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A new genus of Norian involutinid foraminifers: Its morphological, biostratigraphic, and evolutionary significance

SYLVAIN RIGAUD, ROSSANA MARTINI, and ROBERTO RETTORI

The Late Triassic was a time of pronounced radiation in several groups of foraminifers. The rapid evolutionary processes in the Suborder Involutinina caused particularly high diversification of these aragonitic foraminifers, which became a key group for Upper Triassic biostratigraphy. Among them, *Triasina hantkeni* and *Triasina oberhauseri* are regarded as the most precise guide fossils. However, while these species are widely used, a poor documentation of the detailed test structure of *T. oberhauseri* has resulted in misidentifications. The exceptional preservation and abundance of *Triasina oberhauseri* in the Upper Triassic deposits of the Black Marble Quarry (Wallowa terrane, Oregon, USA) has allowed us to make the first detailed observations of its coiling, innermost structure and lamellae arrangement and to recognize morphological features that were either wrongly interpreted or not described in the original systematic definition of the species. In this paper, we demonstrate that the species possesses characteristics that hamper its assignment to *Triasina* and we propose a new genus, *Aulosina*, to accommodate this taxon. Placing emphasis on the accuracy of the morphological description, the diagnosis and the systematic definition of the species are here improved. The identification of innovative features in *Aulosina oberhauseri* (strengthenings, shortened lamellae) highlights new evolutionary trends for the lineage of Involutinina that have proved useful for the establishment of phylogenetic links between involutinid genera and for understanding the evolutive steps leading to the formation of inner-pillars in tubular foraminifers. The increasing complexity of Involutinina representatives at the end of the Triassic, notably marked by the appearance of internal structures in Triasininae, leads us to regard them as probable symbiont-bearing foraminifers.

Key words: Foraminifera, strengthening, shortened lamellae, symbiosis, Triassic, Wallowa terrane, Oregon, USA.

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Introduction

The original systematic description of the species *Triasina oberhauseri* is based on about twenty specimens in thin sections from upper Norian deposits in Austria (Koehn-Zaninetti and Brönnimann 1968). In this type material, the strong recrystallisation of the foraminiferal test, peculiar to aragonitic foraminifers (see Zaninetti and Brönnimann 1971; Hohenegger and Piller 1975), hindered the examination of the species detailed structure. For example, in the sections illustrated by Koehn-Zaninetti and Brönnimann (1968) and Koehn-Zaninetti (1969), only the last whorls are partially preserved while the test periphery is generally missing. Furthermore, the illustrated holotype (Koehn-Zaninetti and Brönnimann 1968: pl. 1; Koehn-Zaninetti 1969: pls. 10: D, 11: C) and paratypes (Koehn-Zaninetti 1969: pls. 10: C, E, F,

11: A, B, D) show only oblique, non-centred to transverse sections in which the elements essential for a correct taxonomic assignment cannot be adequately distinguished. Through lack of information concerning its test construction, their new species has been assigned to the genus *Triasina* (type species *Triasina hantkeni* Majzon, 1954) because of internal structures observed within the tubular chamber that were interpreted as inner-pillars. However, unlike *T. hantkeni*, *T. oberhauseri* is characterized by a lenticular test and thickenings in the umbilical region, features then considered more typical for the Aulotortinae. Consequently, to accommodate this species, the genus *Triasina*, up to then monospecific, required an emendation (Koehn-Zaninetti 1969). According to Koehn-Zaninetti and Brönnimann (1968) and the following authors (Koehn-Zaninetti 1969; Piller 1978; Gaździcki 1983), the presence of characteristics shared with

the Aulotortinae and the Triasininae rendered *T. oberhauseri* equivalent to the hypothetical form conceived by Oberhauser (1964), representing the phylogenetic missing link between *Aulotortus* Weynschenk, 1956 (= *Permodiscus* according to Oberhauser 1964) and *T. hantkeni*.

Since its discovery, *Triasina oberhauseri*, mostly reported from Peritethys, has been encountered in deposits of Norian to early Rhaetian ages (Abate et al. 1984 with bibliography; Salaj 1987; Salaj et al. 1988; Kristan-Tollmann 1990; He and Wang 1990; Röhl et al. 1991; Zaninetti et al. 1992; Villeneuve et al. 1994; Salaj and M'Zoughi 1997; Vuks 2007). Despite its widespread distribution, the species has been observed only rarely and none of the specimens found improved its systematic description. As it has never been encountered together with the Rhaetian marker *T. hantkeni*, *T. oberhauseri* is regarded as a Norian guide fossil and used as such in Geological Time Scale charts (Hardenbol et al. 1998: chart 8). Its stratigraphic value is especially significant since the species is typical of subtropical Upper Triassic lagoonal deposits that lack good biostratigraphic markers.

Although the Norian marker *Triasina oberhauseri* is one of the most widely distributed foraminifers, our understanding of this form is still incomplete. As a result of the discovery of remarkably well-preserved specimens in Oregon and the restudy of the original material, it is now possible to clarify the systematic definition of *Triasina oberhauseri* and to discuss its position in the lineage of Involutinina.

Institutional abbreviations.—MHNG, Museum of Natural History, Geneva, Switzerland; NHMB, Museum of Natural History (Naturhistorisches Museum), Basel, Switzerland.

Studied locality, material, and methods

The studied outcrop (Fig. 1) is located at N45°22'24", W117°21'14" at an elevation of 1780 m on the northern forested slope of the Wallowa Mountains (Wallowa terrane, Oregon, USA). It consists of an isolated compartmented block, 200 metres wide and 60 metres high, comprising a pure micritic, distinctive black lagoonal limestone succession.

Referred to as the Black Marble Quarry, the upper Carnian?–lower–middle? Norian succession contains abundant calcified sponges, corals, spongiomorphs, molluscs, ostracods, echinoderms, brachiopods, common algae, bryozoans, and problematica (Stanley 1979; Stanley et al. 2008; Rigaud 2012). As indicated by large alatoform wallowaconchid bivalves and reef-type fossils organisms in their life positions, the beds are not inverted (Stanley 1979; Yancey and Stanley 1999). Extensive collections of limestone samples were made during three successive fieldtrips, from 2007 to 2009. Along the first 48 metres of the Black Marble Quarry, astonishingly well-preserved occurrences of *Triasina oberhauseri* have been discovered. By its abundance, this discovery contrasts with other reports of the species.

The associated outstanding foraminiferal assemblages found in the Black Marble Quarry will be documented separately.

Several hundred sections of *Triasina oberhauseri* have been observed among the 200 thin sections made from 130 samples collected at the Black Marble Quarry. On account of a high level of thermal metamorphism induced by the close intrusion of batholiths, limestone beds of the quarry are partially recrystallised. Fortunately, the blackest levels, strongly impregnated by hydrocarbons, seem to have been sheltered from the thermally induced recrystallisation. In most of these protected levels, specimens of *T. oberhauseri* are particularly abundant. Although their tests, originally aragonitic, have been completely recrystallised, an early hydrocarbon impregnation has allowed its indirect preservation (Fig. 2A). The resulting brownish trace underlines the test aspect prior to its whole recrystallisation (appearing grey in the wall of the specimens in the greyscaled Figs. 2–5). Thanks to the preservation of ghosts of the original wall, new features of *T. oberhauseri* have been recognized and help to better define its entire structure.

The revision of the systematic position and definition of *Triasina oberhauseri* is based upon the review of the species type material (Fig. 2B, D–G) and the recent discovery of well-preserved specimens (Figs. 2A, C, 3–5). We draw atten-
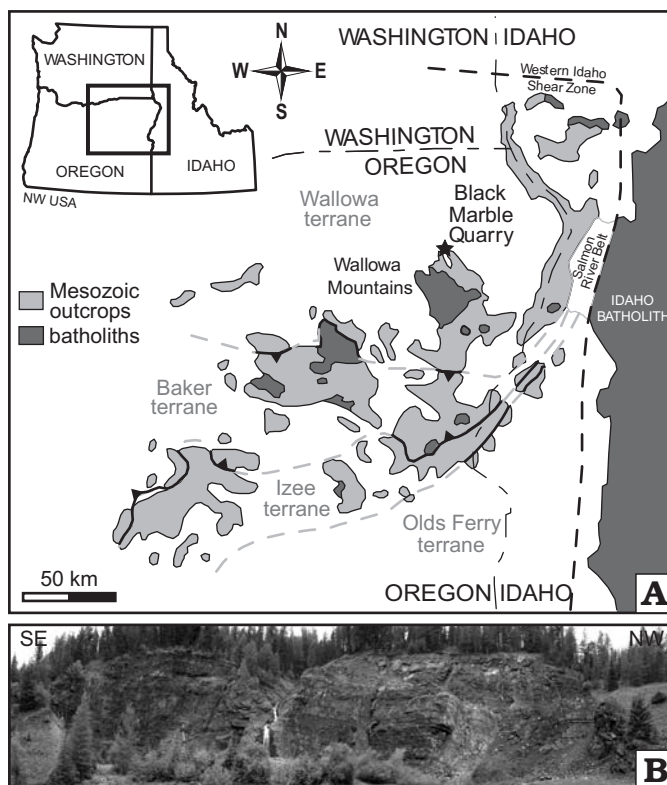

Fig. 1. Location of the Black Marble Quarry. **A**. Geological map of the Blue Mountains Province (North Western USA) modified from Dorsey and LaMaskin (2007). Mesozoic outcrops, mostly covered by the thick Columbia River Basalt, are limited. **B**. Panorama of the Black Marble Quarry. Note the dark colour of the limestone, impregnated by hydrocarbons. The quarry is about 60 metres high.

tion to newly discovered morphological features using numerous illustrations (Figs. 2–5). In view of the large amount of doubtfully identified specimens illustrated in the literature and in order to avoid considerable confusion regarding questionable forms, our synonymy is selective and only comprises forms that have been adequately documented. Fortunately, non-illustrated occurrences of *Aulosina oberhauseri* are rather uncommon (Abate et al. 1984 with bibliography; Salaj et al. 1988; Röhl et al. 1991; Vuks 2007).

