BioOne COMPLETE

New Robertinid Foraminifers from the Early Jurassic of Adnet, Austria and Their Evolutionary Importance

Authors: Rigaud, Sylvain, and Blau, Joachim

Source: Acta Palaeontologica Polonica, 61(4) : 721-734

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.00250.2016

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Editors' choice

New robertinid foraminifers from the Early Jurassic of Adnet, Austria and their evolutionary importance

SYLVAIN RIGAUD and JOACHIM BLAU



Rigaud, S. and Blau, J. 2016. New robertinid foraminifers from the Early Jurassic of Adnet, Austria and their evolutionary importance. *Acta Palaeontologica Polonica* 61 (4): 721–734.

New benthic multichambered foraminifers have been discovered in the Hettangian–Sinemurian of the Northern Calcareous Alps (Adnet, Salzburg, Austria). Originally aragonitic, these forms are completely recrystallized but the early impregnation of their tests by Fe-Mn solutions has, to some extent, allowed an indirect preservation of their primary structure. The most remarkably preserved specimens are found in close vicinity to the marmorea crust, a heavily mineralized multiphased hardground. We describe two new genera, *Velleditsiella* gen. nov., a microgastropod look-alike foraminifer, which includes the species *V. felicitaszae* gen. et sp. nov. and *V. spinaferra* gen. et sp. nov., and *Rossanella* gen. nov., the first known representative of the superfamily Conorboidoidea, which includes the species *R. martinii* gen. et sp. nov. Considering their structural and morphological characteristics, *Velleditsiella* and *Rossanella* phylogenetically derive from two distinct Triassic lineages, respectively the families Trochosiphoniidae and Variostomatidae. The discovery of diverse aragonitic assemblages in earliest Jurassic strata dismisses the long believed hypothesis that all Jurassic aragonitic multichambered foraminifers originated from a single Oberhauserellidae ancestor. It also supports a lower impact of the Triassic/Jurassic biotic crisis on the evolution of aragonitic foraminifers. Hypotheses for the short term and long term evolution of aragonitic multichambered foraminifers are discussed and new phyletic trees are proposed.

Key words: Robertinida, Trochosiphoniidae, Conorboididae, inner-chamber structures, marmorea crust, Jurassic, Austria.

Sylvain Rigaud [SRigaud@ntu.edu.sg], Earth Observatory of Singapore, 50 Nanyang Avenue, 639798 Singapore, Singapore.
Joachim Blau [Joachim.Blau@geolo.uni-giessen.de], Geozentrum, FE Geologie, Altenhöferallee 1, 60438 Frankfurt am Main, Germany.

Received 17 February 2016, accepted 17 August 2016, available online 14 September 2016.

Copyright © 2016 S. Rigaud and J. Blau. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see http://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

The Jurassic was a turning point in the evolution of Foraminifera. According to Fuchs (1975) and Tappan and Loeblich (1988), this geological period records the origination of calcitic Rotaliida and "Buliminida" (sensu Loeblich and Tappan 1992) from aragonitic Robertinida. The first foraminiferal adaptation to a planktonic, meroplanktonic (BouDagher-Fadel et al. 1997; Hart et al. 2003, 2010; Hudson et al. 2005) or tychopelagic (Rigaud et al. 2015b) lifestyle also took place during the Jurassic, through the robertinid family Favusellidae. Despite their great potential to reconstruct and understand the large-scale evolution of foraminifers, aragonitic multichambered forms (order Robertinida) have been so far overlooked in the fossil record, most likely because their tests are rapidly and often severely affected by diagenesis, rendering their study very sensitive.

Representatives of the family Oberhauserellidae have long been believed to be the only Robertinida survivors of the Triassic–Jurassic major extinction event. In consequence, they have been regarded as the most probable direct ancestors of all calcitic Rotaliida, "Buliminida", and "Globigerinida" and all aragonitic Ceratobuliminoidea and Conorboidoidea (e.g., Fuchs 1973, 1975; Tappan and Loeblich 1988; BouDagher-Fadel et al. 1997; Hillebrandt 2010, 2012). This monophyletic hypothesis, however, has been contested by molecular studies (e.g., Darling et al. 1997, 2009; de Vargas et al. 1997; Bowser et al. 2006; Schweizer et al. 2008; Ujiié et al. 2008; Pawlowski et al. 2013) and challenged by the reconstruction of the Robertinida early evolution (Rigaud et al. 2015b).

By the description of new Early Jurassic aragonitic multichambered foraminifers descending from two distinct Triassic non-oberhauserellid lineages, this paper aims at definitely dismissing a potential derivation of all Jurassic Robertinida from a unique oberhauserellid ancestor. This discovery opens new perspectives for the long term evolution of the group and its potential phylogenetic links with

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

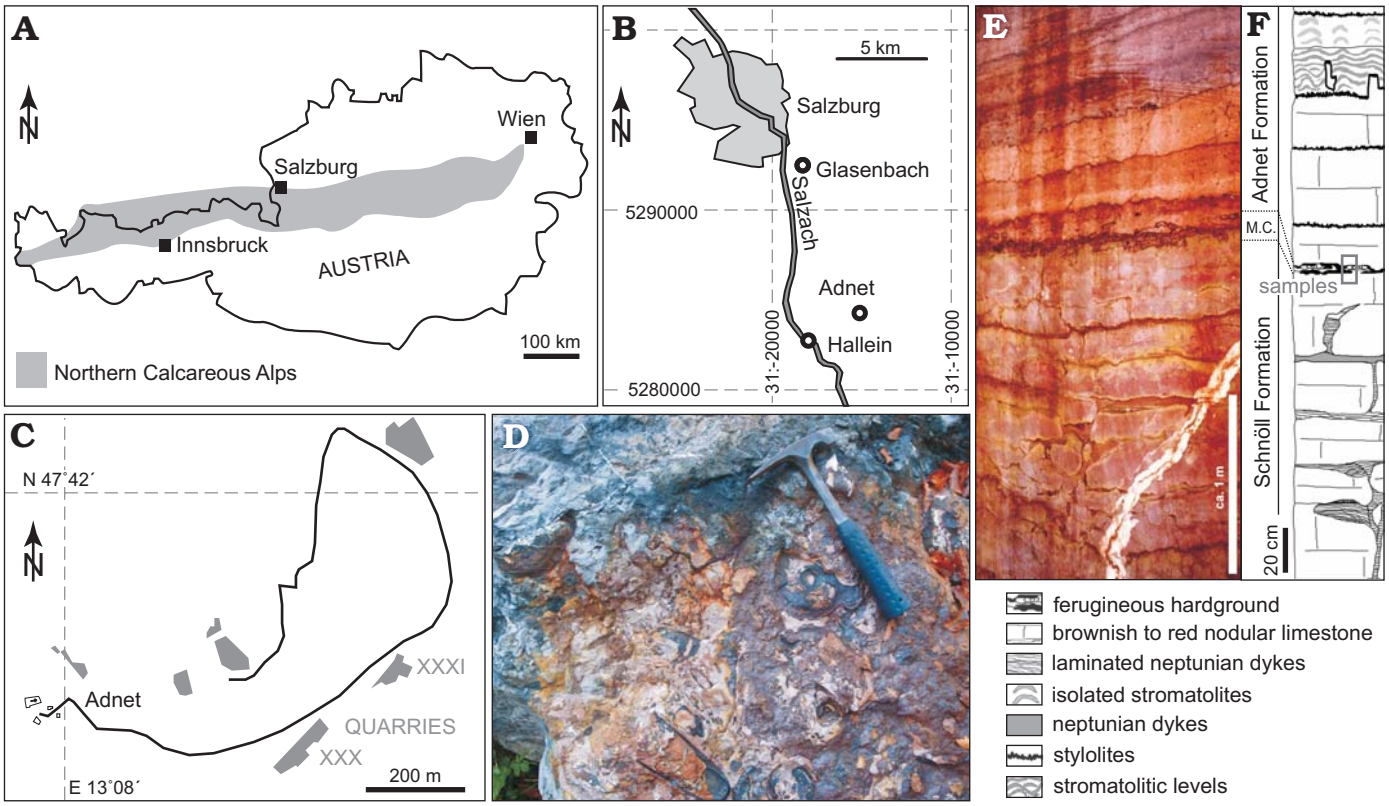


Fig. 1. Studied locality and sampled level. **A**. Map of Austria showing the location of the Northern Calcareous Alps. **B**. Enlargement of the area of Salzburg showing the location of Adnet (Austrian Gauss-Krüger coordinate grid). **C**. Location of the sampled quarries (quarries XXX, XXXI, roman quarry numbering follows Kieslinger 1964). **D**. Picture of the heavily mineralized, ammonite-rich marmorea crust, as exposed in October 2012 in quarry XXXI. **E**. Quarry wall in the Rot-Grau Schnöllbruch (quarry XXXI, situation in 1994) exposing the upper part of the Schnöll Formation, the marmorea crust (M.C.) and the lower part of the Adnet Formation. **F**. Lithologic section of the quarry XXXI and sampling location.

calcitic multichambered foraminifers (i.e., order Rotaliida sensu lato; i.e., sensu Pawlowski et al. 2013).

Institutional abbreviations.—MHNG, The Museum of Natural History of Geneva, Switzerland.

