Early Jurassic aragonitic foraminifers are outstandingly well-preserved in the Marmorea crust, a multiphased ferromanganese layer limiting the Schnöll and Adnet formations (Adnet, Northern Calcareous Alps, Austria). This remarkable preservation, related to the pervasive impregnation of aragonitic tests prior to their recrystallization, allowed observing unknown diagnostic features of the genus Involutina, which typifies the Suborder Involutinina. Thanks to a detailed examination of the Adnet specimens, this paper clarifies the taxonomy, systematic position, and phylogeny of Involutina. A new diagnosis, structural model, and lineage are introduced for the group. Involutina is the direct descendant of Aulotortus and the two taxa probably showed a parallel evolution. As Aulotortus, Involutina presents a high intraspecific variability and its diversity must be revised downward. Current phylogenetic and taxonomic frames of the Suborder Involutinina are firmly questioned as, contrary to previous schemes, the type-genus possesses more than one lamellar deposit per whorl. In Involutina, the height and distribution of papillae on [...]


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Taxonomy, phylogeny, and functional morphology of the foraminiferal genus *Involutina*

SYLVAIN RIGAUD, JOACHIM BLAU, ROSSANA MARTINI, and ROBERTO RETTORI

The genus *Involutina* Terquem, 1862, which typifies the suborder, is a major constituent of latest Triassic and Early Jurassic carbonate rocks. It is particularly abundant in "basinal-like" environments and rapidly recovered from the Triassic–Jurassic extinction event. Although a potential biostratigraphic and paleoecologic marker, it remains an unsatisfactory tool. Its specific to generic recognition, strongly dependent on the wall preservation, is intricate and details of its innermost structure are imperfectly described. Based on the thorough examination of remarkably well preserved specimens, this study aims to improve our knowledge of the morphology, phylogeny, and paleoecology of *Involutina*.


Geological setting

The studied material comes from the Adnet area in the Northern Calcareous Alps (Austria). Located approximately 12 kilometers southeast 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 Schnöll Quarry (Quarry XXXI according to Kieslinger 1964). There, samples have been collected in the “marmorea-crust”, a multiphased ferromanganese layer (hardground) that forms the boundary bed between the Early Jurassic Schnöll Formation (= “Enzesfelder Kalk” in Blau and Grün 1996, 1997) and the Adnet Formation. According to Böhm et al. (1999) and Böhm (2003), the “marmorea-crust” is a guide horizon, latest Hettangian to earliest Sinemurian in age.

The red limestone of the “marmorea-crust” is particularly rich in echinoderms, gastropods, ammonites, and foraminifers. In our thin sections, foraminiferal assemblages are dominated by aragonitic foraminifers, and Involutina liassica is the most common form. Like other aragonitic fossils, specimens of Involutina are completely recrystallized but locally, an early, pervasive ferromanganese impregnation of their wall-microporosity has permitted the fine preservation of their original wall architecture. This particularity allowed us to observe features generally obliterated by diagenesis.

The Involutinina classification: its origin and limitations

The suborder Involutinina Hohenegger and Piller, 1977 unites tubular foraminifers with an aragonitic wall structure. Piller (1978) and di Bari and Laghi (1994) have defined two major models for the Involutinina mode of test construction. In the “Triadodiscus model”, the laminar deposits or first order lamellae (L1 lamellae sensu Piller 1978) are discontinuous but would form by stacking one continuous laminar extension or second order lamella (L2 lamella sensu Piller 1978) per whorl. In the “Aulotortus model”, the L1 lamellae are continuous but are laterally tapered such that they form two distinct L2 lamellae per whorl (or one L2 lamella per half whorl), which are successively interfingered in the umbilical region. A third model was proposed by Piller (1978, 1983) for Involutina and Trocholina. This model is close to that proposed by di Bari and Laghi (1994) for Triadodiscus and can be considered as a variant of the “Triadodiscus model”, like the “Lamelliconus” and “Prorakusia” submodels of di Bari and Laghi (1994).