In this paper, a new term for internal structures in tubular foraminifers is introduced. We here give its definition: *strengthening*, inner, lateral wall thickening of the tubular chamber sides. This term is purely architectural in opposition to "pillar" and do not necessarily imply a role of support for the test. The strengthenings differ from other internal structures (e.g., pseudosepta, internal pillars) in their lateral position.

Systematic palaeontology

Class Foraminifera d'Orbigny, 1826

Order Spirillinida Gorbatchik and Mantsurova, 1980

Suborder Involutinina Hohenegger and Piller, 1977

Superfamily Involutinoidea Bütschli, 1880

Family Involutinidae Bütschli, 1880

Subfamily Triasininae Loeblich and Tappan, 1986, here emended

Emended description.—The test is free, lenticular to globular, possibly biumbilicate. Proloculus followed by an enrolled tubular chamber strengthened by internal structures and lateral laminar extensions (lamellae sensu Piller 1978). Wall calcareous, perforate, aragonitic. Aperture simple, terminal (open end of the tubular chamber).

Genera included.—The subfamily includes the monospecific genus *Triasina* (type species *Triasina hantkeni* Majzon, 1954) and the here erected genus *Aulosina* (type species *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann, 1968).

Remarks.—The Triasininae differ from the Aulotortinae by the presence of internal structures in the tubular chamber.

Stratigraphic and geographic range.—Upper Triassic: Norian–Rhaetian of Tethys and upper Carnian?–Rhaetian of Panthalassa.

Genus *Aulosina* nov.

Type species: *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann, 1968; Norian Dachstein limestone of the Dolomites; Grünau, Almtal, Austria.

Species included: The type species and probably also "*Aulotortus*" *bulbus* Ho in Ho and Hu, 1977.

Etymology: *Aulo* from *Aulotortus* and *sina* from *Triasina*, the name contraction of the two genera that resemble it the most.

Material.—The description of this genus is based on about 250 sectioned specimens from rock thin sections stored at the MHNG (collection 2011-1).

Association.—Abundant foraminifers (e.g., Involutinidae, Duostominidae, Oberhauserellidae, Polymorphinidae), gastropods, bivalves (e.g., megalodontids, wallowaconchids), brachiopods, echinoderms, sponges, corals, spongiomorphs, ostracods, common algae (e.g., dasycladaceans, Codiacea), calcimicrobes, rare serpulids, bryozoans, and diverse problematica.

Description.—The test is free, lenticular to globular, possibly biumbilicate. Globular proloculus followed by a sigmoidally to planispirally enrolled undivided tubular chamber that gradually enlarged from whorl to whorl. Inner strengthenings of the tube wall laterally constrict the tubular chamber lumen. Lateral laminar extensions of the tube wall (lamellae sensu Piller 1978) are developed on both sides of the tubular chamber, possibly building umbilical masses. Wall calcareous, perforate, probably originally hyaline, fibrous and aragonitic. Aperture simple, terminal (open end of the tubular chamber).

Remarks.—The new genus differs from *Triasina* Majzon, 1954 by its lenticular shape, a different internal tube structure (no pillars), a non overlapping (evolute) tubular chamber and a wider umbilical mass.

Stratigraphic and geographic range.—Norian–lower Rhaetian of Tethys and upper Carnian?–Norian of Panthalassa.

Aulosina oberhauseri (Koehn-Zaninetti and Brönnimann, 1968)

Figs. 2–5.

?1966 *Triasina hantkeni* Majzon; Salaj et al. 1966: pl. 2: 4b.
?1967 *Arenovidalina pragsoides* (Oberhauser); Salaj et al. 1967: pl. 2: 2b.
1968 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Koehn-Zaninetti and Brönnimann 1968: fig. 1.
1969 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Koehn-Zaninetti and Brönnimann 1969: pls. 10: C–F, 11: A–D.
1970 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Brönnimann et al. 1970: pl. 2: 5.
?1970 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Brönnimann et al. 1970: pl. 2: 6.
?1970 *Involutina* sp.; Brönnimann et al. 1970: pl. 2: 7.
?1972 *Involutina?*; Pantić 1972: pl. 5: 7.
1974 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Efimova 1974: pl. 6: 16.
?1976 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Salaj 1976: pl. 1: 2.
1976 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Zaninetti 1976: pls. 14: 23, 15: 1a, b.
1978 *Aulotortus pokornyi* (Salaj); Piller 1978: pl. 11: 2, 3, 6–8.
?1979 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Gaździcki et al. 1979: pl. 1: 9.
1980 *Triasina hantkeni* Majzon; He 1980: pl. 73: 10.
1983 *Aulotortus* sp.; Gaździcki 1983: pl. 33: 14.
?1983 *Aulotortus* sp.; Gaździcki and Reid 1983: pl. 2: 1–3.
?1983 *Aulotortus gaschei* (Koehn-Zaninetti and Brönnimann); Gaździcki and Reid 1983: pl. 2: 4–7.
1983 *Aulotortus* cf. *sinuosus* Weynschenk; Gaździcki and Reid 1983: pl. 2: 8.

1983 *Aulotortus sinuosus* Weynschenk; Gaździcki and Reid 1983: pl. 2: 9.

?1983 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Gaździcki and Reid 1983: pl. 3: 1, 2.

?1983 ?*Triasina* sp.; Gaździcki and Reid 1983: pl. 3: 3,4.

?1983 *Glomospirella ammodiscoides* (Rauser-Chernousova); Salaj et al. 1983: pl. 1: 14, 15.

?1983 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Salaj et al. 1983: pl. 123: 4c.

?1983 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Salaj et al. 1983: pl. 126: 1.

1984 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Abate et al. 1984: fig. 1.

?1987 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Salaj 1987: pl. 2: 4, 5.

1989 *Aulotortus* sp.; Matarangas and Skourtis-Coroneou 1989: fig. 4.

?1990 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; He and Wang 1990: pl. 10: 12, 13.

1990 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; He and Wang 1990: pl. 10: 14, 15.

?1990 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Kristan-Tollmann 1990: pl. 8: 11.

1991 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Röhl et al. 1991: pl. 62: 3.

1992 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Zaninetti et al. 1992: pls. 1: 3, 4: 1.

?1992 *Aulotortus sinuosus pragsoïdes* (Oberhauser); Zaninetti et al. 1992: pl. 2: 2.

1993 *Pilamminella* gr. *gemerica–kuthani*; Peybernès et al. 1993: figs. 13–15.

1994 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann;Villeneuve et al. 1994: pl. 4: 1.

?1994 *Aulotortus* ex gr. *sinuosus* Weynschenk; Villeneuve et al. 1994: pl. 3: 1.

?1994 *Aulotortus* sp.; Villeneuve et al. 1994: pl. 4: 2.

?1997 *Triasina oberhauseri* Koehn-Zaninetti and Brönnimann; Salaj and M'Zoughi 1997: pl. 9: 2.

2007 *Triasina hantkeni* Majzon; Roniewicz et al. 2007: pl. 2: 4.

Holotype: NHMB-C27488, Koehn-Zaninetti and Brönnimann (1968); see Fig. 2B herein.

Type locality: Grünau, Almtal, Austria.

Type horizon: Norian Dachstein limestone of the Dolomites.

Diagnosis.—Triasininae presenting a non-overlapping (evolute), mostly sigmoidally coiled tubular chamber regularly constricted by strengthenings.