Geological setting

The studied material comes from Hettangian–Sinemurian limestone rocks of Adnet (Northern Calcareous Alps, Austria). Located approximately twelve kilometers SSE of the city of Salzburg, the village of Adnet is well-known for its Early Jurassic fossil-rich rocks, which are exposed in neighboring quarries (Fig. 1). Our material comes from the Eisenmann Quarry and the Schnöll Quarry (see Fig. 1C: quarries XXX and XXXI according to Kieslinger 1964, respectively). There, the marmorea crust (= "Brandschicht" in the terminology of local quarrymen), an uppermost Hettangian to lowermost Sinemurian guide horizon (*Schlotheimia angulata* Zone; see Dommergues et al. 1995; Böhm et al. 1999; Böhm 2003), represents a multiphased ferromanganese hardground, which rests directly on Upper Triassic reefal limestone (Oberrhätkalk) in quarry XXX and separates the Schnöll Formation from the Adnet Formation in quarry XXXI (Fig. 1D–F). This condensed, heavily mineralized horizon is particularly well-known for its richness in ammonites (dominated by *Schlotheimia marmorea*) and exceptionally diversified foraminiferal assemblages (Blau 1987; Blau and Grün 1997; Ebli 1997; Böhm et al. 1999; Rigaud et al. 2013, 2015a).

We sampled the marmorea crust and the uppermost part of the Schnöll Formation, near the marmorea crust. The red to grey limestone rocks of the marmorea crust are rich in echinoderms, ammonites, gastropods, and foraminifers dominated by *Involutina* (Rigaud et al. 2015a) and other aragonitic forms (i.e., diverse Involutinida and Robertinida). Although these rocks have been a subject of extensive foraminiferal studies in the past (see references above), the forms introduced in the present paper have neither been mentioned nor figured by previous authors.

Material and methods

Aragonite is metastable and particularly susceptible to dissolution. Aragonitic fossils are therefore very rarely recovered in a preserved state. Only few robertinid fossil tests have been directly analyzed by mineralogical determination methods (Wiewióra 1964; Fuchs 1969; Gorbatchik and Kuznetsova 1986; di Bari and Rettori 1996; BouDagher-Fadel et al. 1997; di Bari and Laghi 1998; di Bari 1999). However, since all

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

fossil types do not respond equally to diagenesis, a detailed textural analysis of diagenetic results can allow the successful identification of originally aragonitic components (e.g., Wernli 1987; Rigaud et al. 2013, 2015b).

In our thin sections, gastropods, ammonites, involutinid and robertinid foraminifers show a very distinctive and atypical state of preservation. Despite their complete recrystallization to sparry calcite, these originally aragonitic fossils may display, in the vicinity of the marmorea crust, ghost relics of the primary structure of their shells (e.g., Figs. 2A, B, 3M, 4A, H). This conspicuous state of preservation is exceptional for originally aragonitic fossil components, which primary architectural and structural features are usually obliterated by diagenetic processes. It is related to a more or less pervasive impregnation by Fe-Mn fluids, which occurred prior to the test (?full) recrystallization. Unique to aragonitic tests and shells in Adnet, this preservation state permits the unequivocal identification of originally aragonitic components (Rigaud et al. 2013, 2015a).

In both involutinid and robertinid foraminifers, impregnated parts are strongly dependent on the test primary microporosity. Perforations and interstices between two lamellae or two whorls are the most impregnated parts of the tests. They appear as dark reddish-brownish thin lines under natural light (Figs. 2–4). This preservation of fine structures is uneven, localized in some specimens, prevalent in others. Intensely perforated specimens display the best preservation (Fig. 4). However, when specimens are too heavily mineralized (e.g., in the most impregnated parts of the marmorea crust), tests are too dark and structures are barely recognizable. Non-impregnated specimens are uncolored and lack structural details. Similar preservation states have been described in Cenomanian trocholinids of the Altamira and Bielba formations of Spain (Schlagintweit et al. 2015).

Thanks to the early impregnation of foraminiferal tests by Fe-Mn fluids, important structural details are indirectly preserved, allowing in-depth description. However, the original aragonitic wall of our specimens is not preserved and information concerning the primary arrangement of aragonite needles cannot be provided. In the following section, we thus assume that the wall of the examined foraminifers was originally fibrous and radially arranged, as it has been observed and defined in Robertinida (e.g., Reiss and Schneidermann 1969; di Bari and Laghi 1998).

The following classification has been developed after Cavalier-Smith (2003) and recent classifications proposed by Pawlowski et al. (2013) and Rigaud et al. (2015b).

Systematic palaeontology

Subphylum Foraminifera d'Orbigny, 1826

Class Globothalamea Pawlowski, Holzmann, and Tyszka, 2013

Order Robertinida Mikhalevich, 1980

Suborder Duostominina Rigaud, Martini, and Vachard, 2015b

Superfamily Duostominoidea Brotzen, 1963

Family Trochosiphoniidae Rigaud, Martini, and Vachard, 2015b

Subfamily Trochosiphoniinae Rigaud, Martini, and Vachard, 2015b

Genera included: *Trochosiphonia* Rigaud, Martini, and Vachard, 2015b and *Velleditsiella* gen. nov.

Stratigraphic and geographic range.—Upper Carnian (Upper Triassic)–lower Sinemurian (Lower Jurassic) of Tethys and Panthalassa.

Genus *Velleditsiella* nov.

Etymology: In honor of Felicitász Velledits (Institute of Mineralogy and Geology, University of Miskolc, Hungary) for her paleontological contributions.

Type species: *Velleditsiella felicitaszae* gen. et sp. nov.; see below.

Species included: The type species and *V. spinaferra* gen. et sp. nov.

Diagnosis.—Trochosiphoniinae with pear-shaped chambers directly open on the siphon.

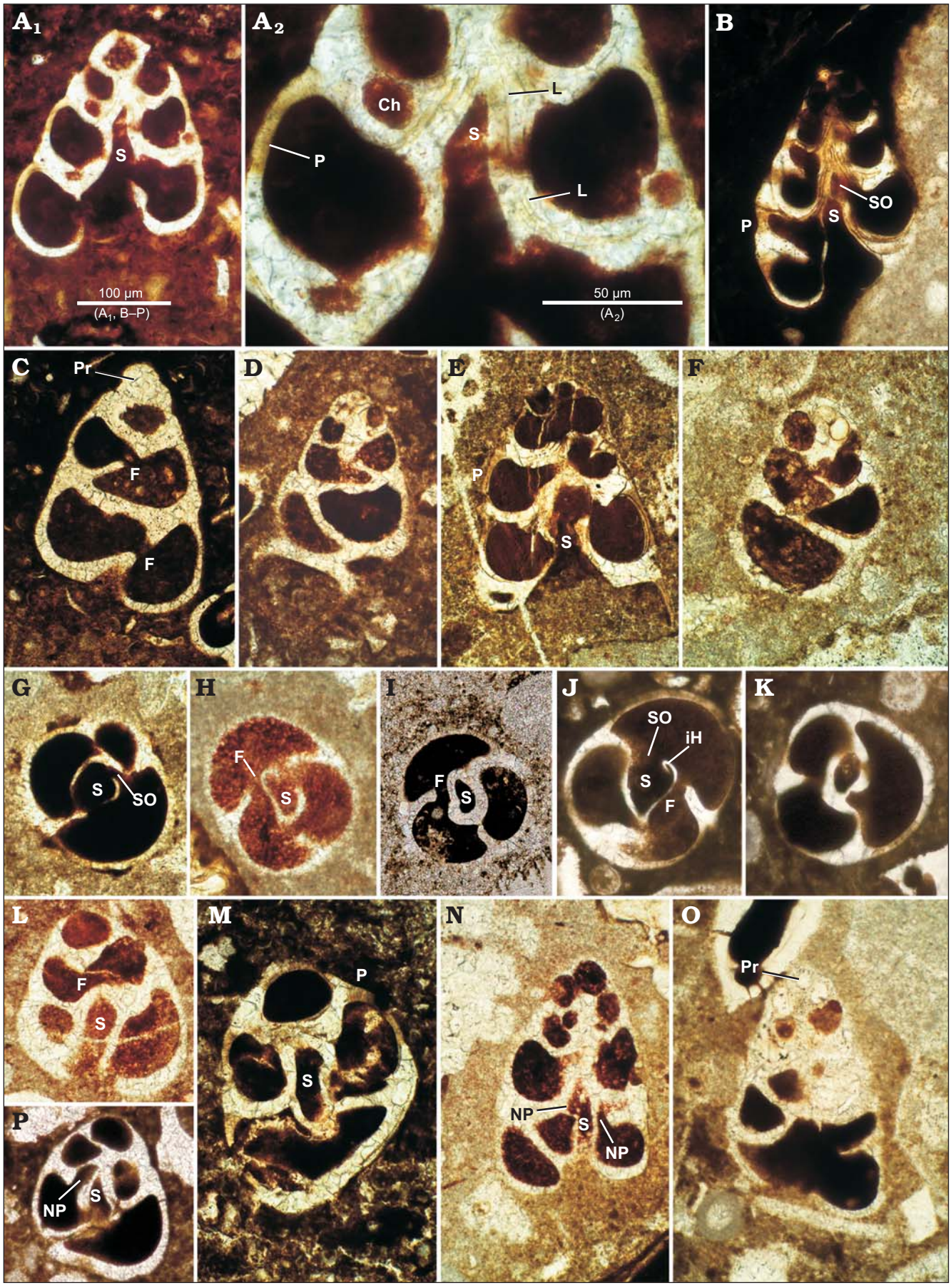
Remarks.—*Velleditsiella* gen. nov. shows similarities to the agglutinated genus *Siphovalvulina* Septfontaine, 1988 from which it differs mainly in its wall composition, in the smoothness and straighter morphology of its siphon (in *Siphovalvulina*, the siphon is twisted), and in its direct openings on the siphon, which are distinct from the aperture.

From its Late Triassic homeomorphic ancestor *Trochosiphonia* Rigaud, Martini, and Vachard, 2015b, it differs only in its pear-shaped chambers (chambers are ovoid in *Trochosiphonia*) and in the presence of an opening between each chamber and the siphon.