The aim of this paper is not to discuss these two major models. However, it has to be noted that the reliability of each model has not been irrefutably proved. The distinction between the two modes of test construction results from the observation of a small number of very well-preserved specimens. As inadequately oriented sections can be misleading for the observer (see Piller 1983: fig. 4), a model established only on a few specimens is unreliable. In addition, the correspondence between the “Triadodiscus model” (di Bari and Laghi 1994: pl. 4: 2) and the associated high-quality illustrations of Triadodiscus (di Bari and Laghi 1994: pl. 3: 4; pl. 4: 1) is questionable. Finally, in specimens known to represent the “Aulotortus model” (e.g., Aulotortus, Coronipora, Frentzenella), the diagenesis often obliterates the lamellae, giving the impression that only one L2 lamella is formed per whorl. This diagenetic alteration particularly affects the L1 lamellae, which are especially minute and discontinuous in Triadodiscus.

The present high rank Involutinina systematic subdivision is partly based on these two major models (Zaninetti 1984; Zaninetti et al. 1987; Loeblich and Tappan 1987). Nevertheless, because of preservation problems, architectural models have been identified in only few forms. The suborder is typified by the genus Involutina in which the lamellae arrangement remains uncertain, entailing confusion in the lineage classification. Actually, the systematic position of the involutinins is for the most part hypothetical and phylogenetic links between different lineages are speculative. In spite of that, in the latest proposed phylogenetic tree (di Bari and Laghi 1994: fig. 7), the majority of Involutinina taxa, Involutina included, have been postulated to have originated from Triadodiscus (“Triadodiscus model”).
Structure and morphology of *Involutina*

In *Involutina*, the test architecture is unvarying. All involutins are non-septate, perforate, and possess papillose lamellae in the umbilical region. As explained by Piller (1978, 1983), papillae are originated by local elongations of the aragonite needles forming the laminae (L1 lamellae). The resulting laminar thickenings render difficult the examination of the L2 lamellae that may, according to the section orientation, appear falsely interrupted. Contrary to the previous schemes (Piller 1978, 1983), our examination of numerous centered, axial sections clearly shows that *Involutina* possesses at least two L2 lamellae per whorl that are, as in the “Aulotortus model”, successively interfingered in the median part of the umbilical region (Fig. 2A, B, D, E, H).

In contrast to the test architecture, the morphology of elements constituting the test of involutins varies considerably. In *Involutina liassica* (Jones in Brodie, 1853), the type-species of *Involutina*, a large range of variability in the test size and shape, the tubular chamber morphology and its position related to the previous whorl, the lamellae thickness, the papillae size, number, and repartition, and the perforations size and their connection exists (Fig. 2A–G). Dimorphism is well- pronounced (see Schweighauser 1951: figs. 5–8). Megalospheric forms display a larger proloculus and a lower number of coils than microospheric forms but, as for other involutins (Koehn-Zaninetti 1969), always show smaller tests. Within the same morphotype, the test may be more than twice as big or as thick, depending on the tubular chamber height and the laminar deposits thickness. The mode of coiling, generally planispiral, may also show some irregularities or oscillations (e.g., Schlagintweit and Piller 1990: pl. 1: 1, 14). The papillose lamellae may be more or less pronounced, forming more or less prominent and numerous papillae on the test surface. The perforations are highly variable in diameter, randomly distributed, and possibly form large canals that may merge (Fig. 2A, C, E, F). Lastly, along the ontogeny of the same specimen, the tubular chamber morphology may change significantly due to the optional development of a tube floor (Fig. 2A–F). The latter observation contests the model proposed by Piller (1978, 1983) for the mode of construction of the tubular chamber.