Description.—The test is free, lenticular with a rounded periphery (Fig. 4C, I) to slightly biumbilicate (Fig. 4E, H). A probable polyembryonism has been documented (Fig. 5J–L). The test is formed by a globular proloculus with a simple opening (Fig. 5I) followed by an enrolled undivided tubular chamber, mostly sigmoidally coiled. Gradually enlarging alongside its 7 to 11 whorls, the tubular chamber, non overlapping (evolute), appears oval in axial section, later possibly becoming kidney-shaped to chevron-shaped against the preceding whorl. Numerous inner strengthenings of the wall regularly constrict both sides of the interior tube from the floor to the roof (Fig. 4). Reduced in the first whorls (Fig. 4K, L), these structures increase in size whorl by whorl but never project beyond the half of the tubular chamber lumen. In tangential sections of the tubular chamber, these strengthenings may appear falsely to represent subdivisions into chamberlets or "inner-pillars" (e.g., Fig. 4B, C). Developed on both sides of the tubular chamber, the laminar extensions of the tube wall (lamellae sensu Piller 1978) increase in length whorl by whorl such as in the last whorls, lamellae may laterally interfinger, building umbilical masses (Fig. 5C–F).

Among centred-specimens, four distinct morphological groups have been identified:

Morphotype 1 (Fig. 3A–C): This form shows a compact sigmoidal stage of coiling becoming almost planispiral in 2 to 6 whorls. The number of coils never exceeds 7.5 whorls.

Morphotype 2 (Fig. 3D–F): With up to 11 whorls, this form has a first compact sigmoidal stage of 3–4 whorls followed by another sigmoidal stage (in inverse order or in another axis of coiling) becoming almost planispiral in 2 to 5 whorls.

Morphotype 3 (Fig. 3G–I): Form distinct by a first streptospirally coiled stage of 2–3 whorls, possibly with a 90° change in coiling direction between whorls, followed by a compact sigmoidal stage becoming almost planispiral in 2 to 5 whorls. The number of coils only rarely exceeds 9 whorls.

Morphotype 4 (Fig. 3J–L): It presents a first streptospirally coiled stage of 2–3 whorls, possibly with a 90° change in coiling direction between whorls, followed by a compact sigmoidal stage of 2–4 whorls and another sigmoidal stage (in inverse order or in another axis of coiling) that becomes almost planispiral in 2 to 4 whorls. The number of coils is about 7–9 whorls.

Some additional irregularities exist: (i) in the morphotype 1, the proloculus is larger than in other morphotypes; (ii) lamellae are more developed in the first whorls of the morphotype 1, other morphotypes are distinguished by lamellae that firstly scarcely cover the test (Fig. 5G, H), such as juvenile forms may appear evolute.

Fig. 2. Involutinid foraminifer *Aulosina oberhauseri* (Koehn-Zaninetti and Brönnimann, 1968), Black Marble Quarry, Oregon (upper Carnian?–lower–middle? Norian); Grünau, Austria (Norian: holotype and paratypes). **A**. Peculiar preservation of the Black Marble Quarry: hydrocarbon impregnation versus test recrystallisation. Apparently well-preserved specimen (MHNG 2011-1-341a, oblique section). The early hydrocarbon impregnation outlines the foraminiferal test (A_1); SEM image of the same specimen after thin section etching (A_2) (diNaEDTA, 1% by volume). Calcitic crystals are limited by graphitic flakes (white arrowheads). Outlines of the test are still visible but do not fit with the crystals limits. Recrystallisation state (A_3). Note that without hydrocarbon impregnation, the foraminiferal test would not be identifiable. **B**. Holotype, NHMB-C27488a, thin section 583; oblique section. B_1. Photograph of original material of Koehn-Zaninetti and Brönnimann (1968). The white arrowhead points out the apparent protuberant, convex umbilical mass. Note the strong recrystallisation of the test and the micritisation of its periphery. B_2. Reconstitution of the holotype after restudy of the original material. See perforations (in grey) and ghosts of the test periphery (dotted lines). The here restored specimen is lenticular in shape. **C**. Comparable section in a specimen from the Black Marble Quarry (MHNG 2011-1-440a). **D–G**. Selected paratypes. **D**. Paratype, NHMB-C27487a, thin section 582; oblique, centred section (D_1) and associated reconstituted drawing (D_2). The first stage of coiling is streptospiral. **E**. Paratype, NHMB-C27488b, thin section 583; oblique section. →
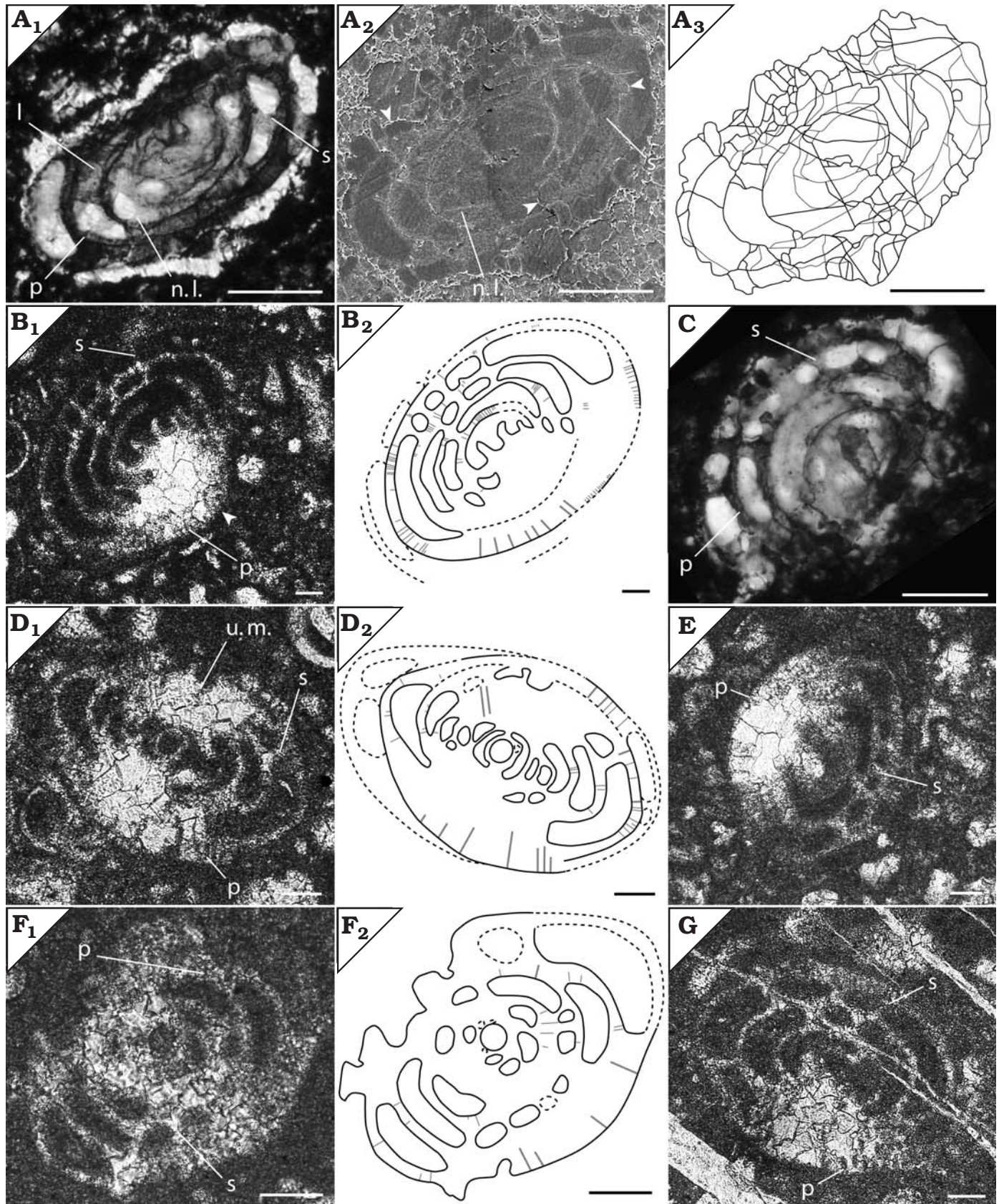
F. Paratype, NHMB-C27488c, thin section 583; oblique, centred section (F_1) and associated reconstituted drawing (F_2). The first stage of coiling is sigmoidal. **G**. Paratype, NHMB-C27487b, thin section 582; oblique section. Abbreviations: l, lamella; n. l., narrowed lumina; p, perforation; s, strengthening; u. m., umbilical mass. Scale bars 50 μm.

Wall calcareous, perforate, commonly recrystallised but probably originally hyalino-radial, fibrous, aragonitic. Several perforations, radially-arranged, riddle the tube wall and the lamellae without ever crossing the internal tube structures (Fig. 4A). Aperture simple, terminal (open end of the tubular chamber).

Dimensions.—Specimens of *Aulosina oberhauseri* from the Black Marble Quarry vary in size from 100 to 300 μm in diameter and 75 to 150 μm in height, the largest being adult forms. The proloculus is globular with a diameter ranging from 20 to 38 μm (20 to 26 μm in the morphotypes 2, 3, 4 and 24 to 38 μm in the morphotype 1). The tubular chamber and associated lamellae gradually increase in size. Lumen of the first stage being generally from 4 to 8 μm in height whereas lumen of the last whorls reach up to 28 μm. Wall perforations are about 2–4 μm in diameter. The strengthenings thicken the tubular chamber wall on a length of 1–2 μm in the first whorls and up to 30 μm in the last whorls. Their thickness is proportional and never exceeds 14 μm.