The foraminiferal affinity of this new genus is incontestable as *Velleditsiella* gen. nov. possesses a proloculus (Figs. 2C, O, 3L) and well-distinct chambers, which are clearly separated by septa and all connected by a foramen (Figs. 2C, F, H–K, 3G, I). However, when specimens of *Velleditsiella* gen. et sp. nov. are tangentially or obliquely sectioned, on account of their aragonitic lamellar wall and trochospiral coiling, they may be confused with microgastropods. Microgastropods are larger (even their larval shells), not primarily bilamellar and do not possess so thin and tightly distributed perforations. Tangential sections of the tube of a microgastropod will never show septation. Moreover, the variability observed through ontogeny in the dimension (Figs. 2A$_1$, N, 3A, B, D–G, K–N) and number of lumina (compare the number of lumina on both sides of the siphon in Figs. 2B, N, 3A, E–G, M) would be aberrant for a microgastropod.

Like other aragonitic fossils found in our samples, all specimens of *Velleditsiella* gen. nov. are completely recrystallized into calcisparite. The apparent, relatively good state of preservation in the structure of some specimens is related

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use



Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

to Fe-Mn impregnation processes (e.g., Figs. 2A, B, E, M, 3H, M).

In Robertinida, the presence of a siphon is unique to the family Trochosiphoniidae and the connection of each chamber with the siphon is limited to the genera *Pragsoconulus* and *Velleditsiella* gen. nov. In these two taxa, additional openings have been most likely used as secondary apertures, allowing shorter connections between each chamber and the surrounding environment.

Stratigraphic and geographic range.—Uppermost Hettangian–lowermost Sinemurian (Lower Jurassic) of Austria.

Velleditsiella felicitaszae sp. nov.

Fig. 2.

Etymology: In honor of Felicitász Velledits (Institute of Mineralogy and Geology, University of Miskolc, Hungary) for her paleontological contributions.

Type material: Holotype: MHNG-75631-1, fully recrystallized adult test in subaxial section partly impregnated by Fe-Mn solutions (Fig. 2B). Paratypes: few hundreds of specimens from the type locality (mainly in MHNG-7563; others in MHNG-2011-1; e.g., Figs. 2A, C–P).

Type locality: Rot-Grau Schnöll Bruch, Adnet, Austria (see Fig. 1).

Type horizon: Hettangian–Sinemurian (Lower Jurassic) of the Schnöll Formation and the marmorea crust (see Fig. 1D–F).

Material.—Type material only.

Diagnosis.—A non-ornamented *Velleditsiella* forming up to 6–7 predominantly triserially arranged whorls.

Description.—The test is smooth, conic elongate, with a rounded outline. The proloculus is globular (Fig. 2C, O), followed by about three trochospirally arranged pear-shaped chambers per whorl (Fig. 2G–K). Moderately enlarging on up to six-seven whorls, chambers are connected by a single interiomarginal opening (foramina in Fig. 2C, F, H–L) and separated by slightly curved, oblique septa. Loosely coiled, chambers delimit a straight, median siphon, roughly rounded tubular in shape (Fig. 2A, B, G–N, P). The narrow end of each chamber is directly open on the siphon (Fig. 2B, G, P, N). This additional opening, probable secondary aperture, is related to a small hook, local inner wall deformation of the siphon edge (Fig. 2J). The siphon is secondarily laminar (i.e., lined by umbilical lateral laminar extensions of the wall of each additional chamber; Fig. 2A, B). On the spiral side, the suture is covered by thick but short lateral outer laminar extensions of the wall (Fig. 2A, B, E). In our material, tests are entirely recrystallized into calcisparite. The original wall structure, primarily bilamellar, finely laminated and very finely perforate (e.g., Fig. 2A), is indirectly preserved in parts finely impregnated by Fe-Mn solutions. This peculiar type of preservation is unique to primarily aragonitic tests and shells (Rigaud et al. 2013, 2015a). The primary aperture is simple, interiomarginal.

Dimensions.—The observed specimens of *Velleditsiella felicitaszae* gen. et sp. nov. reach a maximum of 300 μm in height and 220 μm in width. The spiral angle varies around 60º. The siphon is about 20–25 μm in width.

Remarks.—On account of strong morphological similarities, the Triassic species *Trochosiphonia stanleyi* Rigaud, Martini, and Vachard, 2015b can be regarded as a solid direct ancestor for *Velleditsiella felicitaszae* gen. et sp. nov. (Fig. 5). Externally, *Velleditsiella felicitaszae* gen. et sp. nov. and *Trochosiphonia stanleyi* are homeomorphic. Internally, however, the two species strongly differ in the chamber–siphon relationship (chambers are slightly appressed, not connected to the siphon and ovoid in *Trochosiphonia stanleyi*). The species occurs with representatives of the aragonitic orders Involutinida (i.e., *Coronaserra*, *Coronipora*, *Frentzenella*, *Involutina*, *Kristantollmanna*, *Licispirella*, *Papillaconus*, *Semiinvoluta*, *Trocholina*) (Rigaud et al. 2013) and Robertinida (i.e., *Velleditsiella spinaferra* gen. et sp. nov., *Rossanella martinii* gen. et sp. nov., *Oberhauserella*). Other foraminifers are calcitic nodosariids and miliolids. Involutinida dominate the association, mainly with representatives of the genus *Involutina* (Rigaud et al. 2015a).

Stratigraphic and geographic range.—Only known from the uppermost Hettangian–lowermost Sinemurian (Lower Jurassic) of the Adnet quarries (Austria).

Velleditsiella spinaferra sp. nov.

Fig. 3.

Etymology: From the Latin *spina*, spine and ferre, to carry; for the spiny external morphology displayed by the new species.

Type material: Holotype: MHNG-75631-2, fully recrystallized adult test in subaxial section, slightly impregnated by Fe-Mn solutions (Fig. 3E). Paratypes: dozens of specimens from the type locality (MHNG-75631 and MHNG-2011-1; e.g., Fig. 3A–D, F–Q).

Type locality: Rot-Grau Schnöll Bruch, Adnet, Austria (see Fig. 1).

Type horizon: Hettangian–Sinemurian (Lower Jurassic) of the Schnöll Formation and the marmorea crust (see Fig. 1D–F).

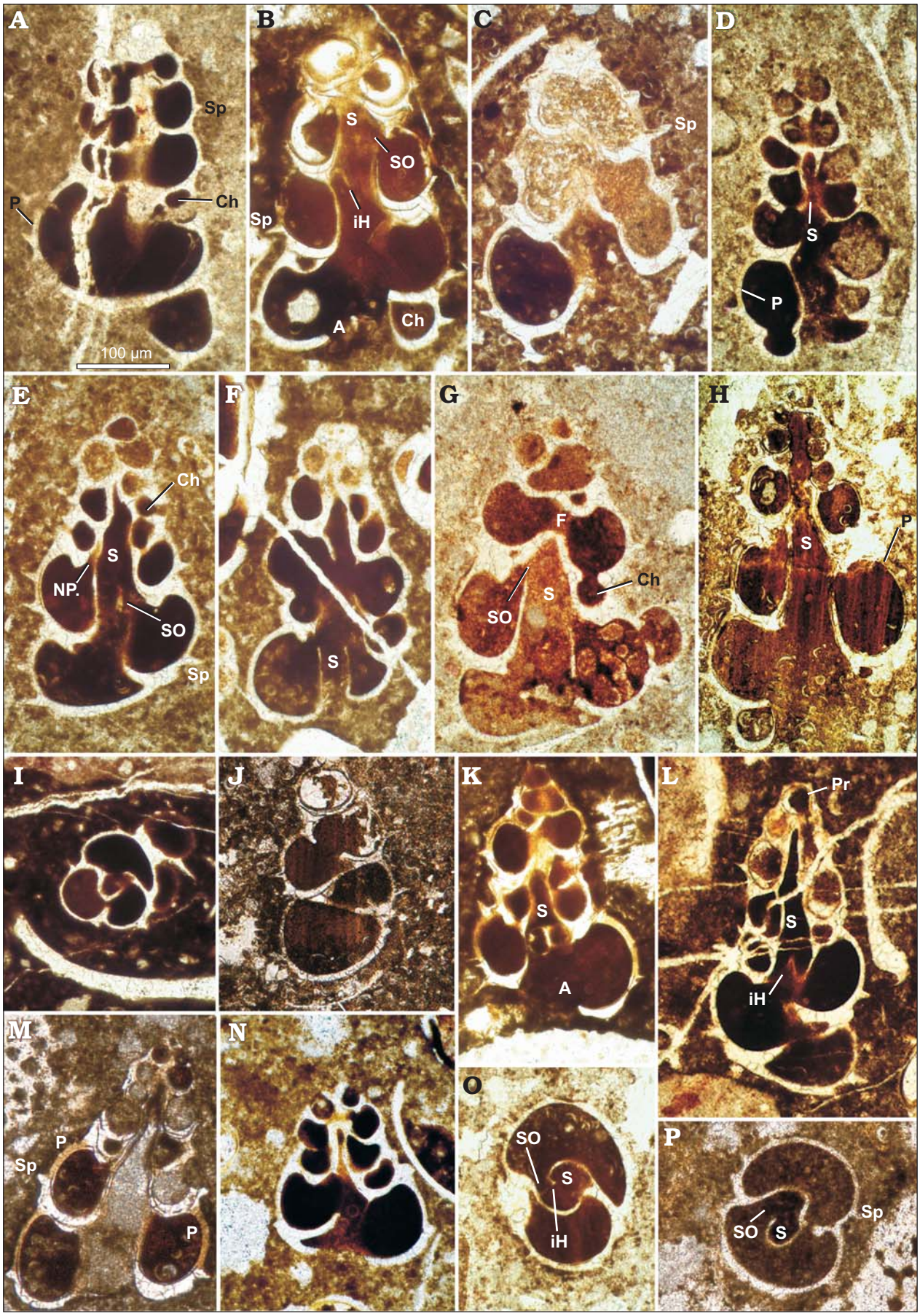
Material.—Type material only.