**Involutina model**

The current models of test construction of *Involutina* (Koehn-Zaninetti 1969; Piller 1978; Blau 1987b) do not integrate the whole complexity of the form. They are based on specimens in which the aragonite needles, laminar deposits (L1 lamellae), and lateral laminar extensions of the tube wall (L2 lamellae) are only partially preserved. In our material, only relics of the aragonite needles and the laminar deposits are preserved but in some specimens, the outline of the laminar extensions is entirely emphasized by the ferromanganese impregnation. Based on a detailed examination of *Involutina liassica*, we herein propose a new model for the *Involutina* structure (Fig. 3). This structural model derives from the study of several randomly oriented sections and does not correspond to a single specimen. Its difference from previous models is largely founded on the arrangement of the laminar extensions that are interfingered in the umbilical region (as in the “Aulotortus model”). Our model clearly contrasts with Piller’s model (1978) in which only one lamella is formed per whorl and contests the latest Involutinina phylogenetic tree proposed by di Bari and Laghi (1994).

**Taxonomy of *Involutina***

The genus *Involutina* was introduced by Terquem (1862: 450), prior to the advent of the International Rules for Zoological Nomenclature (IRZN). Terquem (1862) described two species within the genus: *Involutina silicea* Terquem, 1862 and *Involutina jonesi* Terquem and Piette in Terquem, 1862 (Terquem 1862: 450–451 and 461, respectively), but did not mention which one was the type-species for the genus. Some authors have considered *I. silicea* as the type-species (e.g., Loeblich and Tappan 1954). However, in an earlier work, Bornemann (1874) recognized differences in the wall composition of the two species and, by placing *I. silicea* into *Ammodiscus* Reuss, 1862, he only retained *I. jonesi* in *Involutina*. Because, as stated by Brady (1864), *I. jonesi* is a junior synonym of *I. liassica* (Jones in Brodie, 1853), *Nummulites liassicus* Jones in Brodie, 1853 (= *Involutina liassica*) must be regarded as the type-species of *Involutina* (Brady 1864; Bornemann 1874; Wicher 1952; Kristan 1957; Koehn-Zaninetti 1969; Gušić 1975; Piller 1978; Loeblich and Tappan 1987).

It is generally believed that the genus *Involutina* is characterized by a high interspecific variability and numerous species have been introduced into the genus based on differences observed in the test and tubular chamber morphology. Our study, however, emphasizes that these traits display a large range of variability at the specific level, calling into question the validity of these species. Very few forms can be convincingly separated from *I. liassica* even with a thorough statistical analysis. For example, there is no reliable criterion that permits the distinction between *I. farinacciae* Brönnimann and Koehn-Zaninetti, 1969 and *I. liassica*. Likewise, in our material, along the ontogeny, the tubular chamber section of *I. liassica* appears oval to triangular (e.g., Fig. 2F) and is either formed either by a complete or a semi tube (see Piller 1978 for definition) (Fig. 2A–F). Therefore, the validity of *I. turgidana* Kristan, 1957 based either on the interpretation of Kristan (1957) or Piller (1978) is dubious (see also Gušić 1975).

In the literature, the diversity of *Involutina* had already been revised downwards. Some species (*I. silicea* Terquem, 1862, *I. aspera* Terquem, 1864, *I. polymorpha* Terquem, 1864, and *I. limitata* Terquem, 1864) have been excluded.
from *Involutina* on account of the agglutinated nature of their wall (Bornemann 1874) and the Early Cretaceous species *Involutina stinemeyeri* Church, 1968 as it would not possess the morphological characteristics of the genus (Brönnimann and Koehn-Zaninetti 1969). Among the remaining species, most have been placed into synonymy with the type-species *Involutina liassica* (Jones in Brodie, 1853) (see Bornemann 1874; Wicher 1952; Kristian 1957; Koehn-Zaninetti 1969; Gušić 1975; Piller 1978). For example, the species *Involutina ticinensis* (Schweighauser, 1951) is regarded as the microspheric form of *I. liassica* (Kristian 1957; Koehn-Zaninetti 1969).

**Systematic palaeontology**

The classification here used has been developed after Cavalier-Smith (2003) for the subphylum and Zaninetti et al. (1987) for the suborder, superfamily, family, and subfamily. The class and order ranks of the *Involutina* are still a matter of debate and will not be discussed in this manuscript.

**Subphylum Foraminifera d’Orbigny, 1826**

**Suborder Involutinina Hohenegger and Piller, 1977**

**Superfamily Involutinoidea Bürtschli, 1880**

**Family Involutinidae Bürtschli, 1880**

**Subfamily Involutininae Bürtschli, 1880**

**Genus Involutina** Terquem, 1862

Fig. 2A–I.