The documented Tethyan specimens of *Aulosina oberhauseri* vary in size from 265 to 600 μm in diameter (the 1 mm specimen illustrated by Salaj and M'Zoughi 1997, strongly recrystallised, is here considered to be doubtful). Forms of the original material are, on average, 400 μm in diameter (Koehn-Zaninetti and Brönnimann 1968). However, involutinids of the Black Marble Quarry apparently represent a dwarfed fauna. Small sizes are observed for representatives of the genera *Auloconus*, *Aulosina*, *Aulotortus*, *Frentzenella*, *Licispirella*, *Parvalamella*, and *Trocholina*. Moreover, juvenile forms are rarely illustrated in the literature.

Microfacies and palaeoecology.—The dark grey to black limestone beds of the Black Marble Quarry are mostly composed by muddy microfacies (mudstone, wackestone and packstone) typical of a quiet, periodically restricted, shallow-water lagoonal environment (Rigaud 2012). In some beds small corals or sponge thickets occur.

Foraminiferal association.—*Aulosina oberhauseri* is found in association with representatives of the Family Involutinidae (*Auloconus*, *Aulotortus*, *Frentzenella*, ?*Lamelliconus*, *Licispirella*, *Parvalamella*, *Trocholina* and *Wallowaconus*), Duostominidae (*Cassianopapillaria*, *Variostoma*), Oberhauserellidae (*Praegubkinella*, *Oberhauserella*, *Schmidita*), Polymorphinidae (*Eoguttulina*, *Guttulina*), Trochamminidae (*Trochammina*), Endothyridae, Ophthalmidiidae (*Gsollbergella*) and indeterminate lagenids, miliolids and ?lituolids.

Remarks.—In the original systematic description of *Aulosina oberhauseri*, Koehn-Zaninetti and Brönnimann (1968) de-

scribed: (i) pillars limited to the periphery of the tubular chamber; (ii) embracing lumen in the adult stage; (iii) convex, protuberant umbilical masses. These traits have not been observed in sections of specimens from the Black Marble Quarry and the revision of the original material leads us to reconsider these observations: (i) in opposition to pillars, the internal tube structures of *A. oberhauseri* only laterally thicken the tube wall such that they are justifiably limited to the periphery of the lumen (Fig. 4B–J); (ii) like in *Aulotortus*, the tubular chamber of *A. oberhauseri* is only gradually enlarged so that in section, the lumen are laterally restricted (evolute or non-overlapping tubular chamber). The described embracing lumen are in fact morphological misinterpretations related to oblique sections (Fig. 4D); (iii) the diagenetic result subsequent to the recrystallisation, dissolution or micritisation of the test periphery, sometimes gives the erroneous impression that the umbilical masses are protuberant (Figs. 2B, 5F, I). For example, in the holotype, partly micritised, a part of the test periphery is lacking suggesting that its umbilical masses are protuberant (Fig. 2B$_1$) but remnants of its perforations reveal an initial lenticular geometry (Fig. 2B$_2$).

Despite the fact that majority of the illustrated Tethyan specimens have a larger size, their shape and innermost structure fit in every respect with specimens from the Black Marble Quarry (e.g., Fig. 2C). In the original material, the discovery of paratypes in which the first stage of coiling and the proloculus are preserved (Fig. 2D, F) reveals that the coiling arrangement is equally similar (e.g., sigmoidal coiling in Fig. 2F). In the literature, most illustrations of *A. oberhauseri* lack the juvenile part (non-centred or recrystallised specimens). Since the last whorls of the species are almost planispiral, it is understandable that the form was first thought to be planispirally coiled.

Aulosina oberhauseri differs from *Triasina hantkeni* by its reduced size, a more lenticular shape, a non overlapping (evolute) tubular chamber, different kind of internal tube structures (strengthenings instead of internal pillars), wider umbilical masses and probably a more complicated coiling arrangement (the juvenile coiling of *T. hantkeni* is still unknown). In equatorial and sub-equatorial sections, slightly tangential to the tube lumen, *A. oberhauseri* strongly resembles *T. hantkeni* (Figs. 2C, 3H). The only criteria discerning the two species are the lumen shape of the initial stage and, if the juvenile part is not preserved, the sigmoidal coiling of the last whorls; both pieces of evidence being based on the dissimilarity existing in the tubular chamber lateral overlapping of the two species. In other sections, the observation of inner-pillars in tangential sections of *T. hantkeni* (never ob-

Fig. 3. Involutinid foraminifer *Aulosina oberhauseri* (Koehn-Zaninetti and Brönnimann, 1968), centred to sub-centred sections; Black Marble Quarry (upper Carnian?–lower–middle? Norian). **A–C**. Morphotype 1: macrospheric form? Note the large proloculus and the relatively wide lateral development of lamellae in the juvenile part. **A**. MHNG 2011-1-440b, axial section. Note the lamellae interfingering. **B**. MHNG 2011-1-440c, sub-equatorial section. **C**. MHNG 2011-1-440d, oblique section. **D–L**. Microspheric forms? Note the smaller proloculus, the limited lateral extension of lamellae in the juvenile stage, the high number of convolutions in adult forms (E, H, K, L) and the more complicated coiling arrangement. **D–F**. Morphotype 2. **D**. MHNG 2011-1-440e, sub-axial section. **E**. MHNG 2011-1-440f, sub-equatorial section. Some strengthenings appear slightly oblique to the lumen (arrowheads). **F**. MHNG 2011-1-440g, oblique section. **G–I**. Morphotype 3. **G**. MHNG 2011-1-440h, axial section. Lamellae are laterally restricted in the first whorl →
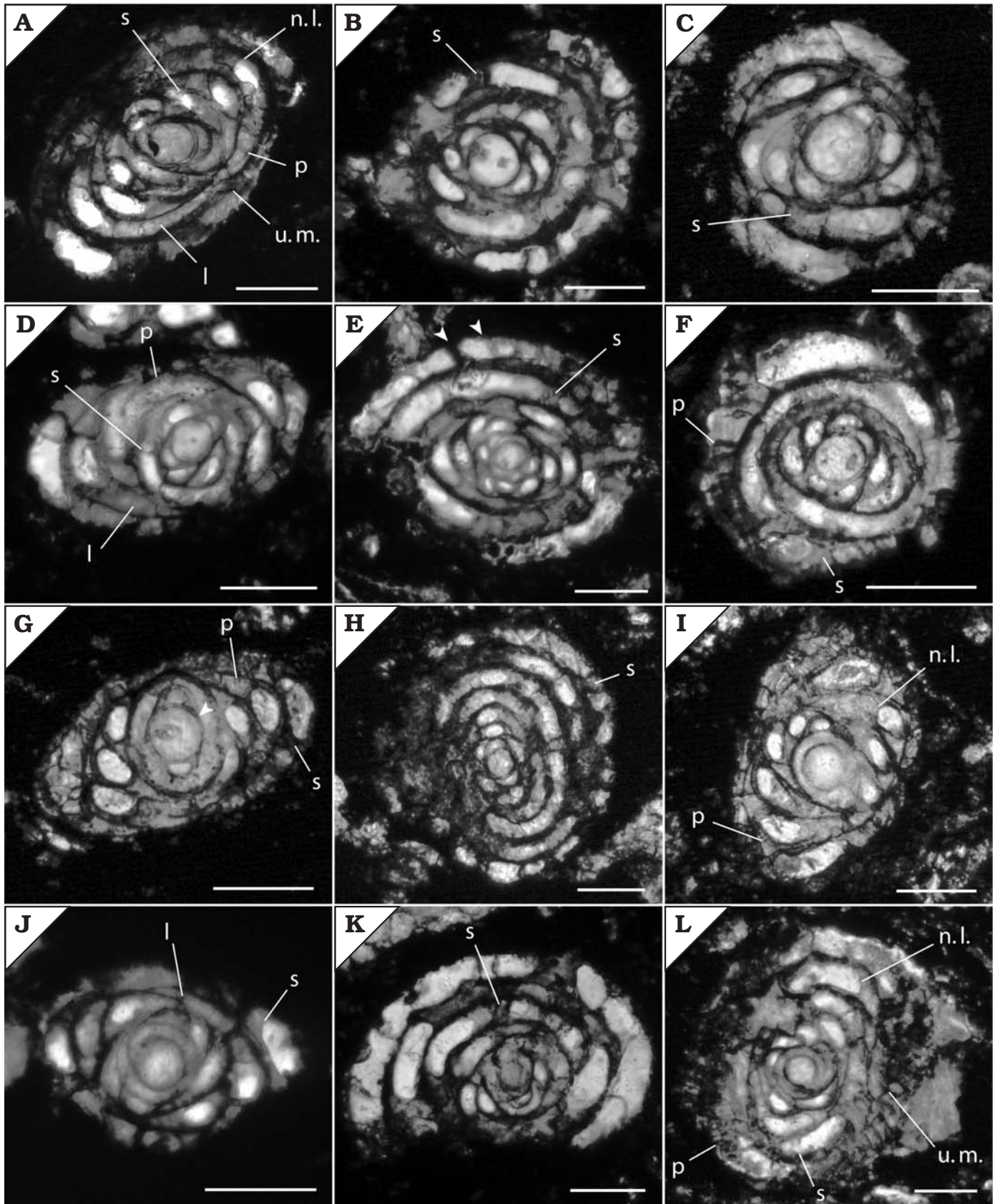
(arrowhead). **H**. MHNG 2011-1-440i, equatorial section. **I**. MHNG 2011-1-440j, slightly oblique section. **J–L**. Morphotype 4. **J**. MHNG 2011-1-440k, axial section. **K**. MHNG 2011-1-440l, sub-equatorial section. **L**. MHNG 2011-1-440m, slightly oblique section. Abbreviations: l, lamella; p, perforation; s, strengthening; n. l., narrowed lumen; u. m., umbilical mass. Scale bars 50 μm.

served in *A. oberhauseri* sections; Fig. 5A, B) hampers any confusion.

