassic; *K. lavanta* (Blau, 1987a) n. comb., Early Jurassic; *K. licia* (Blau, 1987a) n. comb., Early Jurassic; *K. stibanei* (Blau and Haas, 1991) n. comb., Early Jurassic; and *K. truncata* (He and Wang, 1990) n. comb., Norian–Rhaetian.

Comparison and remarks. Kristantollmanna is the only Trocholinidae possessing reduced lamellae on both sides of the test. It differs from *Licispirella* by the size of its lamellae, which are limited to the suture area (reduced lamellae) and do not overlap the previous whorl.

Kristantollmanna is partially homeomorphic with *Turrispirillina* Cushman. The wall composition of *Turrispirillina* is uncertain, but according to the illustrated topotypes (Loeblich and Tappan, 1987, pl. 319, figs. 8–10), the genus is marked by more depressed sutures indicative of a simple tube (without lamellae). In *Kristantollmanna* the base of the tube wall is thickened by reduced lamellae, giving the test a smoother periphery. Similarly, the new genus differs from the monocrystalline genera *Conicospirillina* Cushman and *Mychostomina* Berthelin in its less depressed suture area. Morphological similarities also exist with calcitic Paleozoic forms such as *Eolasiodiscus* Reytlinger, which possesses a double-layered wall.

Genus *Wallowaconus* n. gen.
Type species: *Wallowaconus oregonensis* n. gen., n. sp.
Figs. 6.10–6.15

Derivatio nominis. From the place where it was discovered (Wallowa Mountains, Wallowa terrane, Oregon, U.S.A.) and the conic shape of the test.

Material. Rock thin sections stored in the Museum of Natural History, Geneva, Switzerland (collection MHNG 2011-1).

Diagnosis. A Trocholinidae with shortened lamellae on the spiral side and straight, uniform to slightly uneven, interfingered lamellae on the umbilical side.

Description. The test is free, flat trapezoid to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. Shortened on the spiral side, the lateral laminar extensions of the tube wall (L2 lamellae) are straight, uniform to slightly uneven (Figs. 6.10, 6.11) on the umbilical side, and, at least in the juvenile part, well-developed and interfingered in the umbilical region. Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Stratigraphic and geographic distribution. The genus is only known from the late Carnian?–early/middle? Norian of the Martin Bridge Formation (Wallowa terrane, Oregon, U.S.A.) and from the late Norian–Rhaetian of China (He and Yue, 1987; He and Norling, 1991).

Included species. Wallowaconus oregonensis n. gen., n. sp., late Carnian?/Norian–Rhaetian, and *W. rotundatus* (He and Norling, 1991) n. comb., Rhaetian.

Comparison and remarks. Wallowaconus is the only Trocholinidae possessing shortened lamellae on the spiral side and well-developed, interfingered lamellae on the umbilical side. It differs from *Coronipora* by the absence of sutural perforations. Contrary to *Lamelliconus*, the new genus does not have well-developed, interfingered lamellae on the spiral side.

Wallowaconus rotundatus (He and Norling) is morphologically close to *Coronipora austriaca* (Kristan) and *Coronipora kristantollmannae* Blau. In *W. rotundatus* the absence of sutural pores (or canals) and the partial overlapping of the suture area by the spiral-side lamellae help to differentiate the latter species from them.

Wallowaconus oregonensis n. gen. n. sp.
Figs. 6.10–6.15

Coronipora austriaca (Kristan, 1957). He and Yue, pl. I, figs. 17, 18.

Holotype. No. 2011-1-39, Fig. 6.10.

Derivatio nominis. The new species is named after the state where it was discovered (Oregon, U.S.A.).

Material. The description of this species is based on ~350 specimens from rock thin sections stored in the Museum of Natural History, Geneva, Switzerland (collection MHNG 2011-1).

Type locality. Black Marble Quarry, Wallowa Mountains, Oregon, U.S.A.

Type level. Upper Triassic (upper Carnian?–lower/middle? Norian) of the Martin Bridge Formation.

Description. The test is free, flat trapezoid to low conical with a rounded periphery. It is formed by a globular proloculus with a simple opening followed by a trochospirally enrolled, undivided tubular chamber. Low trochospiral throughout, with an obtuse apical angle, the coiling may show irregularities but whorls never oscillate. Gradually enlarging during growth, the tubular chamber initially appears oval in section, later possibly becoming almost kidney- to chevron-shaped against the previous whorl, and forms up to 10 whorls. Developed on both sides of the tubular chamber, the lateral laminar extensions of the tube wall (L2 lamellae) are asymmetric. Shortened on the spiral side, they may become more and more restricted during ontogeny. Straight, uniform to slightly uneven, and well-developed on the umbilical side, lamellae are interfingered, building an umbilical mass. Wall calcareous, perforate, commonly recrystallized, but probably originally hyaline, fibrous aragonitic, and perforate. On the spiral side of well-preserved specimens, several large perforations, probable secondary apertures, radially-arranged, riddle the tube wall. Primary aperture simple, terminal.

Dimensions. Specimens of *W. oregonensis* from the BMQ may reach up to 600 μm in diameter (usually 100–500 μm). Their height does not exceed 100 μm. The proloculus is small, globular, with a diameter generally between 15–20 μm. The tubular chamber gradually increases in size. Lumens of the first volutions are generally 3–5 μm in height, while those in the last whorls reach up to 50 μm. About 2–3-μm diameter in the juvenile part, perforations attain 6 μm in the last whorls of adult forms, a dimension larger than the tubular chamber in the juvenile part. The apical angle varies from 140–175°.

Microfacies and paleoecology. Muddy microfacies (mudstone/wackestone) typical of a quiet, periodically restricted, shallow-water lagoonal environment (Rigaud, 2012).

Fossil association. Abundant gastropods, ostracods, microproblematica, common algae (e.g., dasycladaceans, codiaceans), bivalves, bryozoans, brachiopods, echinoderms, sponges, and corals.

Foraminiferal association. Wallowaconus oregonensis is found in association with representatives of the suborder Robertinina (e.g., *Cassianopapillaria*, *Praegubkinella*, *Schmidita*) and the suborder Involutinina (*Aulosina*, *Aulotortus*, *Frentzenella*, *Lamelliconus*, *Licispirella*, *Parvalamella*, *Trocholina*), as well as with indeterminate lagenids, polymorphinids, and lituolids.

Stratigraphic and geographic distribution. In Panthalassa, the species is only known from the late Carnian?–early/middle? Norian of the Martin Bridge Formation (Oregon, U.S.A.). In the Tethys, it occurs in the Norian–Rhaetian? of China.

Comparison and remarks. The species resembles *Coronipora austriaca* (Kristan) and *Coronipora etrusca* (Pirini), but differs by the presence of pores that are not limited to the vicinity of the suture and by the absence of erect lamellae. From *Lamelliconus semivacuus* (He and Yue), it differs only by the absence of interfingered lamellae on the spiral side.

Subfamily TROCHOLININAE Kristan-Tollmann, 1963, emend. herein

Type genus: *Trocholina* Paalzow, 1922

Emended description. The test is free, sublenticular to conical. Proloculus followed by a trochospirally enrolled, undivided tubular chamber. Laterally restricted, the laminar extensions of the tube wall (L2 lamellae) are either locally thickened, forming papillae at the test surface, or distorted. They are limited by a relatively complex canal system and form polygonal nodes at the test surface. Wall hyaline, fibrous aragonitic, and perforate. Primary aperture simple, terminal.