1965 *Pachyspirillina* Ruggieri and Giunta; Ruggieri and Giunta 1965: pl. 2: 2, 4, 6; type species *Pachyspirillina lacunosa* Ruggieri and Giunta, 1965.


**Type species:** *Nummulites liassicus* Jones in Brodie, 1853; *Lias* at Fretherne; Gloucestershire, United Kingdom, by subsequent designation of Brady (1864).

**Species included:** As previously mentioned, *Involutina liassica* displays a large range of variability in its test size and shape, tubular chamber morphology and position relative to the previous whorl, lamellae thickness, papillae size, number, and repetition, and perforation size and connection. Herein we consider that *I. liassica* (Jones in Brodie, 1853) (Rhacitian–Early Middle Jurassic) and *I. hungarica* (Sidó, 1952) (Aptian–Albian) are the only described species presenting distinct morphological characteristics. In *I. liassica*, the test is dominantly lenticular, the papillae are uneven, and the wall perforations may merge in the umbilical mass whereas in *I. hungarica*, the test is mostly subglobular (Schlagintweit and Piller 1990), the papillae are equidimensional, and the perforations are radially distributed and straight (Brönnimann and Koehn-Zaninetti 1969). An additional, non-described species, which is very rare in our Early Jurassic material, also shows intrinsic features. Its test is discoidal, its lamellae are thin and only slightly undulated (forming short papillae), and its perforations are rather small in length and diameter (Fig. 2H, I).

**Emended diagnosis.**—Test free, discoidal, sub-globular. Globular proloculus followed by a planispirally enrolled and undivided tubular chamber with successive coils possibly showing irregularities or oscillations. Well-developed, at least in the juvenile part and on both sides of the tubular chamber, the lateral laminar extensions of the tube wall (L2 lamellae sensu Piller 1978) are laterally tapered, interfingering in the umbilical region (Fig. 2A, B, D, E, H), and locally thickened, forming papillae at the test surface. Wall calcareous, perforate, originally fibrous aragonitic (see Hohenegger and Piller 1975). Aperture simple, terminal.

**Remarks.**—The type-species of *Involutina* (*Nummulites liassicus* Jones in Brodie, 1853) was first included into the genus *Nummulites* Lamarck, 1801. Numerous criteria allow the distinction between *Involutina* and *Nummulites*. The most striking dissimilarities are in the wall composition (aragonitic in *Involutina*, calcitic in *Nummulites*), the chamber arrangement (undivided tubular chamber in *Involutina*, multichambered in *Nummulites*), and the higher level of complexity in the canal system of *Nummulites*.

In the literature, confusion exists between the genera *Involutina* and *Ammodiscus* Reuss, 1862 (e.g., in Loeblich and Tappan 1954). Doubts have been cleared up following the works of Kristian (1957) and Hohenegger and Piller (1975). The latter authors have irrefutably demonstrated the aragonitic nature of the *Involutina* wall. It is now assumed that the aragonitic, involute, laminar, and perforate test of *Involutina* is clearly different from the agglutinated, evolute, and imperforate test of *Ammodiscus*.

The genus *Radiospirillina* Blau and Wernli, 1999 is a perfect homeomorphic of *Involutina*. Their difference is only based on their wall composition and structure. In *Radiospirillina*, the wall is calcitic with hyaline radial umbilical masses and a monocrystalline tubular chamber whereas in *Involutina* the wall is entirely fibrous aragonitic.
MHNG-2011-1-9; J₁, isolated specimen with distinct bumps; J₂, enlarged view of J₁; J₃, sectioned, polished, and etched specimen; J₄, enlarged view of J₃ showing significant laminae discontinuities; J₅, enlarged view of J₄ showing detail of a bump. Note the limited lateral extension of the bump and the good preservation of the aragonite needles. Abbreviations: e-h, rudimentary egg-holder; i, interfingered (lamellae); m.c., merged canals; p, perforation; pap, papilla; p.l., papillose lamella; s.c., straight canal; t.f., tube floor. Scale bars 50 μm.

