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

SYLVAIN RIGAUD and JOACHIM BLAU


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., the first known representative of the superfamily Conorbioidea, which includes the species *R. martini* 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, Conorbioidea, inner-chamber structures, marmorea crust, Jurassic, Austria.

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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 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 Conorbioidea (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; Ujić 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
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 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
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 recrystal- lization 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 Mikhailевич, 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. spiniferra 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, 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 Pragosconidus 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 unbilabial 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 60°. 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, Frenztenella, Involutina, Kristantollmannia, Licpisrella, Papillacous, 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 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-7563-1-2, 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., Figs. 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. 3L, 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
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 sec-
ondary 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 recrys-
tallized 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 spinaffera gen. et sp. nov. reach a maximum of about 400
μm in height and 250 μm in width. The spiral angle varies
around 40°. The siphon is about 20–25 μm in width. In section,
spines commonly reach 10–40 μm in length.

Remarks.—Velleditsiella spinaffera 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 spinaffera 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 Mikhailievich, 1980
Superfamily Conorboidoidea Thalmann, 1952
Family Conorboididae Thalmann, 1952 (emended)

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

Genus Rossanella nov.

Etymology: In honor of Rossana Martini (Department of Earth Sci-
ences, 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-cham-
er, 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-cham-
ber structures whereas Conorboides presents a slightly more
complex apertural system (e.g., low interiomarginal slit par-
tially 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 Hettan-
gian–lowermost Sinemurian (Lower Jurassic) of Adnet
(Austria).

Rossanella martini sp. nov.

Fig. 4.

Etymology: In honor of Rossana Martini (Department of Earth Sci-
ences, 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
whorl on up to three-four whorls. Chambers, ovoid, slightly appressed in the juvenile part, progressively become sub-ellipsoidal 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, 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* Broten, 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. felicitasae*.

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 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 *Asymmetrina*, *Involvina*, and *Plagiostomella*, (ii) the materialization of a siphon in *Pragsoconulus* and *Trochosiphonia*, (iii) the increasing folding of umbilical lamellae (papillole 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).
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 Oberhauerella 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 Oberhauerellae (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.
**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), 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, Ceratobuliminidae, and Conorboiidae) and progressively more complex apertural system (Duostominidae, Trochosiphonidae, Ceratobuliminidae, and Conorboiidae). 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.
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 Ceratobuliminioidea and Conoroibioidea. 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, 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 Globothalamia. 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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