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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 ground. We describe two new genera, *Velleditisella* gen. nov., a microgastropod look-alike foraminifer, which includes the species *V. felicitaszae* gen. et sp. nov. and *V. spinaffera* gen. et sp. nov., and *Rossanella* gen. nov., the first known representative of the superfamaly Conorboidoidea, which includes the species *R. martini* gen. et sp. nov. Considering their structural and morphological characteristics, *Velleditisella* 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.

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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 Rotalida 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; Ujiï 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, 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.

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 foraminiferal 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 robaritinid fossil tests have been directly analyzed by mineralogical determination methods (Wiewióra 1964; Fuchs 1969; Gorbachik 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 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 Pawłowski et al. (2013) and Rigaud et al. (2015b).

### Systematic palaeontology

**Subphylum Foraminifera d’Orbigny, 1826**

**Class Globothalamea Pawłowski, Holzmann, and Tyszka, 2013**

Order Robertinida Mikhailевич, 1980

Suborder Duostomininina 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:** *V. spinifera* 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 foraminifer 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 Pragosconulus 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 wall of each additional chamber; Fig. 2A, B). On the spiral side, the suture is covered by thick but short lateral outer wall of each additional chamber; Fig. 2A, B).

The species occurs with representatives of the aragonitic orders Involutinida (i.e., Coronaserra, Coronipora, Frenzenella, Involutina, Kristantollmania, Licispirella, Papillacomus, Semiinvoluta, Trocholinia) (Rigaud et al. 2013) and Robertinida (i.e., Velleditsiella spinaferra gen. et sp. nov., Rossanella martini gen. et sp. nov., Oberhauerserella). 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...
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 40°. 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 Duostominioidea 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 Mikhailievich, 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 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 *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.

**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, I1, 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- 

rhomboid 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. martini reach 280 μm in 

height and 450 μm in width. The proloculus shows a di- 

meter 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 an-

cestor of the subfamilies Garantellinae, Epistomininae, and 

Reinholdellinae (see Rigaud et al. 2015b). As Rossanella gen. 

nov., the genera Epistoma 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–lowest Sinemurian (Lower Jurassic) of Adnet (Austria).

The phylogeny of Robertinida

Until recently, our knowledge of the evolution of the arago-

natic 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 pos- 

sess entirely evolve tests, which contrast with the rather 

sturdily laminar tests of post-Triassic robertinid, non-ober-

hauserellid lineages (superfamily Duostominoidae).

Rigaud et al. (2015b) entirely revised the taxonomy 

and early Triassic evolution of Robertinida, separating the 

oberhauserelloids and duostomoids at the superfamily 

level, and proposing other alternatives for the post-Triassic 

evolution of the group. In contrast to Oberhauserellidae, 

Duostominoidae 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 Pragosconulus 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 ac-
quisitions, and on account of their stratigraphic distribu-

On account of their morphological and structural char-

acteristics, the newly described Early Jurassic Robertinida 

constitute evidence that additional Triassic Robertinida lin-

eages (not only the family Oberhauserellidae) survived the 

Triassic–Jurassic biotic crisis. With their distinctive conic 

elongate test and median siphon, Early Jurassic represen-

tatives 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 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 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.
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, Ceratobuliminioidea, and Conorboidoidea) and progressively more complex apertural system (Duostominidae, Trochosiphoniidae, Ceratobuliminioidea, 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.
(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-olate foraminifers may in fact possess monocrystalline or aragonitic walls (see Blackmon and Todd 1959; Wernli 1971; Pizzi 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 phylectic links between the aragonitic family Oberhauerellidae 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” between the chambers of calcitic Middle Jurassic “Turrilinidae” might indeed represent the result of the evolution of the Trochosiphoninae siphon or the Conorbitidae 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 boli-
vinds (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 phylectic links between agglutinated and calcitic forms have been disregarded. Some Cretaceous rotilalids (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 Fusulinata 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 Oberhauerellidae 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 Oberhauerellids, the subfamilies Trochosiphoninae and Prae reinholdellinae survived the end-Triassic major biotic crisis, and the latter group notably gave rise to the super-
families Ceratobuliminoida and Conorbitidae. 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 phyloge-
etic 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 “ro-
taliid” 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 “Bovilina” 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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