The species *A. oberhauseri* differs from representatives of the genus *Aulotortus* by its coiling arrangement, the shortened lateral extension of its lamellae in the juvenile stage and the occurrence of strengthenings constricting its tubular chamber. In axial, sub-axial to oblique sections, strengthenings are almost not discernible so that the specimens resemble *Aulotortus sinuosus* (Figs. 3A, 4L, 5D) or *Parvalamella friedli* (Fig. 3C, F) in which gentle tube undulations may falsely appear to represent strengthenings. In such peculiar sections, the coiling arrangement and the narrowed lumen (Fig. 5C, H) are the only features allowing the recognition of *A. oberhauseri*.

Comments on morphotypes.—The investigated material of *Aulosina oberhauseri* revealed the presence of four morphotypes. These forms differ in the coiling arrangement, the proloculus size, the lamellae lateral overlapping and the number of coils. All these features are easily identifiable in centred sections.

All morphological groups show a similar stratigraphic and palaeoenvironmental distribution along the Black Marble Quarry succession and display no evolution or variability between their first and last occurrences. Pending further investigations of morphotype distribution in other areas of the world, we refrain to argue that these forms express sexual polymorphism, intraspecific variability, environmental stress peculiar to the Black Marble Quarry depositional environment or even the existence of two or more distinct species.

Nevertheless, the absence of the first stage of coiling in the morphotype 1, its larger proloculus and lower number of whorls combined with its relative abundance, may suggest that this morphotype corresponds to a megalospheric or A form (Fig. 3A–C). As the measured size of the proloculus strongly depends on the section orientation, the resulting values should be treated with utmost care. We assume, however, that owing to the large number of studied individuals and the fact that the half size of the proloculus does not exceed the thickness of our thin sections (30–35 μm) the measured differences are significant. The microspheric or B form, known to show a more varied morphology (Loeblich and Tappan 1964), would correspond to one or more of the other identified morphotypes (Fig. 3D–L). Dimorphism is well known in the Involutinina. It has been, for example, described in *Aulotortus* (Koehn-Zaninetti 1969) and *Involutina* (Gaździcki 1983).

Geographic and stratigraphic range.—Cosmopolitan in the Tethys and in American Panthalassan terranes of Oregon (this study) and the Yukon (Gaździcki and Reid 1983). In the

Tethyan domain, *Aulosina oberhauseri* is referred to the Norian–early Rhaetian. In Oregon, the species occurs within the first 48 metres of the Black Marble Quarry, part of the Martin Bridge Formation, late Carnian? to early–middle? Norian in age.

Discussion on the systematic position of *Aulosina oberhauseri*

Following the first description of *Aulosina oberhauseri* gen. nov., the family position of the genus *Triasina* has never been reviewed. Indeed, widely considered to represent the missing link between *Aulotortus* and *Triasina hantkeni* (Koehn-Zaninetti and Brönnimann 1968; Koehn-Zaninetti 1969; Piller 1978; Gaździcki 1983) and always discovered in close association with Involutinidae (Koehn-Zaninetti and Brönnimann 1968; Koehn-Zaninetti 1969; Zaninetti 1976; Gaździcki et al. 1979; Gaździcki 1983; Abate et al. 1984; He and Wang 1990; Zaninetti et al. 1992; Villeneuve et al. 1994; Vuks 2007), *A. oberhauseri* has unanimously been assigned to the Involutinidae.

The specimens encountered at the Black Marble Quarry confirm this family assignment: (i) *Aulosina oberhauseri* always shows a preservation similar to that of well-known aragonitic forms such as gastropods, dasycladacean green algae, Involutinidae (e.g., *Auloconus*, *Aulotortus*), and Duostominidae (e.g., *Cassianopapillaria*, *Variostoma*) whereas the species never shows a comparable preservation with fossils that have a different mineralogical composition (i.e., sponges, spongiomorphs, ostracods, echinoderms, brachiopods and hyalino-radial, agglutinated, and porcelaneous foraminifers). We consider such a similarity in the diagenetic result as an indirect evidence of the original aragonitic composition of the test of *A. oberhauseri*; (ii) in the adult individuals of *A. oberhauseri* the lateral lamellae development covers the test so that lamellae are step by step interfingered in the umbilical region, as illustrated in the *Aulotortus* model proposed by Di Bari and Laghi (1994) and as observed by Di Bari and Rettori (1996) in *Triasina hantkeni*. This partial overlapping of the test helps to explain the biumbilicate morphology (eight-shape morphology in section) of some Involutinidae. This characteristic is well-pronounced in *Triasina hantkeni* or in *Aulotortus impressus* that are both endowed with only slightly interfingered lamellae.

On the other hand, the systematic position of *Aulosina oberhauseri* as far as its subfamily is concerned has always