Diagnosis.—A spiny, high trochospiral *Velleditsiella* with 2–3 bulged chambers per whorl.

Description.—The test is spiny, high conic elongate, with two to three bulged chambers per whorl (Fig. 3I, O, P). The proloculus is globular (Fig. 3L), followed by trochospirally arranged pear-shaped chambers, moderately enlarging on up to seven whorls. Chambers, loosely coiled and separated

← Fig. 2. Robertinid foraminifer *Velleditsiella felicitaszae* gen. et sp. nov., uppermost Hettangian–lowermost Sinemurian, Adnet, Austria. Holotype (B), paratypes (A, C–P). **A**. MHNG-75631-1, subaxial section. **B**. MHNG-75631-1, subaxial section. **C**. MHNG-75631-1, oblique centered section. **D**. 4a1(2), subaxial, slighty oblique section. **E**. 1620(2), oblique section. **F**. 1620(1), oblique section. **G**. 4a2(8), transverse section. **H**. 4a2(5), transverse section. **I**. 1620(2), transverse section. **J**. AU1P, transverse section. **K**. AU1E, transverse section. **L**. 4a2(6), oblique section. **M**. 4a1(2), oblique section. **N**. 4a2(8), subaxial section. **O**. 4a2(7), centered, slightly oblique section. **P**. 4a2(5), oblique section. Abbreviations: Ch, chamber; F, foramen; iH, inner hook; L, lamellae; NP, narrowest part of the chambers (open on the siphon); P, perforations; Pr, proloculus; S, siphon; SO, secondary opening.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use



Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

by slightly curved oblique septa, are connected by a single interiomarginal opening (foramina in Fig. 3A, G, I, L) and delimit a median siphon (Fig. 3B, D–I, K–P). The narrow end of each chamber is directly open on the siphon (e.g., Fig. 3B, E, G, O–P). This additional opening, probable secondary aperture, is related to a small hook, local inner wall deformation of the siphon edge (Fig. 3B, L, O). The siphon is secondarily laminar (Fig. 3H, M). On the spiral side, the suture is slightly overlapped by dorsal extensions of the wall (see Fig. 3H, M). In our material, tests are entirely recrystallized into calcisparite but easily recognizable thanks to the distinctive spines, even when tests are non-impregnated. The original wall structure, primarily bilamellar, finely laminated and very finely perforate, is indirectly preserved in parts finely impregnated by Fe-Mn solutions (e.g., Fig. 3B, E, H, M). This peculiar state of preservation is unique to primarily aragonitic tests and shells (Rigaud et al. 2013, 2015a). The primary aperture is simple, interiomarginal (Fig. 3B, K).

Dimensions.—The observed specimens of *Velleditsiella spinaferra* gen. et sp. nov. reach a maximum of about 400 μm in height and 250 μm in width. The spiral angle varies around 40º. The siphon is about 20–25 μm in width. In section, spines commonly reach 10–40 μm in length.

Remarks.—*Velleditsiella spinaferra* gen. et sp. nov. differs from *V. felicitaszae* gen. et sp. nov. in its bulged chambers, more irregular coiling, spiny ornamentation and more acute apical angle. It is the only known Duostominoidea with a spiny test.

Thanks to its distinctive spines, which may have played a role of protection, *Velleditsiella spinaferra* gen. et sp. nov. is easily recognizable in thin section and thus possesses a high biostratigraphic potential. The foraminiferal association is identical to that of *V. felicitaszae*.

Stratigraphic and geographic range.—Only known from the uppermost Hettangian–lowermost Sinemurian (Lower Jurassic) of Adnet (Austria).

Suborder Robertinina Mikhalevich, 1980

Superfamily Conorboidoidea Thalmann, 1952

Family Conorboididae Thalmann, 1952 (emended)

Remarks.—The family Conorboididae differs from the families Variostomatidae and Epistominidae sensu lato (i.e., including the subfamilies Epistomininae, Garantellinae, and Reinholdellinae) in its apertural system, which is fused to a scroll-shaped, inner-chamber structure.

Stratigraphic and geographic range.—Hettangian (Lower Jurassic) to Albian (Lower Cretaceous); Eurasia, North America. The genus *Rossanella* described herein is the oldest known representative of the family. The type-genus *Conorboides* has been mentioned from the Pliensbachian (e.g., Nikitenko and Mickey 2004).

Genus *Rossanella* nov.

Etymology: In honor of Rossana Martini (Department of Earth Sciences, University of Geneva, Switzerland) for her contributions to foraminiferal studies and biostratigraphy.

Type species: *Rossanella martinii* gen. et sp. nov.; monotypic, see below.

Diagnosis.—Involute Conorboididae with an inner-chamber, scroll-shaped structure fused to the aperture floor and an arch-like, interiomarginal aperture.

Remarks.—Morphologically, *Rossanella* gen. nov. appears as an intermediate form between Triassic *Praereinholdella* and Jurassic–Cretaceous *Conorboides*. Contrary to *Rossanella* gen. nov., *Praereinholdella* does not possess inner-chamber structures whereas *Conorboides* presents a slightly more complex apertural system (e.g., low interiomarginal slit partially covered by a flap in *Conorboides*).

The new genus shows strong morphological similarities with the ?calcitic genus *Placentulina* Kasimova, 1978, but differs in its less conic shape and arch-like aperture.

Stratigraphic and geographic range.—Uppermost Hettangian–lowermost Sinemurian (Lower Jurassic) of Adnet (Austria).

Rossanella martinii sp. nov.

Fig. 4.

Etymology: In honor of Rossana Martini (Department of Earth Sciences, University of Geneva, Switzerland) for her contributions to foraminiferal studies and biostratigraphy.

Type material: Holotype: MHNG-2011-1-716a, fully recrystallized, Fe-Mn impregnated test in subaxial section, showing the scroll-shaped inner-chamber structure (Fig. 4B). Paratypes: dozens of specimens from the type locality (MHNG-75631 and MHNG-2011-1; e.g., Fig. 4A, C–M).

Type locality: Rot-Grau Schnöll Bruch, Adnet, Austria (see Fig. 1).

Type horizon: Hettangian–Sinemurian (Lower Jurassic) of the Schnöll Formation and the marmorea crust (see Fig. 1D–F).

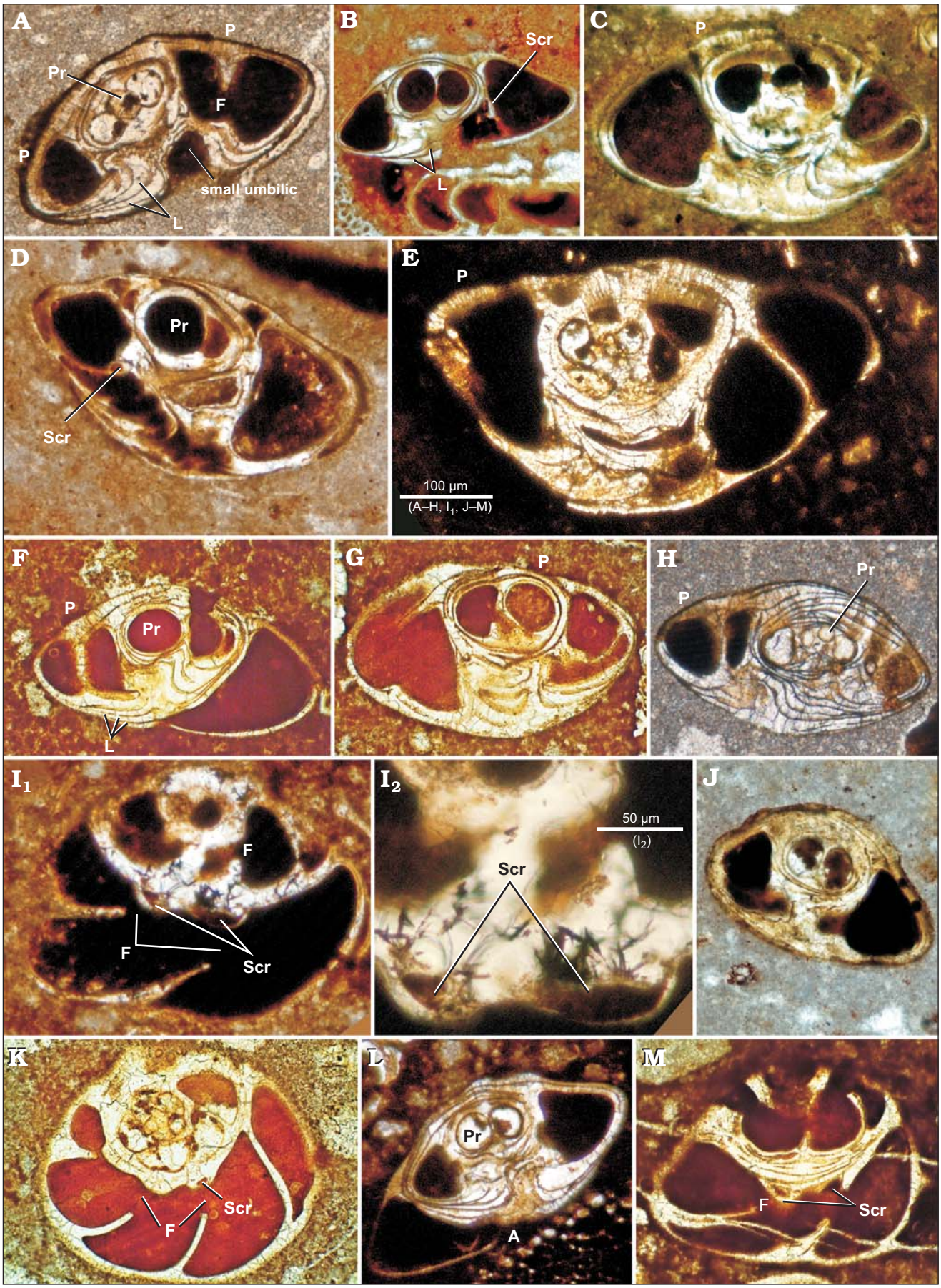
Material.—Type material only.