Composition. The subfamily includes the genera *Coscinoconus* Leupold *in* Leupold and Bigler, 1936; *Semiinvoluta* Kristan, 1957; *Trocholina* Paalzow, 1922; and the newly erected genera *Frentzenella* and *Papillaconus*.

Stratigraphic distribution. Middle?/Late Triassic–Late Cretaceous (Cenomanian).

Comparison and remarks. The present emendation places emphasis on the lamellae architecture and definitively excludes trochospiral involutinins without papillose lamellae from the Trocholininae.

Our work shows that the wall architecture of *Frentzenella* n. gen. and possibly of *Trocholina* Paalzow is characterized by a lamellae organization similar to that of the "*Aulotortus* model." Up to now, the lamellae arrangement of *Coscinoconus* Leupold, *Semiinvoluta* Kristan, and *Papillaconus* n. gen. has never been observed. However, the strong morphological similarities existing between *Trocholina* and *Coscinoconus* and between *Frentzenella* n. gen., *Semiinvoluta*, and *Papillaconus* n. gen. lead us to place them within the same subfamily. Papillae or polygonal nodes have been clearly observed in these five genera, allowing their unequivocal distinction from the Lamelliconinae.

Within the Involutinina, the Trocholininae differ from the Aulotortinae Zaninetti (planispiral forms) and the Parvalamellinae Rigaud and others, 2012 (glomospiroid forms), by the trochospiral mode of coiling. Additionally, they do not possess the internal tubular chamber structures (pillars or strengthenings) that are typical of the Triasininae Loeblich and Tappan.

Genus *Coscinoconus* Leupold *in* Leupold and Bigler, 1936, emend. herein

Type species: *Coscinoconus alpinus* Leupold *in* Leupold and Bigler, 1936

Figs. 4.3–4.11

Hottingerella Piller, 1983, p. 197 (type species = *Trocholina chouberti* Hottinger, 1976, p. 819, pl. I, figs. 1–15).

Andersenolina Neagu, 1994, p. 126 (type species = *Andersenolina bancilai* Neagu, 1994, p. 120, 124, 128, 129, 140, pl. 2, pl. 4, figs. 23, 24, pl. 6, fig. 23, pl. 12, figs. 6, 7, text-fig. 2).

Septatrocholina BouDagher-Fadel and Banner *in* BouDagher, 2008, p. 161 (type species = *Septatrocholina banneri* BouDagher-Fadel, 2008, p. 162, pl. 4.2, figs. 1–4).

Diagnosis. A Trocholinidae showing reduced lamellae on the spiral side and, on the umbilical side, well-developed lamellae endowed with a relatively complex canal system.

Emended description. The test is free, low to high conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber, possibly slightly constricted by endoskeletal structures or wall thickenings (rudimentary septa sensu BouDagher-Fadel, 2008). Reduced on the spiral side, the lateral laminar extensions of the tube wall (L2 lamellae) are, on the umbilical side, well-developed and laterally distorted, forming polygonal nodes at the umbilical mass surface. A relatively complex canal system riddles the umbilical mass (see Hottinger, 1976, pl. 1, figs. 1, 2). This canal system is interspersed with the laminar deposits.

Mainly developed from the sutural pores and limiting the L2 lamellae, it forms levels of polygonal networks. Each level is connected by large canals, generally straight, perpendicularly crossing the successive lamellae (Figs. 4.4, 4.8, 4.10). Wall hyaline, fibrous aragonitic, and perforate. The primary aperture, sometimes described as the open end of the tubular chamber (e.g., Henson, 1947; Emberger, 1955), sometimes not observed (e.g., Leupold and Bigler, 1936; Hottinger, 1976), would be, according to Neagu (1994), "substituted" by umbilical pores.

Stratigraphic and geographic distribution. Bathonian–Cenomanian of Tethys.

Included species. Coscinoconus alpinus Leupold *in* Leupold and Bigler, 1936, Kimmeridgian–Valanginian; *C. altispirus* (Henson, 1947) n. comb., late Albian–early Cenomanian; *C. aptiensis* (Iovcheva, 1962) n. comb., Barremian–Aptian; *C. bancilai* (Neagu, 1994) n. comb., Berriasian–Valanginian; *C. banneri* (BouDagher-Fadel and Banner *in* BouDagher, 2008) n. comb., Callovian–Oxfordian; *C. burgeri* (Emberger, 1955) n. comb., Valanginian; *C. burlini* (Gorbatchik, 1959) n. comb., Valanginian–Barremian; *C. campanellus* (Arnaud-Vanneau and others, 1988) n. comb., Berriasian–Valanginian; *C. cherchiae* (Arnaud-Vanneau and others, 1988) n. comb., Berriasian–Valanginian; *C. chiocchinii* (Mancinelli and Coccia, 1999) n. comb., late Berriasian–Valanginian; *C. chouberti* (Hottinger, 1976) n. comb., late Berriasian–Valanginian; *C. delphinensis* (Arnaud-Vanneau and others, 1988) n. comb., Berriasian–Valanginian; *C. elongatus* Leupold *in* Leupold and Bigler, 1936, Tithonian–Valanginian; *C. floridanus* (Cushman and Applin, 1947) n. comb., late Early Cretaceous; *C. giganteus* (Gorbatchik and Mantsurova *in* Mantsurova and Gorbatchik, 1982) n. comb., Berriasian; *C. limognensis* (Pelissié and Peybernès, 1982) nom. nov., n. comb., Bathonian–Oxfordian; *C. histeri* (Neagu, 1994) n. comb., Berriasian–Valanginian; *C. intermedius* (Henson, 1947) n. comb., Albian–Cenomanian; *C. lenticularis* (Henson, 1947) n. comb., late Albian–early Cenomanian; *C. molestus* (Gorbatchik, 1959) n. comb., Berriasian–Barremian; *C. palastiniensis* (Henson, 1947) n. comb., Bathonian–Callovian; *C. perconigi* (Neagu, 1994) n. comb., Berriasian–Valanginian; *C. sagittarius* (Arnaud-Vanneau and others, 1988) n. comb,. late Berriasian–Barremian; and *C. vasserodi* (Guillaume, 1963) n. comb., Valanginian–Hauterivian.

Comparison and remarks. Our emendation mainly concerns the innermost structure of the wall and test architecture. All species here included in the genus *Coscinoconus* possess a relatively complex canal system. In isolated specimens, the canal system is revealed by the presence of polygonal nodes at the test surface (Figs. 4.3, 4.11) that indicate the location of the youngest canal system. These nodes are particularly well-preserved in forms illustrated by Magniez and Sigal (1985, pl. 1, figs. 12, 14, 17, pl. 2, fig. 3). In sectioned specimens, the canal system, generally obliterated, is sometimes preserved due to early micritic cementation or infiltration of fine sediments into the porous network (prior to test recrystallization). In section, it appears arranged in levels (Hottinger, 1976) such as only one complete canal network level is formed per whorl, delimiting the L2 lamellae. Additional network levels may be observed but their lateral extension within the umbilical mass appears limited.

No canal systems are apparent in the poorly illustrated specimens of *Septatrocholina* BouDagher-Fadel and Banner (BouDagher-Fadel, 2008, pl. 4.2, figs. 1–4). However, the endoskeletal structures, interpreted as rudimentary septa by BouDagher-Fadel (2008), are also observable in *Coscinoconus chouberti* (Hottinger) n. comb., a form known to possess a canal system [see reillustration of Hottinger (1976) specimens in Figs. 4.7, 4.10], most probably indicating that these two forms are related. Similar structures, limited to the tube edge, are rare in the involutinins but also observed in the involutininid genus *Aulosina* Rigaud, Martini and Rettori (Rigaud and others, 2013).