Fig. 4. Strengthenings in involutinid foraminifer *Aulosina oberhauseri* (Koehn-Zaninetti and Brönnimann, 1968), Black Marble Quarry (upper Carnian?–lower–middle? Norian). **A**. MHNG 2011-1-341b, oblique section. Note that the perforations do not cross the strengthenings. The white arrowhead indicates a slight tube undulation. **B**, **C**. Sub-equatorial, sub-centred sections, MHNG 2011-1-440n (**B**) and MHNG 2011-1-440o (**C**). The strengthenings are visible only where the tube lumen appear reduced, attesting their marginal position. **D**. MHNG 2011-1-332, oblique, sub-centred section. The strengthenings are arranged on both sides of the here obliquely-sectioned tubular chamber (arrowheads). **E**. MHNG 2011-1-341c, sub-axial, centred section. See the width of the strengthenings. **F**, **G**. Oblique, sub-centred sections, MHNG 2011-1-440p (**F**) and MHNG 2011-1-440q (**G**). Note that the strengthenings are not differentiated from the tube wall (arrowheads). **H**. MHNG 2011-1-440r, tangential section. In the central part, the black arrowhead points the strengthenings of the other side of the interior tube. Lamellae only slightly cover the umbilical region (white arrowhead), giving a biumbilicate →
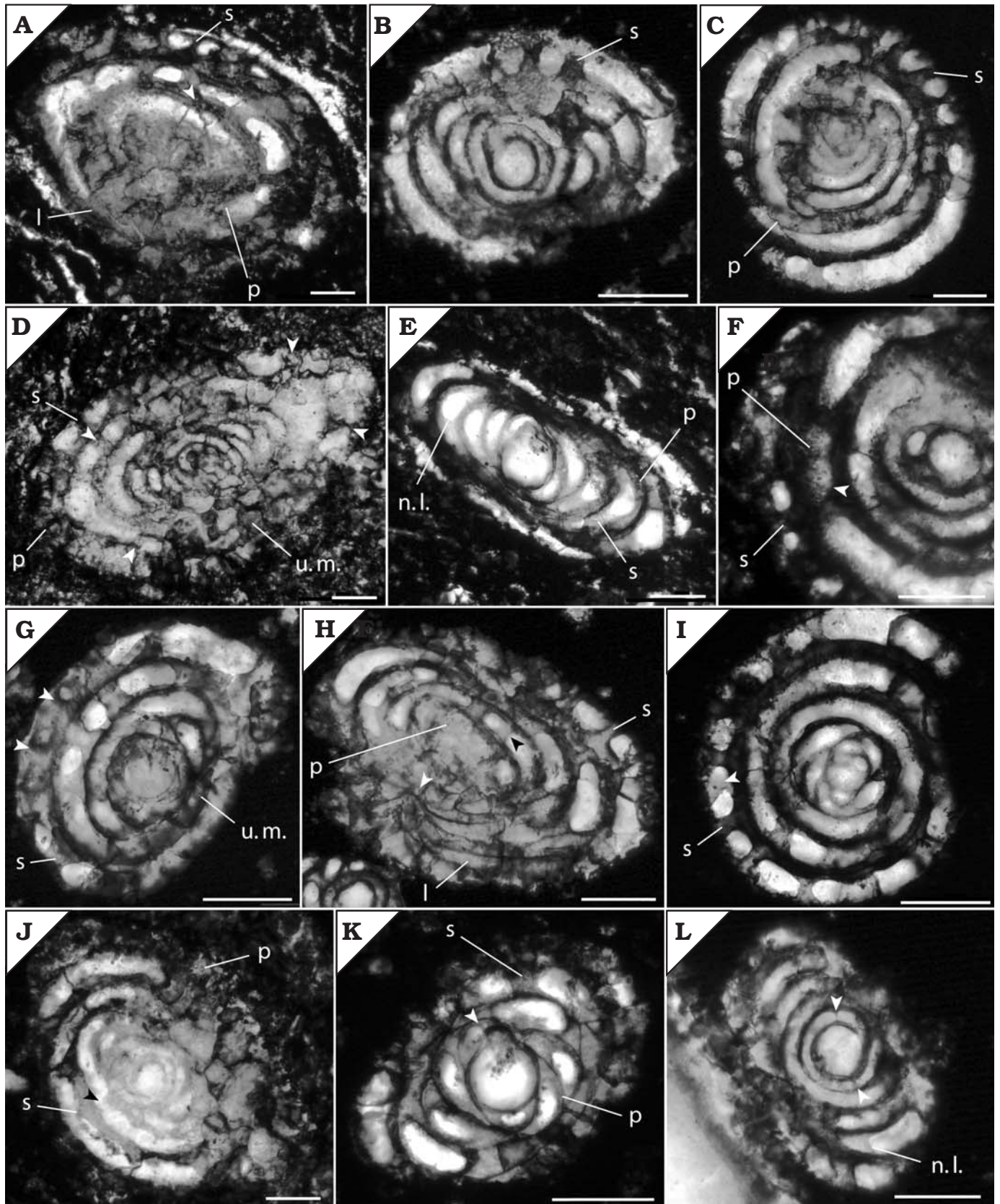
shape to the test. **I**. MHNG 2011-1-440s, equatorial, sub-centred section. The white arrowhead indicates a strengthening of the other side of the interior tube. **J**. MHNG 2011-1-340, oblique, sub-centred section. The black arrowhead points a tangentially-sectioned strengthening. **K**, **L**. Centred, sub-axial sections MHNG 2011-1-440u (**K**) and MHNG 2011-1-440v (**L**). Note the small strengthenings in the first two whorls (arrowheads). Abbreviations: l, lamella; n. l., narrowed lumina; p, perforation; s, strengthening; u. m., umbilical mass. Scale bars 50 μm.
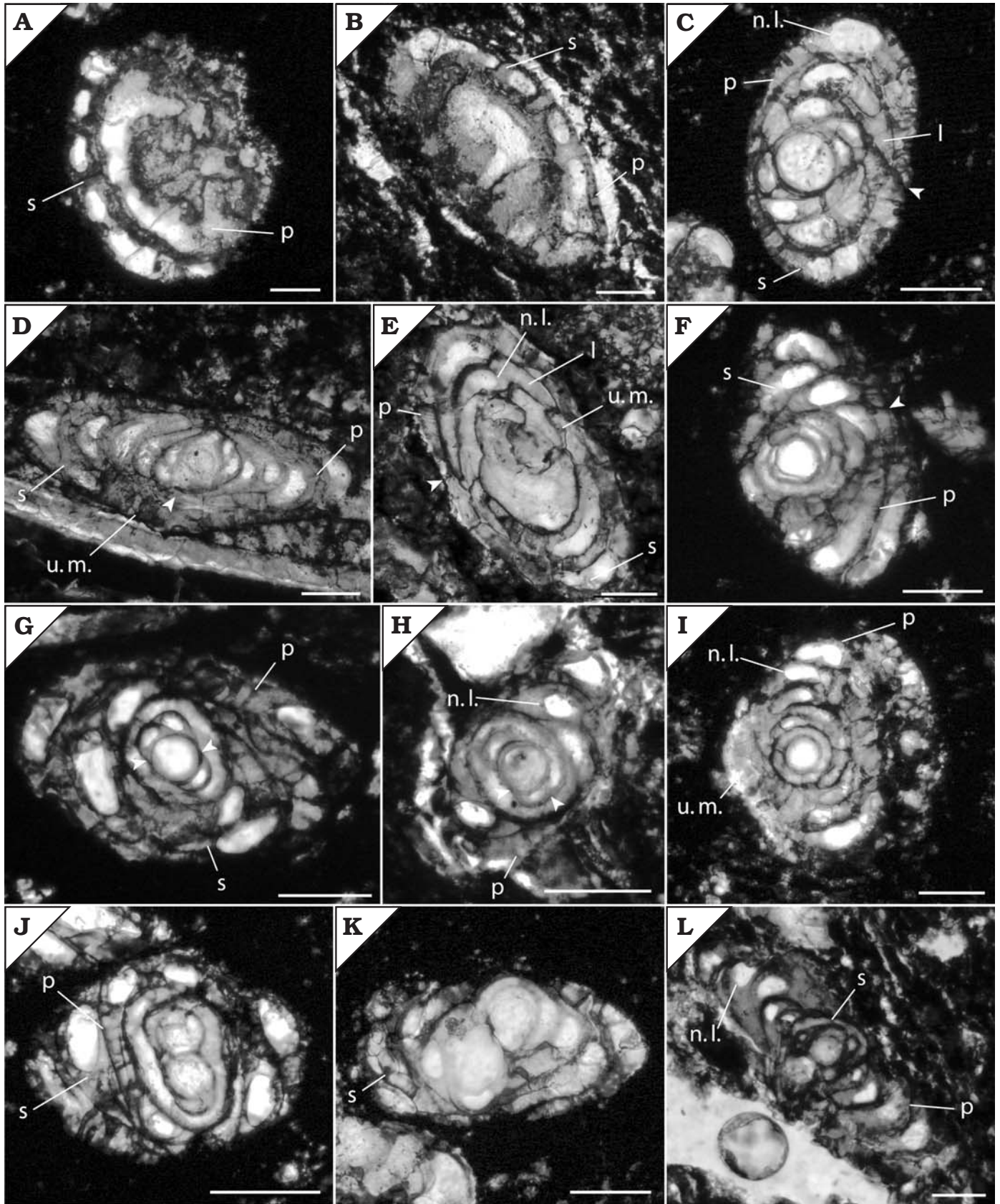
http://dx.doi.org/10.4202/app.2011.0072

Fig. 5. Involutinid foraminifer *Aulosina oberhauseri* (Koehn-Zaninetti and Brönnimann, 1968), Black Marble Quarry (upper Carnian?–lower–middle? Norian). **A**, **B**. Tangential sections, MHNG 2011-1-440w (**A**) and MHNG 2011-1-341c (**B**). Note the absence of transversely sectioned inner-pillars. **C–F**. Lamellae interfingering in the umbilical region (white arrowheads). **C**. MHNG 2011-1-440x, sub-axial; centred section. **D**. MHNG 2011-1-391a, thin →
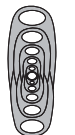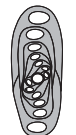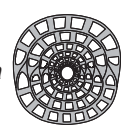
	Triadodiscus	Aulotortus	Aulosina	Triasina
umbilical mass	+	+	+	−
lamellae interfingering	−	+	+	+
reduced/shortened lamellae	−	−	+	+
involute tubular chamber	−	−	−	+
internal tube structures	−	−	+	+
internal pillars	−	−	−	+
strenghtenings	−	−	+	−

Fig. 6. Innermost structure differences in Upper Triassic Involutinina. Only genera morphologically closed to *Aulosina* are here taking into account; each form being hyaline, aragonitic, perforated, with a lenticular to globular test.

been a subject of controversy and discussion. First positioned among the Aulotortinae (Salaj et al. 1967; Piller 1978; Gaździcki 1983), the genus *Triasina* was later moved within the newly introduced Subfamily Triasininae (Loeblich and Tappan 1986) and more recently within the Triadodiscinae (Di Bari and Laghi 1994). Our observations revealed that *A. oberhauseri* possesses interfingered lamellae and thus, would show fewer affinities with the genus *Triadodiscus* than with the genera *Aulotortus* and *Triasina* (Fig. 6). Regarding the form as a whole, it is more plausible to place *A. oberhauseri* in the Triasininae than in the Aulotortinae which do not possess scarcely developed lamellae and are devoid of internal structures. Moreover, in section, the lateral strenghtenings, internal tube structures distinguishing *A. oberhauseri* from the Aulotortinae, are morphologically close to *Triasina* inner-pillars (see Fig. 7: the tangential section of *Aulosina* and the axial vertical section of *Triasina* are almost identical). Accordingly, until phylogenetic relationships between these genera are not fully clarified, it seems more plausible to keep *A. oberhauseri* and *T. hantkeni* together in the emended herein subfamily Triasininae.