Diagnosis.—As for the genus, by monotypy.

Description.—The test is involute, low convexoplane to subplanoconcave, circular in outline, with a subrounded margin. The proloculus is globular (Fig. 4A, D, F, H, I_1, L), followed by about six to seven trochospirally coiled chambers per

← Fig. 3. Robertinid foraminifer *Velleditsiella spinaferra* gen. et sp. nov., uppermost Hettangian–lowermost Sinemurian, Adnet, Austria. Holotype (E), paratypes (A–D, F–P). **A**. MHNG-75631-1, subaxial section. **B**. 1620(2), oblique section. **C**. 1620(2), oblique section. **D**. 1620(2), subaxial section. **E**. MHNG-75631-2, subaxial section. **F**. 1620(8), subaxial section. **G**. MHNG-75631-2, oblique section. **H**. 1620(3), subaxial, slightly oblique section. **I**. 4a2(8), transverse, slightly oblique section. **J**. 1620(2), oblique section. **K**. MHNG-75631-2, oblique section. **L**. 1620(2), centered, subaxial section. **M**. 1620(9), oblique section. **N**. 1620(8), oblique section. **O**. 1620(3), transverse, slightly oblique section. **P**. 1620(2), transverse section. Abbreviations: A, aperture; Ch, chamber; F, foramen; iH, inner hook; NP, narrowest part of the chambers; P, perforations; Pr, proloculus; S, siphon; SO, secondary opening; Sp, spine.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use



Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

whorl on up to three-four whorls. Chambers, ovoid, slightly appressed in the juvenile part, progressively become subrhomboid and more angular. Separated by curved, oblique septa, they gradually increase in size and communicate via a wide, arch-like interiomarginal opening, as the aperture (Fig. 4A, I_1, K–M). Each chamber develops wall extensions that rapidly cover the spiral side of the test and progressively fill the umbilical depression (compare Fig. 4A, B, F, H, L). The test surface, usually not ornamented, may present minor protuberances (bumps) on the spiral side, related to local thickenings of the wall lateral extensions (e.g., Fig. 4L). An inner-chamber, scroll-shaped structure is fused to the aperture floor and extends, in a subvertical to oblique position, to the opposite wall of the chamber (e.g., Fig. 4B, D, I, K, M). Our specimens are all recrystallized into calcisparite. The ghost preservation of fine details of the original wall structure, such as laminae and fine perforations (e.g., in Fig. 4A–C, H) is due to an early Fe-Mn impregnation of walls.

Dimensions.—Specimens of *R. martinii* reach 280 μm in height and 450 μm in width. The proloculus shows a diameter ranging from 40–60 μm and chambers may attain 170 μm in height. Perforations, very fine, are about 2 μm in diameter.

Remarks.—The new species *R. martinii* is morphologically close and most likely phylogenetically related to the Upper Triassic species *Praereinholdella galei* Rigaud, Martini, and Vachard, 2015b. *Praereinholdella galei* only differs from *R. martinii* in its round aperture, internally simple chambers, and more angular test periphery. The subfamily Praereinholdellinae is also considered as the probable ancestor of the subfamilies Garantellinae, Epistomininae, and Reinholdellinae (see Rigaud et al. 2015b). As *Rossanella* gen. nov., the genera *Epistomina* Terquem, 1883, *Reinholdella* Brotzen, 1948, and *Garantella* Kaptarenko-Chernousova, 1956 also acquired their inner-chamber structures in the Lower Jurassic. The foraminiferal association is identical to that of *V. felicitaszae*.

Stratigraphic and geographic range.—The new species is only known from the uppermost Hettangian–lowermost Sinemurian (Lower Jurassic) of Adnet (Austria).

The phylogeny of Robertinida

Until recently, our knowledge of the evolution of the aragonitic order Robertinida was mostly founded on the pioneer works by Fuchs (1973, 1975). The family Oberhauserellidae was therefore regarded as the only survivor of the Triassic–Jurassic major extinction event and the unique ancestor of all post-Triassic Robertinida. Yet, Oberhauserellidae possess entirely evolute tests, which contrast with the rather sturdily laminar tests of post-Triassic robertinid, non-oberhauserellid lineages (superfamily Duostominoidea).

Rigaud et al. (2015b) entirely revised the taxonomy and early Triassic evolution of Robertinida, separating the oberhauserelloids and duostominoids at the superfamily level, and proposing other alternatives for the post-Triassic evolution of the group. In contrast to Oberhauserelloidea, Duostominoidea have showed a rapid diversification during the Triassic, giving rise to a large range of morpholotypes. Their evolution is notably marked by (i) the development of a planispiral coiling in *Asymmetrina*, *Involvina*, and *Plagiostomella*, (ii) the materialization of a siphon in *Pragsoconulus* and *Trochosiphonia*, (iii) the increasing folding of umbilical lamellae (papillose lamellae) in *Cassianopapillaria* and *Diplotremina*, and (iv) the formation of a double aperture (in *Variostoma*), possibly separated by a tenon in *Cassianopapillaria*, *Diplotremina*, and *Pillerita*. Based on the increasing complexity of the architecture in Triassic Robertinida, here considered as evolutionary acquisitions, and on account of their stratigraphic distribution, we propose here a new phyletic tree for Triassic–Early Jurassic Robertinida (Fig. 5). This tree combines observations and updates made by Rigaud et al. (2015b) with our new, Early Jurassic data. Robertinida are especially well-documented in the Carnian and, probably for that reason, show their greater generic diversity during this stage. In other Triassic stages, their record is lacunar. Part of their early evolution is most likely undisclosed. On account of their aragonitic, finely perforated and primarily bilamellar wall, high variability in chamber shape, and high trochospiral coiling, the genera *Pragsoconulus*, *Trochosiphonia*, and *Robertonella* are here interpreted as probable descendant of *Variostoma*. An alternative phyletic option would be to consider *Trochosiphonia* as a descendant of a Triassic "*Verneuilinoides*" and *Pragsoconulus* and *Robertonella* as descendants of Triassic Tetrataxidae but this polyphyletic hypothesis would only be founded on superficial morphological similarities (no structural evidence).

On account of their morphological and structural characteristics, the newly described Early Jurassic Robertinida constitute evidence that additional Triassic Robertinida lineages (not only the family Oberhauserellidae) survived the Triassic–Jurassic biotic crisis. With their distinctive conic elongate test and median siphon, Early Jurassic representatives of *Velleditsiella* gen et sp. nov. obviously originated from *Trochosiphonia*, known from Upper Triassic rocks of Tethyan and Panthalassan domains (Rigaud et al. 2015b).

← Fig. 4. Robertinid foraminifer *Rossanella martinii* gen. et sp. nov., uppermost Hettangian–lowermost Sinemurian, Adnet, Austria. Holotype (B), paratypes (A, C–M). Note the shape modifications from juvenile (e.g., A, B, F, J, L) to adult (e.g., I_1, M) and senile (E) forms. **A**. 4a2(8), axial section. **B**. Holotype, MHNG-2011-1-716a, subaxial section, displaying the distinctive scroll-shaped, inner chamber structure. **C**, **D**, **J**. MHNG-2011-1-716b-e, axial and subaxial sections. **E**. AU1L, slightly oblique, centered section. **F**, **G**. 1620(2), axial and subaxial sections. **H**. 4a1, slightly oblique, centered section. **I**. AU1K, subaxial section. **K**. 1620(2), sub-centered, slightly oblique section. **L**. AU1C, axial section. **M**. 1620(2), oblique section. Abbreviations: A, aperture, F, foramen, L, lamellae, P, perforations, Pr, proloculus, Scr, scroll-shaped, inner chamber structure.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