Coscinoconus displays a high morphological variability. As in other Trocholinidae, its apical angle varies considerably. The spiral side is generally devoid of ornamentation (or eroded), but some forms display striae (e.g., *C. altispirus* and *C. bancilai*) or a complex reticulate network, almost hiding the whorls on the spiral side (*C. lenticularis*). Moreover, it is still unclear if all forms with a complex canal system possess a primary aperture (see Neagu, 1994). For now, these morphologic issues cannot be resolved because of the poor preservation (recrystallization and erosion) of studied specimens. Further studies are needed in order to comprehend the complexity of the taxon.

For reasons explained by Arnaud-Vanneau and others (1988), trochospirally coiled *Coscinoconus lenticularis* cannot be included in the genus *Hensonina* Moullade and Peybernès, 1974, which is a junior synonym of *Involutina* (see Schlagintweit and Piller, 1990).

Since the species *Trocholina intermedia* Frentzen and *Coscinoconus intermedius* (Henson) (= *T. arabica* nom. nov. in Arnaud-Vanneau and others, 1988) are no longer considered members of the same genus, the species name *C. intermedius* is here reinstituted.

Coscinoconus limognensis nom. nov. for *Trocholina gigantea* Pelissié and Peybernès, 1982

Remarks. Pelissié and Peybernès (1982) described the new foraminifera *Trocholina gigantea*, whose name was preoccupied by *T. gigantea* Gorbatchik and Mantsurova (*in* Mantsurova and Gorbatchik, 1982), published earlier in the same year. The two species, undoubtedly distinct, are here classified with *Coscinoconus*. Therefore, *C. giganteus* (Pelissié and Peybernès) must be considered a junior homonym, and is renamed *C. limognensis* for the region where the species was discovered (Limogne, France).

Genus *Semiinvoluta* Kristan, 1957, emend. herein

Type species: *Semiinvoluta clari* Kristan, 1957

Fig. 5.14

Diagnosis. A Trocholinidae with shortened lamellae on the spiral side and well-developed, papillose lamellae on the umbilical side.

Emended description. The test is free, sublenticular to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. Shortened on the spiral side, the lateral laminar extensions of the tube wall (L2 lamellae) are well-developed on the umbilical side, at least in the juvenile part, locally thickened, forming papillae at the test surface. Wall hyaline, fibrous aragonitic, and perforate. Aperture, not observed, most likely simple, terminal.

Stratigraphic and geographic distribution. This monospecific genus occurs in Rhaetian–Early Jurassic deposits of the Tethys. Species possibly belonging to the genus, however, have been illustrated up to the Oxfordian (Mantsurova and Gorbatchik, 1982, pl. I, figs. 3, 4, 6).

Included species. Semiinvoluta clari Kristan, 1957, Rhaetian–Early Jurassic, including its junior synonym *"Coronipora" serraforma* Senowbari-Daryan and others, 2010.

Comparison and remarks. Up to now, the lamellar structure of *Semiinvoluta* was unknown and is clarified in the present emendation. The genus is the only Trocholinidae possessing shortened lamellae on the spiral side and papillose lamellae on the umbilical side. Illustrations of the genus are rather rare in the literature. Sections of *Semiinvoluta* have been recently illustrated by Senowbari-Daryan and others (2010, figs. 14n–r) under the name *Coronipora serraforma*.

A remarkably well-preserved *Semiinvoluta* has been found in the Adnet material, Austria (Fig. 5.14). It clearly displays shortened lamellae on the spiral side and papillose lamellae in the umbilical region.

Genus *Trocholina* Paalzow, 1922; emend. Paalzow, 1932; emend. Henson, 1947; emend. Mjatliuk, 1953; emend. Gorbatchik, 1959; emend. Dessauvagie, 1968; emend. Koehn-Zaninetti, 1969; emend. Piller, 1978; emend. Neagu, 1995; emend. herein

Type species: *Involutina conica* Schlumberger, 1898
Figs. 4.1, 4.2

Ornatoconus di Bari, 1998, p. 26 (type species = *Ornatoconus francorussoi* di Bari, 1998, p. 28, pl. 1, fig. 1).

Diagnosis. A Trocholinidae without canal systems, showing reduced lamellae on the spiral side and papillose lamellae on the umbilical side.

Emended description. The test is free, low to high conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. Reduced on the spiral side, the lateral laminar extensions of the tube wall (L2 lamellae) are well-developed on the umbilical side, at least in the juvenile part, locally thickened, forming papillae at the test surface (Fig. 4.2). Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Stratigraphic and geographic distribution. The genus occurs in late Ladinian–Jurassic deposits of the Tethyan domain. Further studies are needed to clarify its potential occurrence in Early Cretaceous rocks.

Included species. Trocholina acuta Oberhauser, 1964, Norian–Rhaetian; *T. blaui* Senowbari-Daryan and others, 2010, Rhaetian–early Early Jurassic; *T. conica* (Schlumberger 1898) n. comb., Bathonian–Kimmeridgian; *T. conosimilis* Subbotina and others, 1960, Callovian–Oxfordian; *T. cordevolica* Oberhauser, 1964, late Ladinian–Carnian; *T. eduardi* Tollmann and Kristan-Tollmann, 1970, Rhaetian; *T. francorussoi* (di Bari, 1998) n. comb., Carnian; *T. gracilis* Blau, 1987b, Rhaetian–Early Jurassic; *T. intermedia* Frentzen, 1941, Early Jurassic; *T. klaipedica* Grigelis, 1985, Callovian; ?*T. krzyżanowiensis* Stzejn, 1957, late Valanginian; *T. nidiformis* (Brückmann, 1904) n. comb., Jurassic; ?*T. nodulosa* (Seibold and Seibold, 1960) n. comb., early Late Jurassic [form considered to belong to *Hungarillina* by Blau and Wernli (1999)], *T. piriniae* Blau, 1987a, Early Jurassic; *T. plagiostoma* Tollmann and Kristan-Tollmann, 1970, Rhaetian; *T. remesiana* Chapman, 1900, Tithonian; ?*T. silvai* Petri, 1962, late Albian; *T. solecensis* Bielecka and Pożaryski, 1954, Kimmeridgian; *T transversarii* Paalzow, 1932, early Late Jurassic; *T. turris* Frentzen, 1941, Early Jurassic; *T. ultraspirata* Blau, 1987a, Early Jurassic; and *T. umbo* Frentzen, 1941, Early Jurassic.

Comparison and remarks. The diagnosis of the genus *Trocholina* has been emended by several authors. Our emendation mostly differs from previous emendations in the description of the spiral-side structure, formed by reduced lamellae. The genus *Trocholina* only differs from *Semiinvoluta* in the length of its spiral-side lamellae, which is reduced in *Trocholina*. It is partially homeomorphic with *Trocholinopsis* Piller, 1983, from which it differs in a more rounded tubular-chamber section and in the position of its spiral-side perforations that are not limited to the suture area. In addition, according to Piller (1983), *Trocholinopsis* does not possess lamellae on its spiral side, whereas *Trocholina* shows reduced lamellae. Furthermore, only one L2 lamella would be added per whorl in *Trocholinopsis* (Piller, 1983). These two characteristics compel us to provisionally exclude *Trocholinopsis* from the Trocholinidae.