North American occurrences

The Late Triassic foraminifers in North America are documented in few publications (Gaździcki and Reid 1983; Kristan-Tollmann and Tollmann 1983; Igo and Adachi 1992).

Foraminiferal assemblages depicted in these papers are relatively poor and not well-diversified. The Black Marble Quarry, for example, was first investigated for its foraminiferal content by Kristan-Tollmann and Tollmann (1983) but only two taxa ("*Diplotremina*? sp." and "*Angulodiscus eomesozoicus*") were mentioned. North American Upper Triassic deposits usually are considered to be poor in foraminifers in respect to Tethyan localities. The most relevant foraminiferal assemblages have been cited in the Upper Triassic sequence of Lime Peak (Yukon, Canada) as far as Involutinidae are concerned (Gaździcki and Reid 1983) and in the Upper Triassic blocks of the San Juan Island (Washington State) documenting porcelaneous foraminifers (Igo and Adachi 1992).

The Black Marble Quarry occurrence of *Aulosina oberhauseri* is a first record of this species from the USA though it has previously been found in North America at the Canadian Lime Peak locality (Gaździcki and Reid 1983). Although illustrations of the species have been considered to be doubtful by Abate et al. (1984) or even to belong to *Triasina hantkeni* by Di Bari and Rettori (1996), these forms fit with the new combination of the species *Aulosina oberhauseri* (see synonymy). The American localities provide the richest occurrences of *A. oberhauseri* ever reported worldwide and, contrary to preconceived ideas, the species seems to be more abundant in Panthalassan than in Tethyan deposits.

Aulosina oberhauseri is well-represented in periodically restricted lagoonal environments of the Wallowa terrane whereas according to Gaździcki and Reid (1983) it also oc-

section; axial, centred section. **E**. MHNG 2011-1-491b, thin section; transverse section. **F**. MHNG 2011-1-440y, thin section; oblique, centred section. **G**, **H**. Lamellae development in the juvenile part of the morphotypes 3 and 4. **G**. MHNG 2011-1-440z, thin section; oblique, centred section. Shortened lamellae (white arrowheads). **H**. MHNG 2011-1-480a, thin section; sub-axial, centred section. Note the reduced size of the lamellae in the first whorls (white arrowheads) and their progressive development. **I**. MHNG 2011-1-440aa, thin section; slightly oblique, centred section. Test formed by a globular proloculus with a simple opening followed by an undivided tubular chamber in contrast with J–L showing a polyembryonism (two proloculus). **J**, K. Slightly oblique, centred sections, thin section MHNG 2011-1-440ab (**J**) and MHNG 2011-1-440ac (**K**). **L**. MHNG 2011-1-480b, thin section; axial, centred section. Abbreviations: l, lamella; n. l., narrowed lumina; p, perforation; s, strengthening; u. m., umbilical mass. Scale bars 50 µm.

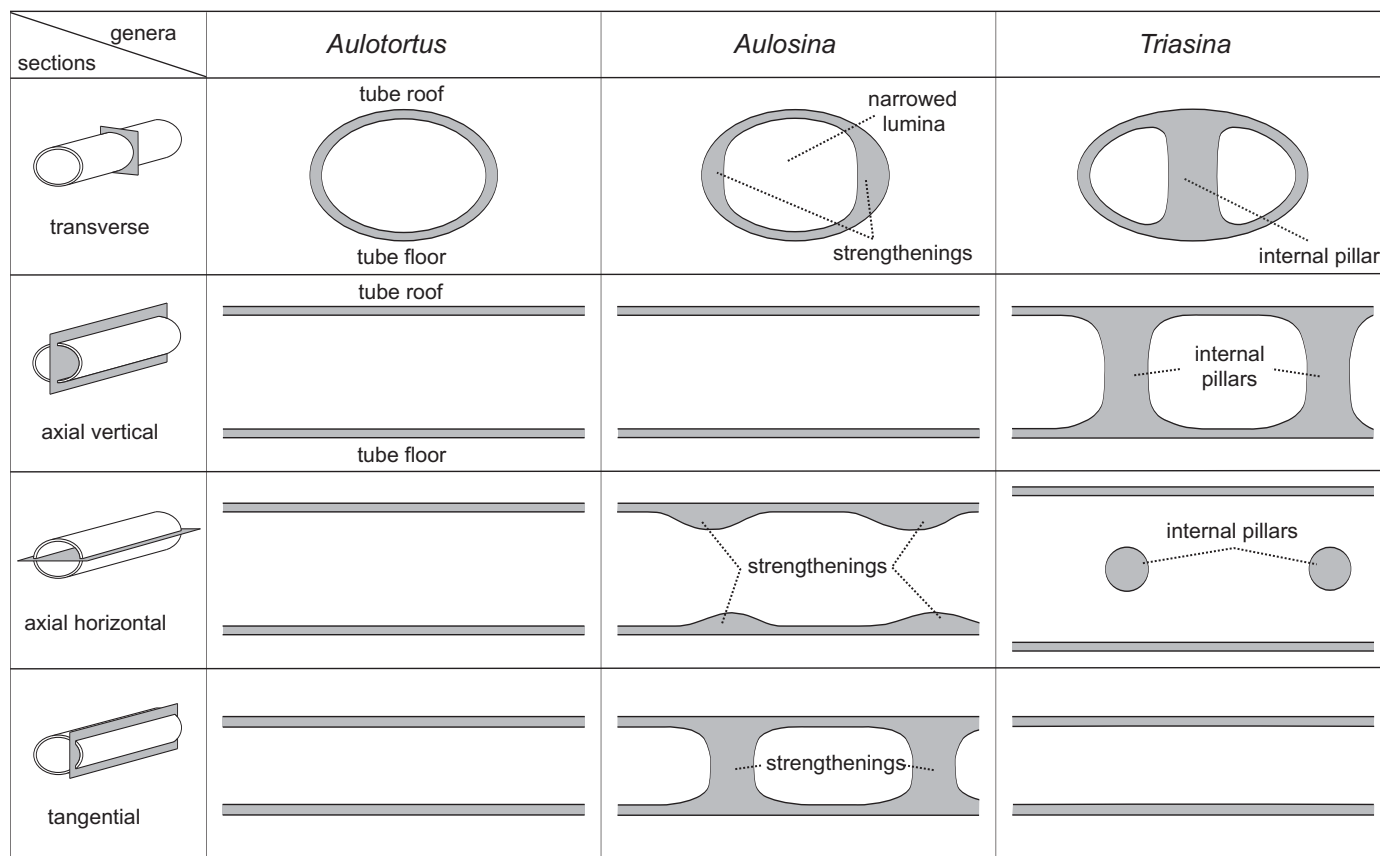| sections \ genera	Aulotortus	Aulosina	Triasina
transverse	tube roof / tube floor	narrowed lumina / strengthenings	internal pillar
axial vertical	tube roof / tube floor		internal pillars
axial horizontal		strengthenings	internal pillars
tangential		strengthenings	

Fig. 7. Tubular chamber section concept in Involutinidae. *Aulotortus*: tubular chamber simple, without internal structures; *Aulosina* gen. nov.: tubular chamber lumen constricted by strenghtenings; *Triasina*: tubular chamber supported by inner-pillars. Note similarities between sections of different genera. The axial horizontal section of the tubular chamber is the most reliable for a generic identification.

curs in slope deposits of the Stikine terrane. If confirmed, the presence of *A. oberhauseri* in such environments might be useful to calibrate platform deposits with deeper environments. Biostratigraphic markers defining precisely the stratigraphy of shallow-water deposits are rare in Upper Triassic rocks (Rigaud et al. 2010).

Phylogeny and evolution

Speculations on the *Aulotortus–Triasina* phylogenetic lineage are hypothetic and scant data exists to establish links between these two genera of involutinids. The derivation of *Triasina* from *Aulotortus* (Koehn-Zaninetti and Brönnimann 1968; Koehn-Zaninetti 1969; Piller 1978; Gaździcki 1983) is only based on the argument that *A. oberhauseri*, regarded as an intermediate form, possesses inner-pillars. Our study emphasizes that the tubular chamber structures of *Aulosina* are in fact strengthenings (and not inner-pillars), limited to the periphery of the tubular chamber. According to this discovery, the phylogenetic link between *Aulotortus* and *Triasina* might be questioned.