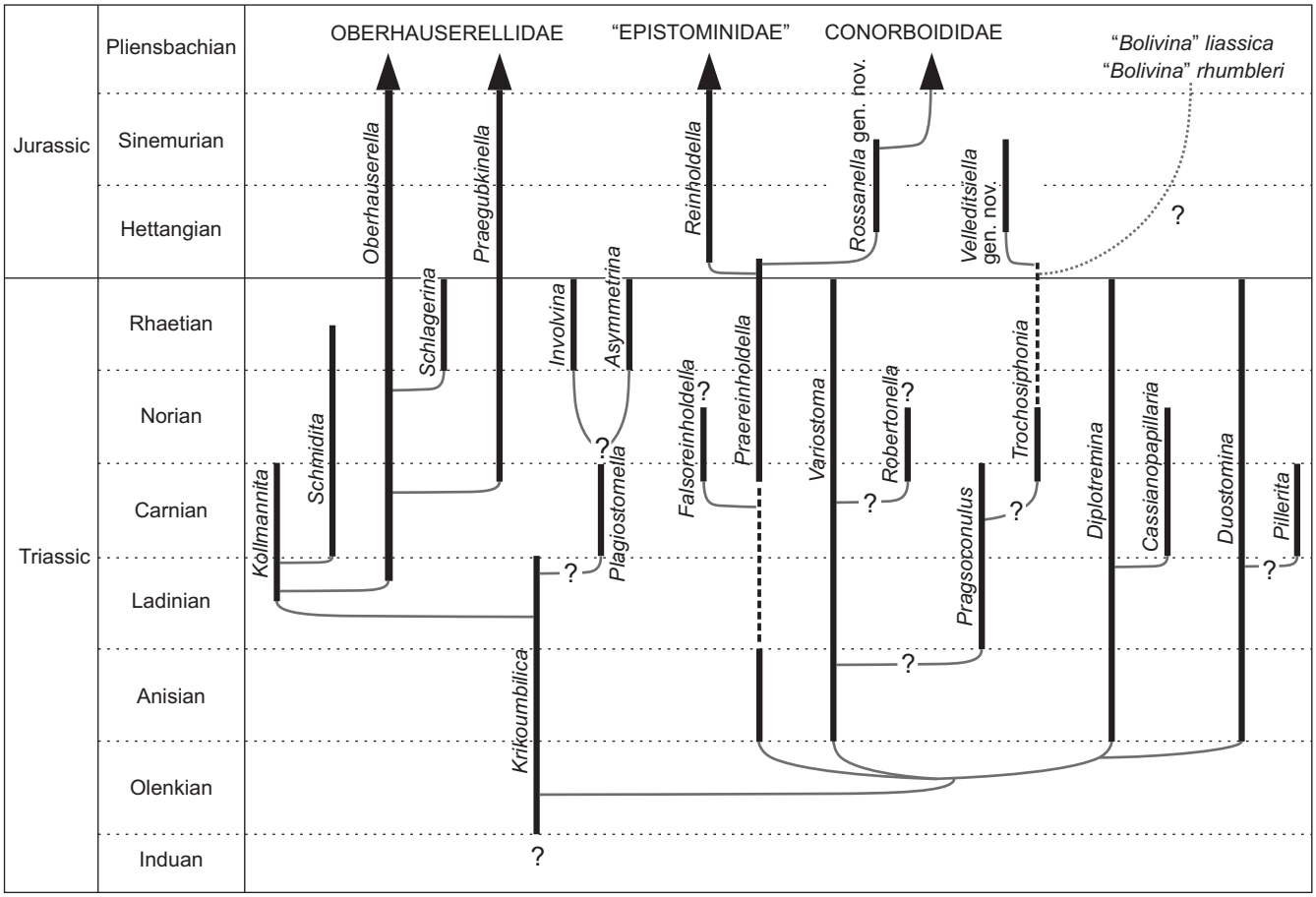


Fig. 5. Triassic–Early Jurassic evolution of the order Robertinida at the genus level (partly based on Rigaud et al. 2015b, with new data). Dashed lines indicate uncertain stratigraphic distribution, dotted lines indicate uncertain phyletic relationship.

Rossanella gen. et sp. nov. does not have affinities with any Oberhauserellidae but shares its distinctive test shape, laminar structure, and chamber morphology with Middle–Late Triassic Praereinholdellinae. This new genus also possesses the characteristic scroll-shaped, inner-chamber structure of the post-Triassic family Conorboididae and only differs from *Conorboides* in its simpler apertural morphology. Therefore, *Conorboides* most likely originated from *Rossanella*, which itself originated from a Praereinholdellinae. The last known Praereinholdellinae has been documented in the lowermost Hettangian of the Northern Calcareous Alps of Austria (Hillebrandt 2010: fig. 1 as "*Reinholdella* sp. A" and Hillebrandt 2012: pl. 4: 1, 4, 5; pl. 6: 3a, b as "cf. *Reinholdella* sp. nov."). This species shows an intermediary apertural system between Triassic Praereinholdellinae and post-Triassic Robertinina (sensu Rigaud et al. 2015b = Robertinida with an inner-chamber structure attached to the aperture), but does not possess a true internal plate yet. It is a good candidate as ancestor for the first Epistominidae sensu lato and/or Conorboididae. Hillebrandt (2010, 2012) incorrectly described an "arcus" (sensu Fuchs 1969) in this transitional species and regarded it as the Hettangian missing link between *Oberhauserella* and *Reinholdella*. The observed structure is in fact a simple thickening of the chamber roof (see Hillebrandt 2012: pl. 4: 5) and not the distinctive wall fold (arcus) characteristic of the family Oberhauserellidae (see Fuchs 1969 for details).

In combining published data (Fuchs 1973, 1975; Rigaud et al. 2015b) with our new observations, we propose a new phyletic tree for Mesozoic–Recent Robertinida families (Fig. 6). Interestingly, this phyletic tree shows that 60% of robertinid families survived the T/J biotic crisis, giving rise to at least two new superfamilies (Conorboididae and Epistominidae), as soon as the Hettangian. The earliest Jurassic records the first appearance of inner-chamber plates in Robertinida, which then rapidly display high morphological variabilities. Following their Early Jurassic development, the position and shape of these "toothplates" remain almost unchanged for several million years in both conorboidoid and ceratobuliminoid lineages. The function of these internal structures is still unknown but their origination is probably linked to environmental constraints, possibly related to the T/J major extinction event. As observed by Scott (1978), toothplate structures further partition the chambers and may impede the passage of cytoplasm. In view of their connection to the aperture, they may have played a role to face hostile environmental conditions, providing a better isolation from the surrounding environment.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

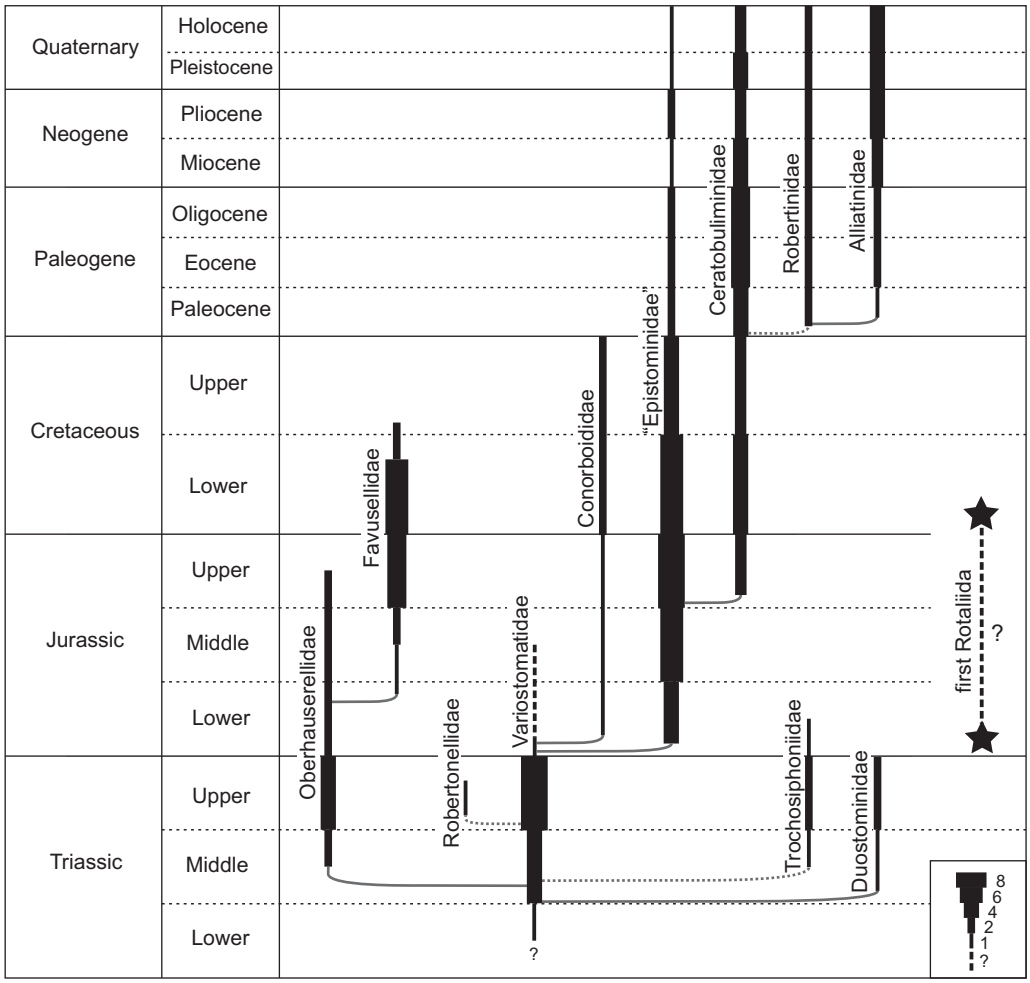


Fig. 6. Mesozoic–Recent phyletic tree of Robertinida, at the family level. Line width indicates the generic diversity for the different families (see bottom-right for associated number of genera). "Epistominidae" include the subfamilies Epistomininae, Garantellinae, and Reinholdellinae. Dashed lines indicate uncertain stratigraphic distribution, dotted lines indicate uncertain phyletic relationship.

Evolutionary implications

Molecular data have challenged traditional taxonomic and phylogenetic views on Foraminifera. The sequencing of calcitic forms has evidenced that the orders Buliminida, Rotaliida, and Globigerinida, as defined in Loeblich and Tappan (1987, 1992), are not monophyletic (e.g., Darling et al. 1997, 2009; de Vargas et al. 1997; Ujiié et al. 2008; Schweizer et al. 2008). Our understanding of the origination and long term evolution of calcitic foraminifers is limited. Molecular studies have demonstrated that, in these foraminifers, the mode of life, the acquisition of inner-chamber structures, and even the wall structure and coiling mode have a lower taxonomic value than previously widely accepted (see review in Schweizer et al. 2011). The adaptation to a planktonic mode of life occurred several times in the foraminiferal evolution (Ujiié et al. 2008; Darling et al. 2009), inner-chamber structures, such as the toothplates, can appear or disappear in the same lineage (Ujiié et al. 2008), and even when morphologically close, two species are not necessarily phylogenetically linked (see Ujiié et al. 2008; Schweizer et al. 2008). It indicates that multichambered calcitic lineages previously classified in the orders "Buliminida", "Globigerinida", and Rotaliida have experienced a parallel evolution.