Interfingered lamellae have not been clearly seen in *Trocholina*, because papillose lamellae show nodosities in several directions, rendering difficult such observation. However, our work shows that lamellae appear frequently interrupted in the middle part of the umbilical region. The recurrence of this pattern favors the "*Aulotortus* model" and contradicts the "*Trocholina* model" proposed by Piller (1978). Moreover, the latter model is based on specimens possessing a thick spiral side (with well-developed lamellae) that must be referred to *Frentzenella* n. gen., which also possesses the lamellae arrangement characteristic of the *Aulotortus* model (see below).

The differences between *Trocholina* and *Ornatoconus* are limited to the dimensions of the papillae and perforations. We consider that these two criteria are of specific value only and herein synonymize the genera.

The genera *Babelispirillina* Ruggieri and Giunta, 1965, and *Cylindrotrocholina* Loeblich and Tappan, 1986, although close to *Trocholina*, cannot yet be considered synonymous because their wall composition and lamellae organization are still unknown. Similarly we do not consider *Ichnusella* Dieni and Massari, 1966, and *Bancilina* Neagu, 1995, to be synonymous with *Trocholina*. According to Dieni and Massari (1966), *Ichnusella* possesses a monocrystalline tube, characteristic of the Spirillinida. Neagu (1995) did not give any information on the wall composition of *Bancilina*, but the fissured umbilical mass observed in thin section resembles that of *Neotrocholina*. If *Bancilina* is aragonitic, however, it would only differ from *Trocholina* by the shape of its tubular chamber, a significantly variable feature and only of specific value. Further studies of the wall composition of these genera are needed to understand taxonomic relationships.

Genus *Frentzenella* n. gen.

Type species: *Frentzenella frentzeni* n. gen., n. sp.
Figs. 5.3–5.13

Derivatio nominis. The name of this genus is dedicated to Dr. Kurt Frentzen for his valuable work on Early Jurassic foraminifers.

Diagnosis. A Trocholinidae with well-developed lamellae on both sides of the tubular chamber and papillose lamellae on the umbilical side only.

Description. The test is free, sublenticular to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. The well-developed lateral laminar extensions of the tube wall (L2 lamellae) are interfingered on both sides of the tubular chamber, at least in the juvenile part, building an apical thickening and an umbilical mass. Lamellae on the umbilical side are locally thickened, forming papillae at the test surface. Wall hyaline, fibrous aragonitic, and perforate. Aperture simple, terminal.

Stratigraphic and geographic distribution. Norian–Cenomanian of the Tethys; Late Triassic of Panthalassa.

Included species. Frentzenella belorussica (Mityanina, 1957) n. comb., Callovian–Tithonian; *F. crassa* (Kristan, 1957) n. comb., Rhaetian; *F. frentzeni* n. gen., n. sp., late Carnian?–early/middle? Norian; *F. granosa* (Frentzen, 1941) n. comb., Norian–Middle Jurassic; *F. involuta* (Mantsurova *in* Mantsurova and Gorbatchik, 1982) n. comb., Tithonian–Valanginian; *F. laevis* (Kristan, 1957) n. comb., Norian–Rhaetian; *F. odukpaniensis* (Dessauvagie, 1968) n. comb., Berriasian–Cenomanian; and *F. perforata* n. gen., n. sp., Early Jurassic.

Comparison and remarks. Frentzenella is the only Trocholinidae without canal systems but with well-developed, straight lamellae on the spiral side and papillose lamellae on the umbilical side.

Remarkably well-preserved specimens of *Frentzenella* from Adnet and the BMQ clearly show interfingering lamellae on both sides of the test (Fig. 5.9; characteristic of the "*Aulotortus* model"). As previously mentioned, this observation contrasts with Piller's (1978) model that most probably was based on altered specimens or inadequately oriented sections. Looking in detail at his illustrations, it appears that the spiral-side lamellae of some specimens are interfingered (Piller, 1978, pl. 17, fig. 2, pl. 18). In specimens known to show an "*Aulotortus* model" (e.g., *Aulotortus*, *Coronipora*), diagenesis often obliterates the lamellae, giving the false impression that only one L2 lamella is formed per whorl and, according to the section, lamellae may not appear interfingered (see Piller, 1983, fig. 4).

The genus *Neotrocholina*, also found up to the Cenomanian, may be confused with *Frentzenella*. *Neotrocholina*, however, clearly shows a calcitic, hyaline-radial wall, and the pillars forming the umbilical mass are more structured, well-defined, and often delimited by cracked fissures. Furthermore, the two genera never show the same preservation in the same material.

The calcitic, double-layered-walled, Paleozoic genus *Monotaxinoides* Brazhnikova and Yartseva, 1956, shows strong morphological similarities with *Frentzenella*, but is unrelated.

Specimens of *Frentzenella* possessing a thick apical buildup have been erroneously assigned to *Trocholina umbo* Frentzen in the literature. All whorls of that species are visible on the spiral side in isolated specimens (Frentzen, 1941), indicating that the species does not possess an apical thickening, as is true for other *Trocholina*.

Frentzenella frentzeni n. gen., n. sp.

Figs. 5.5–5.9

Semiinvoluta clari Kristan, 1957. Senowbari-Daryan and others, 2010, p. 276, figs.17a, b, u.

Holotype. No. 2011-1-48, Fig. 5.5.

Derivatio nominis. As for the genus.

Material. The description of this genus is based on hundreds of specimens from rock thin sections stored in the Museum of Natural History, Geneva, Switzerland (collection MHNG 2011-1).

Type locality. Black Marble Quarry, Wallowa Mountains, Oregon, U.S.A.

Type level. Upper Triassic (upper? Carnian–lower/Middle? Norian) of the Martin Bridge Formation (Wallowa terrane, Oregon, U.S.A.; Rigaud, 2012).

Description. The test is free, lenticular to low conical, with a rounded periphery. It has a globular proloculus with a simple opening followed by a trochospirally enrolled, undivided tubular chamber. Low trochospiral throughout, with an obtuse apical angle, the coiling may be irregular (Fig. 5.8), but whorls never oscillate. Gradually enlarging throughout its 5–9 whorls, the tubular chamber appears oval to slightly kidney-shaped in section. Well-developed on both sides of the tubular chamber, at least in the juvenile part, the lateral laminar extensions of the tube wall (L2 lamellae) are interfingered, building an apical thickening and umbilical mass. Umbilical-side lamellae are locally thickened, forming rounded papillae at the test surface. Spiral-side lamellae are straight, sometimes uneven, possibly forming striae or bumps at the test surface. Wall hyaline, fibrous aragonitic, and perforate. Radially arranged perforations occur mostly at the tubular-chamber periphery in areas not covered by lamellae. Aperture simple, terminal.

Dimensions. Specimens from the BMQ reach up to 450 μm in diameter; their height does not exceed 180 μm. The proloculus is globular with a diameter ranging from 15–30 μm. The tubular chamber gradually increases in size, with lumens increasing initially from 5 μm in height up to 50 μm in the last whorls. Perforations, scarce, may attain 5-μm diameters in the last whorls. The apical angle is generally between 140–170°.

Microfacies and paleoecology. Muddy microfacies (mudstone/wackestone) typical of a quiet, periodically restricted, shallow-water lagoonal environment (Rigaud, 2012).

Fossil association. Abundant gastropods, ostracods, microproblematica, common algae (e.g., dasycladaceans, codiaceans), bivalves, bryozoans, brachiopods, echinoderms, sponges, and corals.