Our material, however, highlights further evidences corroborating the lineage. First, the similarities observed in the lamellae arrangement of *Aulotortus* (Piller 1978; Di Bari and Laghi 1994), *Aulosina* (this study), and *Triasina* (Di Bari and Rettori 1996) prove that these genera have a strong phylogenetic link and most probably a close common ancestor. Then, the new features recognized in *Aulosina oberhauseri* remind structural elements and morphological characteristics distinguishing *Triasina hantkeni* from *Aulotortus* representatives: (i) a large size: although comparatively small compared with coeval Tethyan representatives, *A. oberhauseri* is one of the largest Involutinidae of the Black Marble Quarry; (ii) shortened lamellae: despite non overlapping in *A. oberhauseri*, the tubular chamber is laterally prolonged by lamellae which are, in the first whorls of coiling, comparable in relative size to those of *T. hantkeni* (see Di Bari and Rettori 1996); (iii) inner-tube structures: even though limited to the periphery of the lumen, the strengthenings are internal wall thickenings morphologically closed to *Triasina* inner-pillars. The absence of perforations through the strengthenings might attest to their role of support (Figs. 2C, 4A, G).

Although a direct lineage between *Aulotortus*, *Aulosina*, and *Triasina* cannot be proved, evidences of their strong phylogenetic link are thus undeniable. From *Aulotortus* to *Triasina*, the level of complexity attained in each form increases and innovative features follow the same way: while
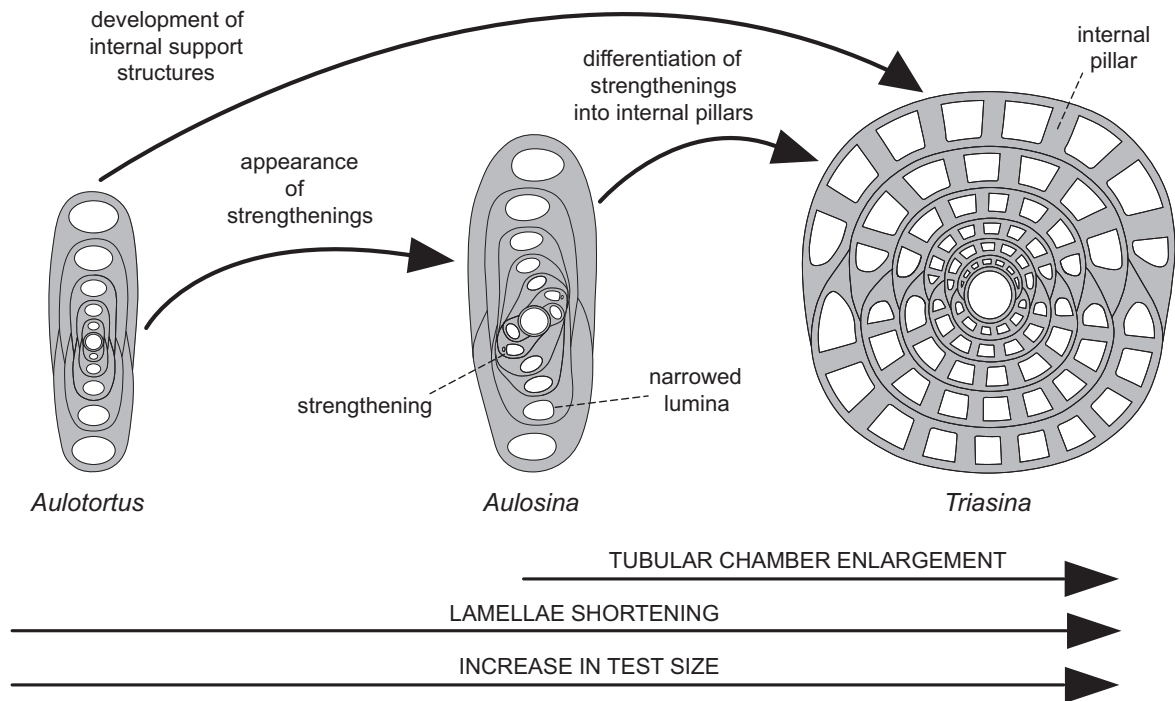
Fig. 8. Sketch showing the theoretical evolutionary steps of the hypothetic *Aulotortus–Triasina* lineage.

the test increases in size, internal tube structures are developed; concurrently, the tubular chamber, supported by internal structures, is enlarged, limiting the lateral development of lamellae (Fig. 8). Considering such an evolution, the lateral strenghtenings constricting the interior tube of *A. oberhauseri* would be the ancestral structures of *T. hantkeni* inner-pillars; the tubular chamber enlargement being responsible for their differentiation into inner-pillars (Fig. 8). This structural evolutionary trend is probably not limited to the Involutinina lineage: similar structures are observed in the Upper Permian with specimens illustrated as *Hemigordiopsis renzi* (Gargouri and Vachard 1988: pl. 1: 1–11) and *Baisalina* aff. *B. pulchra* (Gargouri and Vachard 1988: pl. 2: 1–3, 7–9). Named pseudosepta by Gargouri and Vachard (1988), we consider such structures, in lateral position with regard to the interior tube, to be strengthenings instead.

Several authors believe that *Aulosina oberhauseri* represents only one step of the *Aulotortus–Triasina* phylogeny. Until now, no known specimen convincingly can be proved to represent another intermediate form. According to Salaj (1976), *Arenovidalina pragsoides* (Oberhauser, 1964) would be one of these additional intermediate forms. Nevertheless, the genus first described as agglutinated (Ho 1959) and later emended as microgranular (Salaj et al. 1967) cannot be included in the aragonitic Suborder Involutinina. Moreover, illustrations of the species (*Permodiscus pragsoides* by Oberhauser 1964: pls. 2: 1, 4, 12, 17, 19, 21, 24–26; 4: 7) never show a tubular segmentation so it is impossible to recognize any phylogenetic link between the species *P. pragsoides*, *A. oberhauseri*, and *T. hantkeni*. In contrast, the species "*Aulotortus*" *bulbus* Ho (Ho and Hu 1977: pl. 9: 14–16, 18–25) displays clear inner tube structures. Well illustrated by De Castro (1990: e.g., "*Aulotoruts sinuosus*" in pl. 2: 1), these structures seem to be lateral strengthenings. A further study of the species "*A.*" *bulbus* is required to confirm its assignment to *Aulosina*. The specimen illustrated by He (1980: pl. 73: 11) as *Triasina hantkeni* shows internal tube structures and might thus be considered as an intermediate form. However, observable internal tube structures are more developed on the roof of the interior tube and seem more spaced-out such as they are morphologically closer to pseudosepta, unknown features of the lineage of Involutinina.

Adaptative evolution of Involutinina

Primitive involutinins are lenticular with a wide umbilical mass attesting to their thick laminar test. Throughout the Middle and Late Triassic, many structural and morphological modifications of their test occurred. Although rather simple, the evolutive acquisitions of involutinins show the same kinds of development as majority of larger benthic foraminifers: (i) their size considerably increased reaching more than one millimetre in some Lamelliconinae, Aulotortinae, and Triasininae; (ii) they acquired a more complex morphology moving from lenticular to globular (*Parvalamella*, *Prorakusia*, *Triasina hantkeni*) or conical (e.g., *Auloconus*, *Lamelliconus*, *Ornatoconus*, *Trocholina*); (iii) asymmetric forms showed a tendency to reduce the lateral extension of their spiral side lamellae. This is particularly

well-pronounced in *Coronipora* and *Semiinvoluta*; (iv) internal structures (strengthenings and pillars) allowed the tubular chamber enlargement at the expense of the lamellae development (e.g., in *Triasina hantkeni*).

Late Triassic involutinins occur only in the shallowest regions of oligotrophic tropical seas. In such foraminifers, the nature and complexity of the wall structure (aragonitic, fibrous, laminar, perforate wall) and the thinning of the outer wall achieved by the intercalation of internal support structures are features considered to represent adaptations to the exigencies of a symbiotic life (Haynes 1965; Ross 1974; Leutenegger 1984; Hallock 1985; Hohenegger 2009).

Conclusions

Aulosina oberhauseri is one of the emblematic forms related to the Late Triassic diversification of Involutinina. At the Black Marble Quarry, the exceptional preservation of *Aulosina oberhauseri* allows to observe features generally obliterated by diagenetic processes. The presence of lamellae interfingering in the umbilical region undeniably attests that *A. oberhauseri* is morphologically close to *Aulotortus* and *Triasina*. Phylogenetic links between these three genera have not been fully clarified and although the species shares several characteristics with both genera, the presence of a new inner-tube element raises doubts about its exact systematic placement. Our data suggest that the strengthenings, first internal tube structures appearing during the Late Triassic in Involutinina, would be closely related to inner-pillars. It even seems that the strengthenings would be an indispensable step prior to the formation of inner-pillars in tubular foraminifers, whatever is their wall nature. This would be the case for the *Aulosina–Triasina* lineage with *A. oberhauseri* (this work), and also probably for the *Hemigordius–Shanita* lineage through forms morphologically close to *Hemigordiopsis* and *Baisalina*.

All major evolutive steps of the lineage of Involutinina occurred before the Triassic–Jurassic boundary. This crisis is probably the cause of interruption in involutinin evolution prior to the acquisition of the complex morphology characterizing the informal group known as "Larger Benthic Foraminifera".

Acknowledgments

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