Such an evolutionary pattern is also characteristic of the robertinid lineage. For example, several robertinid lineages developed inner-chamber structures (Duostominidae, Ceratobuliminoidea, and Conorboidoidea) and progressively more complex apertural system (Duostominidae, Trochosiphoniidae, Ceratobuliminoidea, and Conorboidoidea). As for calcitic foraminifers, distinct robertinids may have independently developed a planktonic lifestyle as both low and high conical Favusellidae (probably originated from two Triassic genera: *Oberhauserella* and *Praegubkinella*, respectively) are abundantly found in slope and basinal deposits of Middle–Upper Jurassic environments (BouDagher-Fadel et al. 1997; Wernli and Görög 2007).

In addition to the similarities observed in their evolution mode, the first known calcitic multichambered foraminifers are morphologically close to various Robertinida representatives. According to Fuchs (1973, 1975) and Tappan and Loeblich (1988), aragonitic Robertinida would be the direct ancestors of all calcitic foraminifers previously classified in the orders "Buliminida", "Globigerinida", and Rotaliida by Loeblich and Tappan

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

(1987). This monophyletic hypothesis, contested by molecular data (see molecular trees in Bowser et al. 2006 and Pawlowski et al. 2013, in which *Robertina* branches apart from all "Rotaliida" sensu lato), also lacks strong support in fossil data. The advent and rise of the order Rotaliida sensu lato (i.e., sensu Pawlowski et al. 2013, including the former orders Buliminida, Globigerinida, and Rotaliida of Loeblich and Tappan 1992) is one of the most obscure topics. Prior to the Early Cretaceous radiation of the group, no unequivocal data exists to prove or refute the prior existence of Rotaliida sensu lato, entailing a 100 Myrs uncertainty in their time of origination (Fig. 6). Actually, all Jurassic rotaliid-alike foraminifers may in fact possess monocrystalline or aragonitic walls (see Blackmon and Todd 1959; Wernli 1971; Piuz 2004). Due to common diagenetic alterations of foraminiferal walls, phylogenetic relationships have generally been presumed, at best from rough morphological similarities or stratigraphic compatibilities. Assumed direct phyletic links between the aragonitic family Oberhauserellidae and the calcitic families Turrilinidae (as proposed by Tappan and Loeblich 1988) or Guembelitriidae (as suggested by Fuchs 1975) are not even morphologically supported. With regard to their morphologic characteristics and stratigraphic distribution, the new genera *Velleditsiella* and *Rossanella* would offer more appropriate phylogenetic links. The "toothplate" extending between the chambers of calcitic Middle Jurassic "Turrilinidae" might indeed represent the result of the evolution of the Trochosiphoniinae siphon or the Conorboididae scroll-shaped structure, which are both related to the apertural system. It is, however, unknown whether Jurassic "Turrilinidae" are true turrilinids (i.e., with hyaline-radial calcitic walls). Some Early Jurassic biserial foraminifers originally described as calcitic bolivinids (i.e., "*Bolivina*" *liassica* and "*B.*" *rhumbleri*) are for example proved (by mineralogical determination methods) to be aragonitic in composition (Blackmon and Todd 1959).

Phylogenetic relationships between aragonitic and calcitic multichambered foraminifers lack constraints, but according to our data, a paraphyly and/or polyphyly of the Mesozoic–Recent robertinids and "rotaliids" sensu lato can be envisaged. Potential direct phylogenetic links between agglutinated and calcitic forms have been disregarded. Some Cretaceous rotaliids (e.g., gavelinellids, *Rotorbinella*) display an inner microgranular layer, which could be reminiscent of an unknown (but direct) microgranular/agglutinated ancestor. Similarly, the monophyly of Robertinida is not fully supported by stratigraphic and morphologic evidence (dashed lines in Figs. 5, 6). A polyphyletism cannot be excluded. The acquisition of an aragonitic wall from an agglutinated or microgranular ancestor is not unique to the order Robertinida. It occurred prior to the Triassic in the Fusulinida lineage, with the origination of the aragonitic superfamily Staffelloidea (Vachard 1990; Vachard et al. 2003, 2010) and may have re-happened later through independent lineages.

Conclusions

The discovery of missing links in the Robertinida lineage has improved our understanding of the early evolution and diversity of the order Robertinida. The family Oberhauserellidae should not be considered as the only Robertinida that spanned the T/J boundary, which impact on the Robertinida diversity has been overestimated. Together with oberhauserellids, the subfamilies Trochosiphoniinae and Praereinholdellinae survived the end-Triassic major biotic crisis, and the latter group notably gave rise to the superfamilies Ceratobuliminoidea and Conorboidoidea. In these superfamilies, the development of various inner-chamber structures may have favored survival during the hostile, post-crisis Lower Jurassic period.

The reconstruction of the Robertinida evolution is of primary importance to define potential long term phylogenetic links between aragonitic, microgranular/agglutinated, and calcitic multichambered foraminifers. Up to now, only few Robertinida have been sequenced in molecular studies. These robertinids are found on a branch of multichambered Textulariida (e.g., see Bowser et al. 2006: fig. 5.3), separated from calcitic multichambered foraminifers (= Rotaliida sensu lato, see Pawlowski et al. 2013). Although molecular results on few species must be considered with great caution, this data supports a polyphyletic Mesozoic origination of calcitic and aragonitic Globothalamea. The first calcitic "rotaliid" families are morphologically close to some Jurassic Robertinida but a transition between these forms cannot be reliably supported. The original nature and structure of the wall of most Jurassic foraminifers that have been classified in the calcitic orders Rotaliida and Spirillinida remain undefined. Such forms may, as the Early Jurassic species "*Bolivina*" *liassica* and "*B.*" *rhumbleri*, have possessed aragonitic walls. A re-evaluation of the Jurassic diversity of the aragonitic order Robertinida and its potential relationships with other foraminiferal groups is a requisite.

Acknowledgements

Malcolm Hart (Plymouth University, UK), Valery Vuks (A.P. Karpinsky Russian Geological Research Institute, St. Petersburg, Russia), and an anonymous reviewer are thanked for their helpful comments. SR thanks the Swiss Science National Foundation for the grant PBGEP2-145580.

References

Blackmon, D. and Todd, R. 1959. Mineralogy of some Foraminifera as related to their classification and ecology. *Journal of Paleontology* 33: 1–15.

Blau, J. 1987. Neue Foraminiferen aus dem Lias der Lienzer Dolomiten. Teil II (Schluß): Foraminiferen (Involutinina, Spirillinina) aus der Lavanter Breccie (Lienzer Dolomiten) und den Nördlichen Kalkalpen. *Jahrbuch der Geologischen Bundesanstalt* 130: 5–23.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

Blau, J. and Grün, B. 1997. Neue Involutinen (Foraminifera) aus dem marmorea-Hartgrund (Hettangium/Sinemurium) von Adnet (Österreich). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* 204: 247–262.

Böhm, F. 2003. Lithostratigraphy of the Adnet Group (Lower to Middle Jurassic, Salzburg, Austria). *In*: W.E. Piller (ed.): Stratigraphia Austriaca. *Österreichische Akademie der Wissenschaften* 16: 231–268.

Böhm, F., Ebli, O., Krystyn, L., Lobitzer, H., Rakús, M., and Siblík, M. 1999. Fauna, stratigraphy and depositional environment of the Hettangian–Sinemurian (Early Jurassic) of Adnet (Salzburg, Austria). *Abhandlungen der Geologischen Bundesanstalt* 56: 143–171.

BouDagher-Fadel, M.K., Banner, F.T., and Whittaker, J.E. 1997. *The Early Evolutionary History of Planktonic Foraminifera*. 269 pp. British Micropaleontology Society, London.

Bowser, S.S., Habura, A., and Pawlowski, J. 2006. Molecular evolution of Foraminifera. *In*: L. Katz and D. Bhattacharya (eds.), *Genomics and Evolution of Microbial Eukaryotes*, 78–93. Oxford University Press, Oxford.

Brotzen, F. 1948. The Swedish Paleocene and its foraminiferal fauna. *Sveriges Geologiska Undersökning* 42: 1–140.

Brotzen, F. 1963. Evolutionary trends in certain calcareous foraminifera on the Paleozoic–Mesozoic boundary: *In*: G.H.R. von Koenigswald, J.D. Emeis, W.L. Buning, and C.W. Wagner (eds.), *Evolutionary Trends in Foraminifera*, 66–78. Elsevier, Amsterdam.

Cavalier-Smith, T. 2003. Protists phylogeny and the high-level classification of Protozoa. *European Journal of Protistology* 39: 338–348.

Darling, K.F., Wade, C.M., Kroon, D., and Leigh Brown, A.J. 1997. Planktic foraminiferal molecular evolution and their polyphyletic origins from benthic taxa. *Marine Micropaleontlogy* 30: 251–256.

Darling, K.F., Thomas, E., Kasemann, S.A., Seears, H.A., Smart, C.W., and Wade, C.M. 2009. Surviving mass extinction by bridging the benthic/planktic divide. *Proceedings National Academy of Sciences* 106: 12629–12633.

de Vargas, C., Zaninetti, L., Hilbrecht, H., and Pawlowski, J. 1997. Phylogeny and rates of molecular evolution of planktic Foraminifera: SSU rDNA sequences compared to the fossil record. *Journal of Molecular Evolution* 45: 285–294.

di Bari, D. 1999. *Globigerina* like foraminifera (Oberhauserellidae) from the Triassic (Ladinian Carnian) of the San Cassiano Formation (Dolomites, Italy). *Abhandlungen der Geologischen Bundesanstalt* 56: 49–67.

di Bari, D. and Laghi, G. 1998. Mineralogy and test wall structure in duostominid foraminifers (Triassic, Dolomites, Italy). *Bollettino del Museo Civico di Storia Naturale di Venezia* 48: 247–254.

di Bari, D. and Rettori, R. 1996. *Papillaria laghii* gen. et sp. nov. (Foraminiferida) from the Triassic (Carnian) of the Dolomites, Italy. *Revue de Paléobiologie* 16: 21–28.