Foraminiferal association. The species is found with representatives of the suborder Robertinina (e.g., *Cassianopapillaria*, *Praegubkinella*, *Schmidita*) and the suborder Involutinina (*Aulosina*, *Aulotortus*, *Frentzenella*, *Lamellico-*

nus, *Parvalamella*, *Trocholina*, *Wallowaconus*), as well as with indeterminate lagenids, polymorphinids, and lituolids.

Stratigraphic and geographic distribution. In Panthalassa, the species is only known from the late Carnian?-early/middle? Norian of the Martin Bridge Formation (Wallowa terrane, Oregon, U.S.A.). In the Tethys, it occurs in Iran in rocks of probable Rhaetian age.

Comparison and remarks. The new species may be easily confused with *Semiinvoluta clari*. The lateral extension of the interfingering spiral-side lamellae in *Frentzenella frentzeni* is the only consistent criteria for separating them. Thus, non-centered transverse sections are inadequate to distinguish the two forms. In such sections, the papillae size and morphology (more prominent and rounded in *Frentzenella*) may help in their recognition.

By its obtuse apical angle and sublenticular morphology, *Frentzenella frentzeni* shows superficial homeomorphism with *Coscinoconus lenticularis* (Henson). The absence of reticulate ornamentation on the spiral side, the presence of rounded papillae on the umbilical side, and the absence of a complex canal system in *Frentzenella frentzeni* allow their distinction.

Frentzenella perforata n. gen., n. sp.
Figs. 5.10–5.13

Holotype. No. 75631-424a, Fig. 5.10.

Derivatio nominis. From the Latin "perforata." The new species is named for its distinctive, large perforations.

Material. Thin sections stored in the Museum of Natural History, Geneva, Switzerland (collection MHNG 75631).

Type locality. Schnöll Quarry, Adnet, northern Calcareous Alps, Austria.

Type level. The marmorea crust of the Schnöll Formation, uppermost Hettangian–lowermost Sinemurian.

Description. The test is free, sublenticular, with a rounded periphery. It has a globular proloculus with a simple opening, followed by a trochospirally enrolled, undivided tubular chamber. The coiling is low trochospiral throughout, with an obtuse apical angle. Gradually enlarging throughout its 3–6 whorls, the evolute tubular chamber appears oval to slightly kidney-shaped in section. Well-developed on both sides of the tubular chamber, the lateral laminar extensions of the tube wall (L2 lamellae) build an apical thickening and an umbilical mass. Umbilical-side lamellae are locally thickened, forming rounded papillae at the test surface. Spiral-side lamellae may show small undulations following the tubular chamber morphology, forming a slight spiral bulge at the test surface. Wall hyaline, fibrous aragonitic, and perforate. Large perforations, probably secondary apertures, possibly join together on the umbilical side (Fig. 5.10). They randomly riddle the papillose lamellae and the tubular-chamber periphery. Primary aperture, not observed, most likely simple, terminal.

Dimensions. Specimens reach up to 600 μm in diameter and 300 μm in height. The proloculus is globular with a mean diameter of 50–55 μm. The tubular chamber gradually increases in size. Lumens range from 10 μm in height initially to 50 μm in the last whorls. Perforations are scarce and may attain 10 μm in diameter. The apical angle is 155–175°.

Microfacies and paleoecology. The marmorea crust microfacies are described in detail in Böhm and others (1999, p. 165). Böhm (2003, p. 262) stated that the Schnöll Formation was deposited in "lower slope and basinal settings," but the diverse organisms and abundant oncoids indicate shallower environments.

Fossil association. Abundant echinoderms, ammonites, and foraminifers associated with gastropods, ostracods, bivalves, brachiopods, and *Globochaete alpina*. *Schizosphaerella* is rock-forming in some samples.

Foraminiferal association. The species occurs with representatives of the suborders Robertinina (?epistominids) and Involutinina (*Coronaserra*, *Coronipora*, *Frentzenella*, *Involutina*, *Kristantollmanna*, *Licispirella*, *Papillaconus*, *Semiinvoluta*, *Trocholina*) and with lagenids and miliolids. Involutinids dominate the association and the genus *Involutina* is the most common.

Stratigraphic and geographic distribution. Known only from the Early Jurassic of Austria.

Comparison and remarks. *Frentzenella perforata* mostly differs from *F. frentzeni* by the presence of large canals that are randomly distributed in the umbilical mass. Although the spiral side of *F. perforata* may show slightly undulated lamellae in section, the test surface does not show any papillae. Actually, the lamellae follow the test morphology, which is characterized by depressed sutures. This morphological feature distinguishes the species from forms assigned to *Papillaconus* n. gen. (see below).

By its lenticular geometry and very low trochospiral coiling, *F. perforata* shows similarities with *Involutina liassica* (Jones), but unlike that species the spiral side is neither perforated nor covered by papillae.

Genus *Papillaconus* n. gen.
Type species: *Trocholina verrucosa* Kristan, 1957
Fig. 5.15

Derivatio nominis. From the Latin "papilla" and "conus" (= cone). The new genus is named for the presence of papillae that completely cover its conical test.

Diagnosis. A Trocholinidae with well-developed, papillose lamellae on both sides of the tubular chamber.

Description. The test is free, sublenticular to conical. Globular proloculus followed by a trochospirally enrolled, undivided tubular chamber. The lateral laminar extensions of the tube wall (L2 lamellae) are well-developed, at least in the juvenile part and on both sides of the tubular chamber, and locally thickened, forming papillae at the test surface. Wall hyaline, fibrous aragonitic, and perforate. Aperture, not observed, most likely simple, terminal.

Stratigraphic and geographic distribution. Rhaetian–Early Jurassic of the Tethys.

Included species. *Papillaconus kristani* (Tollmann and Kristan-Tollmann, 1970) n. gen., nom. nov., Rhaetian–Early Jurassic; ?*P. mitrus* (Tollmann and Kristan-Tollmann, 1970) n. comb., Rhaetian; and *P. verrucosus* (Kristan, 1957) n. comb., Rhaetian.

Comparison and remarks. The new genus differs from *Frentzenella* n. gen. in possessing papillose lamellae on the spiral side.

Papillaconus mitrus (Tollmann and Kristan-Tollmann) shows a papillose spiral side, suggesting the presence of papillose lamellae covering the test. In spite of that and according to Tollmann and Kristan-Tollmann (1970), whorls would be visible on the spiral side of isolated specimens. As illustrated by Blau and Grün (1997, fig. 5K), the lamellae undulation can follow the test morphology in forms possessing an apical thickening, rendering whorls indirectly distinguishable. Presuming that *P. mitrus* shows a spiral side covered by papillose lamellae, which follow the depressed morphology of the sutures when added, we have temporarily placed it in the new genus. However, the presence of well-developed spiral-side lamellae in this species has not yet been seen. Further investigations are needed to confirm its taxonomic position.

Papillaconus kristani. nom. nov. for *Semiinvoluta verrucosa* Tollmann and Kristan-Tollmann, 1970

Remarks. Kristan (1957) erected the species *Trocholina verrucosa*. Later, Tollmann and Kristan-Tollmann (1970) described *Semiinvoluta verrucosa*. As we herein place both within *Papillaconus,* the latter species becomes a junior synonym of the former. It is renamed *P. kristani* in honor of Edith Kristan-Tollmann.

TROCHOLINIDAE MORPHOLOGY AND KEYS FOR IDENTIFICATION

The tests of Mesozoic Trocholinidae are only exceptionally found in their original, unaltered state. Sometimes eroded, generally micritized or recrystallized, and often damaged by pressure-dissolution processes, lamellae and perforations are ordinarily obliterated. The taxonomy of Trocholinidae is thus based on rarely or barely visible criteria. Fortunately, some morphological features can help unravel the lamellae and perforations arrangement.