In 1965, Ruggieri and Giunta have introduced the Middle Jurassic genus *Pachyspirillina* that presents the same morphological characteristics as the genus *Involutina*. While Ruggieri and Giunta (1965) have considered that *Pachyspirillina* belongs to the monocristalline Spirilliniidae Reuss, 1862, Loeblich and Tappan (1987) have placed the genus in synonymy with *Involutina* (aragonitic). Doubt remains about the wall composition of *Pachyspirillina* and consequently, its validity cannot be confirmed or contested yet. Two species have been included in *Pachyspirillina* by Ruggieri and Giunta (1965). The type-species *Pachyspirillina lacunosa* Ruggieri and Giunta, 1965 (pl. 2: 4, 6) is perfectly homeomorphous with *Involutina liassica*. Its test is planispirally coiled, perforate, and presents, a waved periphery (probable papillae) in section. If proved to be aragonitic, the species should be placed in synonymy with *I. liassica*. Conversely, the second species, *Pachyspirillina (?) involutinoides* Ruggieri and Giunta, 1965 (pl. 2: 20–22), questionably assigned to *Pachyspirillina*, has a low trochospiral coiling. According to Blau and Wernli (1999), the species must be assigned to the genus *Radiospirillina* Blau and Wernli, 1999, which displays a monocristalline wall. However, if aragonitic, the species should be rather included into the genus *Piriniella* Blau, 1987a (see Rigaud 2012; Rigaud et al. 2013a). It is worth to note that the specimens illustrated by Ruggieri and Giunta (1965) as *Pachyspirillina* n. gen., sp. ind. (1965: pl. 2: 2) shows a sub-centered, oblique section of the species “*Pachyspirillina* lacunosa.”

In 1974, Moullade and Peybernès have introduced the new genus *Hensonina* for planispiral *Involutinidae* presenting a reticulate umbilical ornamentation, a criterion that would allow its distinction from *Involutina*, which shows umbilical masses covered by “pillars” (i.e., papillae). Although they have mentioned that their material permitted them to observe this reticulate ornamentation, none of the illustrated specimens (Moullade and Peybernès 1974: pl. 3: 6–9) has evidenced such structure. A reticulate ornamentation is, however, present on the spiral side of the specimens illustrated by Henson (1947) as *Trocholina lenticularis* Henson, 1947 and *Trocholina lenticularis minima* Henson, 1947 that Moullade and Peybernès (1974) considered as the generotype of their new genus. The latter species, asymmetric in shape and in its ornamentation, has been recently assigned to the genus *Hensonipapillus* Schlagintweit, Riggla, and Wilmser, 2015. *Hensonipapillus lenticularis* is characterized by a trochospiral type of coiling and possesses a complex canal system (see illustrations in Henson 1947; Brönnimann and Koehn-Zaninetti 1969; Arnaud-Vanneau et al. 1988). According to Piller (1978) and Schlagintweit and Piller (1990), the specimens illustrated by Moullade and Peybernès (1974) must be referred to *Involutina hungarica* (Sidó, 1952) and the genus *Hensonina* Moullade and Peybernès, 1974 should be placed into synonymy with *Involutina*.

**Stratigraphic and geographic distribution.**—Late Triassic (late Norian?–Rhaetian), Early–Middle Jurassic, and Aptian–Albian of Tethys.