Dommergues, J.-L., Meister, C., and Böhm, F. 1995. New data on Austroalpine Liassic ammonites from the Adnet quarries and adjacent areas (Oberösterreich, Northern Calcareous Alps). *Jahrbuch der geologischen Bundesanstalt* 138: 161–205.

d'Orbigny, A. 1826. Tableau méthodique de la classe des Céphalopodes: *Annales des Sciences Naturelles* 7: 245–314.

d'Orbigny, A. 1846. *Foraminifères fossiles du Bassin Tertiaire de Vienne (Autriche)*. 312 pp. Gide et Cie, Paris.

Ebli, O. 1997. Sedimentation und Biofazies an passiven Kontinentalrändern: Lias und Dogger des Mittelabschnittes der Nördlichen Kalkalpen und des frühen Atlantik (DSDP site 547B, offshore Marokko). *Münchner Geowissenschaftliche Abhandlungen*, *Reihe A* 32: 1–255.

Fuchs, W. 1969. Zur Kenntnis des Schalenbaues der zu den Trias-"Globigerinen" zählenden Foraminiferengattung *Praegubkinella*. *Verhandlungen der Geologischen Bundesanstalt* 2: 158–167.

Fuchs, W. 1973. Ein Beitrag zur Kenntnis der Jura, "Globigerinen" und verwandter Formen an Hand polnischen Materials des Callovien und Oxfordien: *Verhandlungen der Geologischen Bundesanstalt* 3: 445–487.

Fuchs, W. 1975. Zur Stammesgeschichte der Planktonforaminiferen und verwandter Formen im Mesozoikum. *Jahrbuch der Geologischen Bundesanstalt* 118: 193–246.

Gorbatchik, T.N. and Kuznetsova, K.I. 1986. Study of shells mineral composition of planktonic Foraminifera. *Voprosy Mikropaleontologii* 28: 42–44.

Hart, M.B., Hylton, M.D., Oxford, M.J., and Smart, C.W. 2003. The search for the origin of the planktic Foraminifera. *Journal of the Geological Society* 160: 341–343.

Hart, M.B., Hudson, W., and Smart, C.W. 2010. Origin and early evolution of Jurassic planktic Foraminifera. *Earth Sciences Frontiers, Special Issue* 17: 209–210.

Hillebrandt, A., von 2010. Aragonitic Foraminifera (Robertinina) from the Triassic–Jurassic Boundary Interval of the Northern Calcareous Alps. *Earth Sciences Frontiers*, *Special Issue* 17: 70–72.

Hillebrandt, A. von 2012. Are the Late Triassic to Early Jurassic aragonitic Oberhauserellidae (Robertinina) the ancestors of planktonic Foraminifera? *Neues Jahrbuch Geologie Paläontologie Abhandlungen* 266: 199–215.

Hudson, W., Hart, M.B., Sidorczuk, M., and Wierzbowski, A. 2005. Jurassic planktonic Foraminifera from Pieniny Klippen Belt and their taxonomic and phylogenetic importance (Carpathians, southern Poland). *Tomy Jurajskie* 3: 1–10.

Kieslinger, A. 1964. *Die nutzbaren Gesteine Salzburgs*. xii + 436 pp. Das Bergland Buch, Salzburg.

Loeblich, A.R., Jr. and Tappan, H. 1987. *Foraminiferal Genera and Their Classification*. 1182 pp. Van Nostrand Reinhold, New York.

Loeblich, A.R., Jr. and Tappan, H. 1992. Present status of foraminiferal classification. *In*: Y. Takayanagi and T. Saito (eds.), *Studies in Benthic Foraminifera, Benthos'90*, 93–102. Tokai University Press, Tokyo.

Mikhalevich, V.I. [Mihalevič, V.I.] 1980. Taxonomy and evolution of the foraminifera in the light of the new data on their cytology and ultrastructure [in Russian]. *Trudy Zoologičeskogo Instituta, Akademiâ Nauk SSSR* 94: 42–61.

Nikitenko, B.L. and Mickey, M.B. 2004. Foraminifera and ostracodes across the Pliensbachian–Toarcian boundary in the Arctic Realm (stratigraphy, palaeobiogeography and biofacies). *In*: A.B. Beaudoin and M.J. Head (eds.), The Palynology and Micropalaeontology of Boundaries. *Geological Society of London*, *Special Publication* 230: 137–174.

Pawlowski, J., Holzmann, M., and Tyszka, J. 2013. New supraordinal classification of Foraminifera: Molecules meet morphology. *Marine Micropaleontology* 100: 1–10.

Piuz, A.D. 2004. *Micropaléontologie d'une plate-forme bioclastique échinodermique: Les calcaires à entroques du Bajocien du jura méridional et de Bourgogne*. 267 pp. Thèse n° 3566. Université de Genève, Genève.

Reiss, Z. and Schneidermann, N. 1969. Ultramicrostructure of *Hoeglundina*. *Micropaleontology* 15: 135–144.

Rigaud, S., Blau, J., Martini, R., and Rettori, R. 2013. Taxonomy and phylogeny of the Trocholinidae (Involutinina). *Journal of Foraminiferal Research* 43: 317–339.

Rigaud, S., Blau, J., Martini, R., and Rettori, R. 2015a. Taxonomy, phylogeny, and functional morphology of the foraminiferal genus *Involutina*. *Acta Palaeontologica Polonica* 60: 235–244.

Rigaud, S., Martini, R., and Vachard, D. 2015b. Early evolution and new classification of the order Robertinida (Foraminifera). *Journal of Foraminiferal Research* 45: 3–28.

Schweizer, M., Pawlowski, J., Kouwenhoven, T.J., Guiard, J., and Van der Zwaan, B. 2008. Molecular phylogeny of Rotaliida (Foraminifera) based on complete small subunit rDNA sequences. *Marine Micropaleontology* 66: 233–246.

Schweizer, M., Jorissen, F., and Geslin, E. 2011. Contributions of molecular phylogenetics to foraminiferal taxonomy: General overview and example of *Pseudoeponides falsobeccarii* Rouvillois, 1974. *Comptes Rendus Paleovol* 10: 95–105.

Schlagintweit, F., Rigaud, S., and Wilmsen, M. 2015. Insights from exceptionally preserved Cenomanian trocholinids (benthic foraminifera) of northern Cantabria, Spain. *Facies* 61: 1–27.

Scott, G.H. 1978. Shell design in *Bolivinita quadrilatera*, *B. pohana*, and

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use

B. compressa (Foraminiferida). *New Zealand Journal of Geology and Geophysics* 21: 85–95.

Septfontaine, M. 1988. Vers une classification évolutive des Lituolides (Foraminifères) Jurassiques en milieu de plate-forme carbonate. *Revue de Paléobiologie, Benthos '86*, *Volume Spécial* 2: 229–256.

Tappan, H. and Loeblich, A.R., Jr. 1988. Foraminiferal evolution, diversification and extinction. *Journal of Paleontology* 62: 695–714.

Terquem, O. 1883. Cinquième mémoire sur les foraminifères du système oolithique de la zone à Ammonites parkinsoni de Fontoy (Moselle). *Bulletin de la Société géologique de France, Ser. 3* 11: 339–406.

Thalmann, H.E. 1952. Bibliography and index to new genera, species and varieties of foraminifera for the year 1951. *Journal of Paleontology* 26: 953–992.

Ujiié, Y., Kimoto, K., and Pawlowski, J. 2008. Molecular evidence for an independent origin of modern triserial planktonic foraminifera from benthic ancestors. *Marine Micropaleontology* 69: 334–340.

Vachard, D. 1990. Fusulinoids, smaller foraminifera and pseudoalgae from southeastern Kelantan (Malaysia) and their biostratigraphic and paleogeographic value. *In*: H. Fontaine (ed.), *Ten Years of CCOP Research on the Pre-Tertiary of East Asia, CCOP Technical Publications*, 43–167. CCOP Technical Secretariat, Bangkok.

Vachard, D., Zambetakis-Lekkas, A., Skourtsos, E., Martini, R., and Zaninetti, L. 2003. Foraminifera, algae and carbonate microproblematica from the late Wuchiapingian/Dzhulfian (late Permian) of Peloponnesus (Greece). *Rivista Italiana Paleontologia Stratigrafia* 109: 339–358.

Vachard, D., Pille, L., and Gaillot, J. 2010. Palaeozoic Foraminifera: Systematics, palaeoecology and responses to global changes. *Revue de Micropaléontologie* 53: 209–254.

Wernli, R. 1971. Les Foraminifères du Dogger du Jura méridional (France). *Archives Sciences Genève* 24 (2): 305–364.

Wernli, R. 1987. Les protoglobigérines (foraminifères) du Bajocien inférieur des Sofs (Rif, Maroc). *Eclogae Geologicae Helvetiae* 80: 817–829.

Wernli, R. and Görög, Á. 2007. Protoglobigérines et Oberhauserellidae (Foraminifères) du Bajocien–Bathonien du Jura méridional, France. *Revue de Micropaléontologie* 50: 185–205.

Wiewióra, A. 1964. Rentgenometryczna identyfikacja substancji mineralnej skorupek otwornic jurajskich. *Przegląd Geologiczny* 11: 455–456.

Downloaded From: https://bioone.org/journals/Acta-Palaeontologica-Polonica on 28 Mar 2024
Terms of Use: https://bioone.org/terms-of-use