In well-preserved specimens, perforations and canal systems form empty tubes that extend from the tubular-chamber lumen to the test periphery across the laminar deposits. The L2 lamellae, formed by the stacking of L1 lamellae, extend from the tubular-chamber wall up to an end point, the location of which depends on the L2 lamellae length and orientation. These lamellae may be 1) straight and uniform (Fig. 5.1) as in *Lamelliconus*, 2) straight with surface unevenness (Figs. 6.2, 6.10, 6.11, 6.15) as in *Coronipora*, 3) locally thickened (Fig. 4.1; Figs. 5.3–5.15) as in *Trocholina*, *Semiinvoluta*, *Frentzenella* n. gen., and *Papillaconus* n. gen., or 4) limited by a relatively complex canal system (Figs. 4.4, 4.8, 4.10) as in *Coscinoconus* (see Fig. 7 for nomenclature). When straight and uniform, the lamellae do not form ornamentation and the outer test surface appears smooth. When straight with surface unevenness, they may form thin striae or small bumps at the test surface. When locally thickened, the lamellae form rounded to elongated papillae, whereas they form polygonal nodes when limited by a complex canal system. Both straight-uniform and slightly uneven lamellae may occur in *Wallowaconus* n. gen. Specimens of *Trocholina* and *Frentzenella* n. gen. from the Late Triassic and Early Jurassic show rounded papillae, but, those from the Middle Jurassic and younger may show more elongated papillae.

With intense micritization or recrystallization of the test, lamellae and unfilled perforations are generally obliterated. If the test is not too eroded or affected by pressure-dissolution processes, its outline is generally preserved for examination of its exterior morphology (examples in Fig. 7).

In isolated specimens, striae, bumps, papillae, and polygonal nodes are clearly visible. Whorls are apparent on the spiral side in forms possessing reduced lamellae (limited to the suture area). Though covered by a thin laminar deposit, sutures generally appear slightly depressed between the faintly prominent whorls (Fig. 6.1). The wall of the lectotype of *Trocholina conica* (Fig. 4.1), however, is partially eroded and clearly thinned on its spiral side, hampering observation of the prominent whorls. In forms possessing shortened and well-developed lamellae, the tubular chamber and spiral sutures are not discernible from the exterior. In forms with thickened apices, the lamellae may undulate while following the test morphology such that whorls are indirectly visible in isolated specimens. If lamellae are shortened or only slightly interfingered, the apical thickening appears depressed (Fig. 4.12), but if lamellae are significantly interfingered, the apical thickening may form a bulge (Fig. 5.6). In forms possessing erect lamellae, spiral ridges or flanges follow the test suture, indirectly delimiting the successive whorls.

In section, the whole morphology must be extrapolated, because structural elements are only visible in two dimensions. In taxa without canal systems (e.g., *Frentzenella* n. gen., *Semiinvoluta*, and *Trocholina*), the papillae outline is wavy but may appear irregular, since papillae are randomly sectioned (Fig. 4.1; Figs. 5.3, 5.5–5.15). In taxa with simple or complex canal systems (*Piriniella*, *Coscinoconus*), the umbilical mass shows a toothed (Fig. 4.13) or crenellated periphery (Figs. 4.4, 4.8, 4.10), respectively, owing to the regularity of the canal systems riddling the wall. Perforations and canal systems are indirectly preserved thanks to the presence of micritic cements or fine sediments that have infiltrated their openings. Changes in wall thickness on the spiral side reflect differences in lamellae types. Specimens with reduced lamellae display a thicker wall in the last whorl, and forms possessing shortened lamellae have a thicker wall in median whorls, while those covered by well-developed lamellae show thickened apices (Fig. 7).

To summarize, Trocholinidae exhibit high variability in the lamellae layout and in the size and arrangement of the perforations and canal systems through the lamellae, and their test shape is mostly controlled by these traits. Because of the distinctiveness of these variations, forms can be identified, even if recrystallized. In order to facilitate generic determinations in thin section, specimens in different stages of preservation are illustrated in Figure 7, and an identification key is proposed in Figure 8.

EVOLUTIONARY TENDENCIES AND PHYLOGENY

During the Late Triassic and Early Jurassic, Trocholinidae evolved rapidly. Other radiations probably occurred later, but studies on Trocholinidae are so incomplete that the same precision cannot be found at each geological stage and in each paleogeographic domain. Papers dealing with Trocholinidae from the Middle Jurassic, for example, are

