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

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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. spinafera* gen. et sp. nov., the first known representative of the superfamly Conorboidioidea, which includes the species *R. martinii* gen. et sp. nov. Considering their structural and morphological characteristics, *Velleditsiella* and *Rossanella* gen. nov., 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.


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


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, 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.

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).

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 *Schlotheimia marmorea* and exceptionally diversified foraminifer assemblages (Blau 1987; Blau and Grün 1997; Ebli 1997; Böhm et al. 1999; Rigaud et al. 2013, 2015a).

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
fossil types do not respond equally to diageneisis, a detailed taxonomic 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 whors 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 Mikhailovich, 1980**

Suborder Duostominina Rigaud, Martini, and Vachard, 2015b
Superfamily Duostominoidea Brotzen, 1963
Family Trochosiphoniidae Rigaud, Martini, and Vachard, 2015b
Subfamily Trochosiphoninae 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. spinifera* gen. et sp. nov.

**Diagnosis.**—Trochosiphoninae 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. 2F, 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, 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
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 aper-
tures, allowing shorter connections between each chamber and the surrounding environment.

**Stratigraphic and geographic range.**—Uppermost Hettan-
gian–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 lam
inar (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 *Trouchosiphonia stanleyi* Rigaud, Martini, and Vachard, 2015c 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, Frenzenniala, Involutina, Kristantollmania, Licispirella, Papillaconus, Semiinvoluta, Trocholina*) (Rigaud et al. 2013) and Robertinida (i.e., *Velleditsiella spinaferra* gen. et sp. nov., *Rossanella martini* gen. et sp. nov., *Oberhauserella*). Other foraminifers are calcitic nodosariids and miolids. 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 prolocular is globular (Fig. 3L), followed by trochospirally arranged pear-shaped chambers, moderately enlarging on up to seven whorls. Chambers, loosely coiled and separated...
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 \( \mu m \) in height and 250 \( \mu m \) in width. The spiral angle varies around 40°. The siphon is about 20–25 \( \mu m \) in width. In section, spines commonly reach 10–40 \( \mu m \) 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 Mikhailich, 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, Garantellininae, and Reinholdellininae) 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 martini* 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 *Praereinholdsella* and Jurassic–Cretaceous *Conorboides*. Contrary to *Rossanella* gen. nov., *Praereinholdsella* 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–lowest Sinemurian (Lower Jurassic) of Adnet (Austria).

**Rossanella martini** 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 sub planoconcave, circular in outline, with a subrounded margin. The proloculus is globular (Fig. 4A, D, F, H, I, L), followed by about six to seven trochospirally coiled chambers per
that of Lower Jurassic. The foraminiferal association is identical to and Vachard, 2015b.

Triassic species close and most likely phylogenetically related to the Upper diameter.

test, 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 subventral to oblique position, to the opposite wall of the chamber (e.g., Fig. 4B, D, I, K, M). Our specimens are all recrystallized into calcisparites. 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. martini* 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. martini* 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. martini* 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 *Epistoma* Terquem, 1883, *Reinholdella* Brotzken, 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 were 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 evolve 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 duostominooids at the superfamily level, and proposing other alternatives for the post-Triassic evolution of the group. In contrast to Oberhauserelloidae, Duostominoidea have showed a rapid diversification during the Triassic, giving rise to a large range of morphotypes. Their evolution is notably marked by (i) the development of a planispiral coiling in *Asymemetrina*, *Involvina*, and *Plagiostomella*, (ii) the materialization of a siphon in *Pragsoconulus* and *Trochosphonia*, (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 phylectic 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 undiscovered. On account of their aragonitic, finely perforated and primarily bilamellar wall, high variability in chamber shape, and high trochospiral coiling, the genera *Pragsoconulus*, *Trochosphonia*, and *Robertonella* are here interpreted as probable descendant of *Variostoma*. An alternative phylectic option would be to consider *Trochosphonia* 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 *Trochosphonia*, known from Upper Triassic rocks of Tethyan and Panthalassan domains (Rigaud et al. 2015b).

Fig. 4. Robertinid foraminifer *Rossanella martini* 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., I1, 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. AU1A, 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.
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 Robertinitina (sensu Rigaud et al. 2015b = Robertinitida 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 phylogenetic tree for Mesozoic–Recent Robertinida families (Fig. 6). Interestingly, this phylogenetic tree shows that 60% of Robertinitida 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 Robertinitida, 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 origin 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.

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 phylogenetic 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 foraminifer 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 Robertinida lineage. For example, several Robertinida lineages developed inner-chamber structures (Duostominidae, Ceratobuliminioidea, and Conorboidioidea) and progressively more complex apertural systems (Duostominidae, Trochosiphoniidae, Ceratobuliminioidea, and Conorboidioidea). As for calcitic foraminifers, distinct Robertinida may have independently developed a planktonic lifestyle as both lower and high conical Favusellidae (probably originated from two Triassic genera: Oberhauserella and Praegubkinella, respectively) are abundantly found in slope and basin deposits of Middle–Upper Jurassic environments (BouDagher-Fadel et al. 1997; Wernli and Görög 2007).

In addition to the similarities observed in their evolutionary 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.
(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 Löeblich 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; Piaz 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 Turritiidae (as proposed by Tappan and Löeblich 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 “Turritiidae” might indeed represent the result of the evolution of the Trochosiphoniinae siphon or the Conorroidae scroll-shaped structure, which are both related to the apertural system. It is, however, unknown whether Jurassic “Turritiidae” are true turritinids (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 polyphyley of the Mesozoic–Recent robertinids and “rotaliids” sensu lato can be envisaged. Potential direct phyletic links between agglutinated and calcitic forms have been disregarded. Some Cretaceous robertinids (e.g., gavelinellids, Rotorbixinella) 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 Trochosiphoninae and Praereinholdellinae survived the end-Triassic major biotic crisis, and the latter group notably gave rise to the superfamilies Ceratobuliminoida and Conorboioida. 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 a 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 “rotalid” 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.

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Rigaud and Blau—Robertinid Foraminifers from Early Jurassic of Austria


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