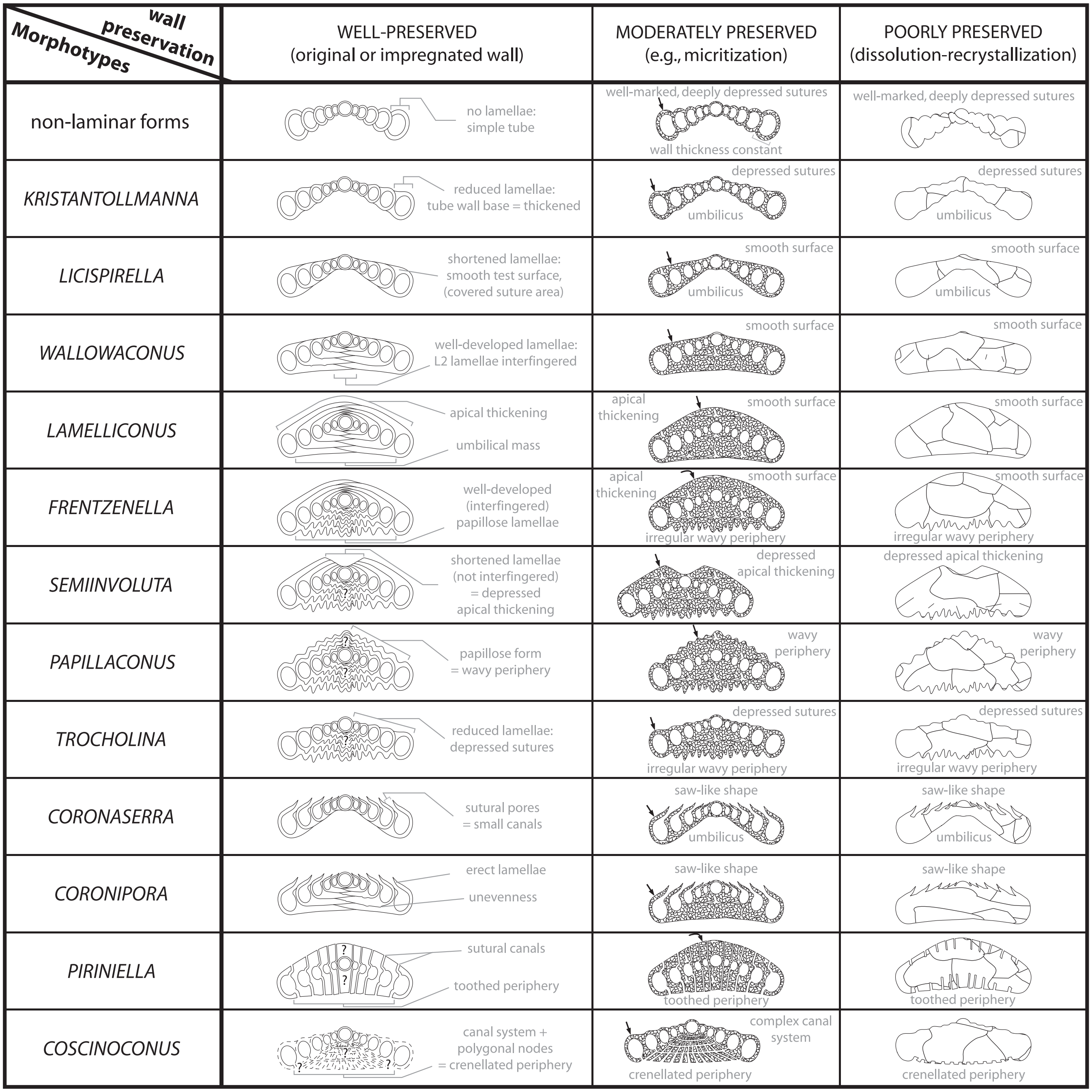

FIGURE 7. Reconstituted models of Trocholinidae (in axial section), from well-preserved to completely recrystallized specimens. To facilitate comparisons, all forms that are not eroded or affected by pressure-dissolution processes are represented with the same apical angle. The laminar extensions (L2 lamellae) are only figured in well-preserved forms (left column). In moderately preserved forms (i.e., with unpreserved lamellae but discernible tube lumens), arrows indicate the thickest part of the wall above the tubular chamber, allowing the distinction between reduced, shortened, and well-developed laminar extensions (see text). The preservation of the test of poorly preserved forms is limited to their outline.

few and only based on Tethyan material. Our knowledge of the stratigraphic range and diversity of each Trocholinidae genera will surely improve with works to come. The present study of only one American terrane (the Wallowa terrane), for example, has underlined the high diversity of the Trocholinidae in part of the Panthalassan Province during the Late Triassic. Some forms are most likely endemic and represent missing links for the lineage. Investigations in other areas of the Panthalassan domain should provide other missing links, which are essential for a deeper understanding of the group.

During their evolution, Trocholinidae showed a gradual shortening, thinning, or deformation of their laminar extensions (L2 lamellae) on one or both sides of the test. The perforations, first limited to the spiral side and tubular-chamber periphery, progressively appeared in the umbilical mass. Their size increased stepwise through time, possibly developing canals, which became more and more structur-

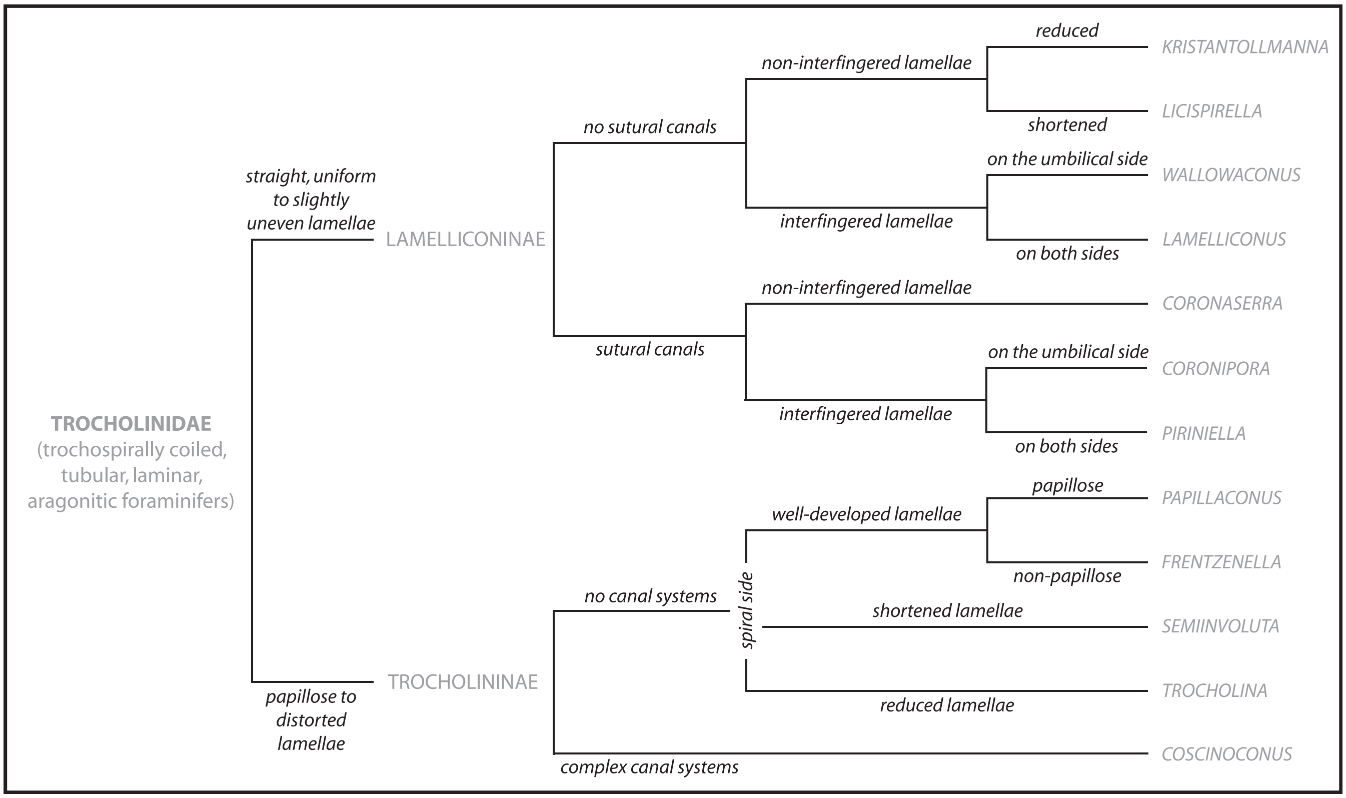

FIGURE 8. Identification key for the Trocholinidae (see the section on systematics for details).

ally complicated. Rarely tackled, the Trocholinidae phylogeny can be developed to a very advanced level. The new classification herein proposed allows a detailed subdivision of the Trocholinidae phylogeny. If the acquisition of a canal system or lamellae deformation is considered as a gain and progressive lamellae shortening as a loss, it is now possible to erect a phyletic tree in which only one morphological character is gained or lost at each evolutionary step (Fig. 9). The above mentioned evolutionary acquisitions, the frameworks of the phylogeny, are recognizable from lineage to lineage. However, to resolve phylogenetic links at a higher resolution, we have also studied differences observed at the specific level. Morphological changes from species to species are more subtle. With time, ornamentation became more and more complex, and the size and quantity of perforations slightly increased, while the laminar extensions were progressively shortened during ontogeny. In the Trocholinidae, the juvenile part of a specimen gives information about the closest ancestor, while the adult stage shows the morphological patterns of the descendant to come. These observations were used for improvements of the phyletic key shown in Figure 9.

As illustrated in Figure 9, the Trocholinidae showed a rapid radiation during the Late Triassic and seem to have been only slightly affected by the Triassic-Jurassic extinction event. Nearly all morphotypes appeared during the Carnian–Norian. The genus *Lamelliconus* is regarded as the common ancestor of all trochospirally coiled Involutinina, and believed to be phylogenetically linked to the genus *Aulotortus* (Oberhauser, 1964; Koehn-Zaninetti, 1969). Our phyletic tree is mostly supported by the recognition of intermediary forms. For instance, the occurrence of specimens showing a gradual increase of their lamellae undulation corroborates the direct phyletic link between *Lamelliconus*, *Frentzenella* n. gen., and *Papillaconus* n. gen. (Figs. 5.1–5.3, 5.10, 5.15).

Although morphologically consistent, our phyletic tree is deficient in that the *Lamelliconus–Frentzenella–Semiinvoluta–Trocholina–Coscinoconus* lineage poses a stratigraphic problem. We surely observe the gradual stepwise acquisition of unique morphologic features (Fig. 9). However, up to now, *Trocholina* has been found prior to *Semiinvoluta* in the fossil record. As the different trocholinid morphotypes show the same kind of evolutionary trends (lamellae shortening, thinning, or deformation), it is impossible to exclude parallel evolution. Therefore, we propose the alternative phyletic hypothesis that representatives of the genus *Trocholina* possibly descended from two different groups (Fig. 9: dashed lines). During the late Ladinian–Carnian, high conical *Trocholina* (*T. cordevolica* and *T. francorussoi*), morphologically close to ?*Lamelliconus multispirus*, arose from the *Lamelliconus* lineage, while at the end of the Triassic, low conical forms (e.g., *T. plagiostoma*), morphologically close to *Frentzenella frentzeni* n. gen., n. sp. and *Semiinvoluta clari*, appeared. The study of the lamellae architecture of ?*Lamelliconus multispirus* and ?*L. procerus* is most probably the key to better constrain the beginning of the Trocholinidae phylogeny.

CONCLUSIONS AND PERSPECTIVES

Due to the poor preservation of their original aragonitic test, trochospirally coiled Involutinina have been disregard-

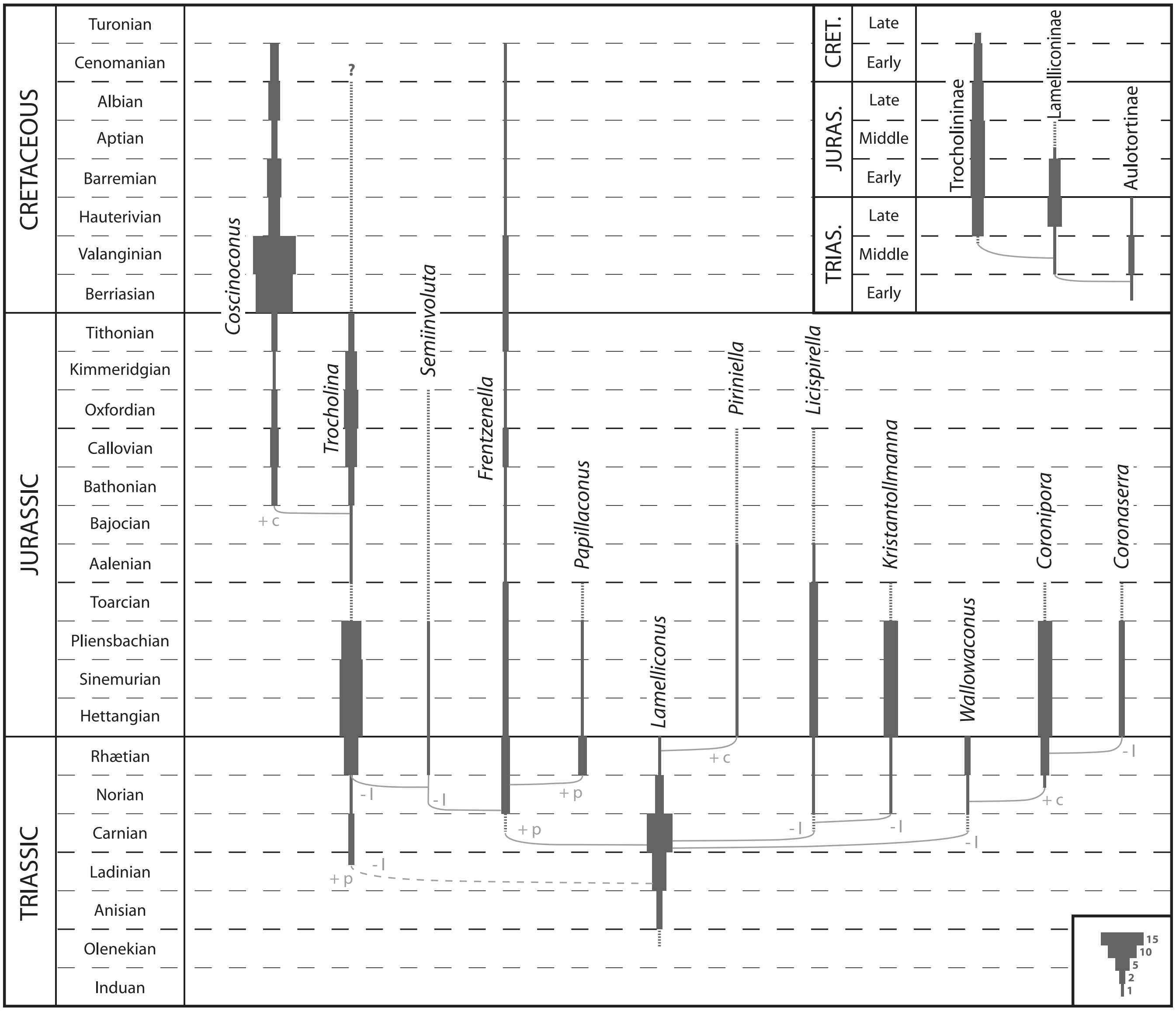

FIGURE 9. Phyletic tree (in light gray) and stratigraphic ranges (in dark gray) of the Trocholinidae. Line width indicates the specific diversity for the different genera (main figure) and the generic diversity for the different subfamilies (top-right figure). The number of species or genera for a specific line width is shown in the lower right corner. Dashed lines correspond to an uncertain link (in gray) or stratigraphic range (in black). + = gain, − = loss, p = papillae, c = canals, l = lamellae lateral extension.

ed. New evidence of their primary structure presented in this paper have allowed us to reconstruct their phylogeny. The Trocholinidae show a gradual evolution over time, and all morphotypes were derived from a common *Lamelliconus* ancestor. Highly diversified, each species presents a characteristic shape, identifiable even in the case of intense recrystallization.

As generic and suprageneric criteria are now well-established for distinguishing the Trocholinidae, it is time to better constrain their stratigraphic, paleogeographic, and paleoenvironmental distribution as well as to initiate the study of their functional morphology. Through their evolution, the Trocholinidae clearly displayed a shortening or deformation of their laminar extensions. Concurrently, perforations increased in size and canal systems, probable secondary apertures, were developed. These evolutionary tendencies were, without doubt, driven by their ecological preferences.

ACKNOWLEDGMENTS

The present report is part of an international collaboration aimed at comparing the Wallowa terrane with other regions of the Tethys and Panthalassa (research funded by the National Swiss Science Foundation grants 200021-113816 and 200020-124402 to R.M. and an Augustin Lombard grant from the SPHN Society of Geneva to S.R.).

The authors wish to thank Roland Wernli and Louisette Zaninetti (University of Geneva) for their constructive comments and suggestions. Michael Knappertsbusch (Natural History Museum of Basel), Annachiara Bartolini (MNHN, Paris), and Jolanta Smoleń and Jolanta Iwańczuk

(Polish Geological Institute, Warsaw) are warmly thanked for their welcome in the frame of this study. Thanks are also due to reviewers Valery J. Vuks (A. P. Karpinsky Russian Geological Research Institute) and Demir Altiner (Middle East Technical University) for their critical comments.

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Received 26 February 2012
Accepted 6 June 2013