**Phylogeny**

There are conflicting theories as far as the position of *Involutina* in the involutinins lineage is concerned. *Involutina* has been either considered to directly derive from trochos-
piral forms (i.e., Lamelliconus) or planispiral forms (i.e., Aulotortus or Triadodiscus). The hypothesis that Lamelliconus is the closest ancestor of Involutina has been proposed by Kristan-Tollmann (1963). However, recent studies have demonstrated that trochospirally coiled involutins (Trocholinidae) are a separate group (Rigaud et al. 2013a), refuting Kristan-Tollmann’s (1963) statement. The possible origination of Involutina from Aulotortus as proposed by Koehn-Zaninetti (1969), Gušić (1975), and Salaj et al. (1983) or from Triadodiscus as postulated by Piller (1978), Gazdzicki (1983), and di Bari and Laghi (1994) is trickier to prove. Aulotortus and Triadodiscus only differ in their laminar deposits architecture (more discontinuous in Triadodiscus) and possibly in their laminar extensions arrangement (interfingered in Aulotortus). These characteristics, strongly dependent on the test preservation, have been only partially documented in Involutina. Our study emphasizes that the laminar extensions of Involutina liassica are interfingered in the median part of the umbilical region, as in the “Aulotortus model”. This observation questions the potential phylogenetic link between Triadodiscus and Involutina and demonstrates that, contrary to Piller’s (1983) opinion, Aulotortus and Involutina do not show a distinct difference in their mode of test formation.

The assumption that Involutina derives from Triadodiscus is mainly based on the observation of bumps (= “bosses” sensu di Bari and Laghi 1994) on the test surface of Triadodiscus inceptus di Bari and Laghi, 1994. In isolated specimens, these features are actually very close to the involutins papillae. This resemblance led di Bari and Laghi (1994) to regard the species as the missing link between the two genera. Our examination of numerous specimens of Triadodiscus inceptus from the collection of di Bari and Laghi (1994), however, allows to incontestably distinguish bumps and papillae, refuting a possible link between the two structures. While papillae are the external expression of local L2 lamellae thickenings (e.g., Fig. 2F; see also Piller 1983), bumps are the external expression of the laminae discontinuity characterizing the wall architecture of Triadodiscus (Fig. 2).

On the other hand, the specimens illustrated by He and Yue (1987: “Aulotortus columnaris”, pl. 5: 21–23) represent a probable missing link between Aulotortus and Involutina. These forms, though devoid of papillose lamellae, display large pores or canals that are comparable in size to those of Involutina liassica. It is noteworthy that the syntypes of Aulotortus columnaris (He 1982: pl. 4: 1–4), however, do not show canals in their umbilical masses (only fine perforations). Hence, the specimens illustrated by He and Yue (1987) cannot be included in A. columnaris He, 1982.

Accordingly, we postulate that Aulotortus is the direct ancestor of Involutina. Their test morphology (discoidal to almost globular), type of coiling (planispiral with possible irregularities or oscillations), laminar arrangement (interfingering), and tubular chamber morphology (oval to crescent-shaped in section and with or without a tube floor) are similar. Additionally, in Aulotortus, it is the thickness of the laminar extensions and not their length that predominantly controls the size of the test. The thinner the laminar extensions are, the more discoidal is the test (e.g., in Aulotortus tumidus). Finally, the high morphological variability observed in Involutina strongly reminds that of Aulotortus representatives.

Stratigraphic and evolutionary implications

Late Triassic and Early Jurassic carbonate platforms lack diagnostically biostratigraphic markers, particularly in shallow-water deposits. Aulotortus is widely used in biostratigraphic studies and Involutina, rich in Tethyan “basinal-like” deposits, might be useful to calibrate platform deposits with deeper environments. However, the genera Aulotortus and Involutina are characterized by significant morphological uneveness, entailing difficulties in their specific recognition.

In Aulotortus and Involutina, species have mainly been established on the basis of the test shape, the laminar development, the mode of coiling, or the tubular chamber morphology. While consistent with studies on other foraminiferal groups, these criteria, single-handedly, have proved to be unreliable for the involutinid taxonomy. For instance, Aulotortus sinuosus, Involutina liassica (e.g., in Böhm et al. 1999: pl. 15: 17), and Involutina hungarica may show either a planispiral or oscillating coiling. In addition, misinterpretation of the wall structure in recrystallized specimens can lead to the establishment of artificial species. For example, the species “Aulotortus tumidus” has been falsely interpreted to possess a last “evolute” whorl (see Piller 1978: pl. 6). Similarly, in Involutina liassica, as the papillose lamellae usually follow the previous whorl outline, the last whorls may appear misleadingly evolute.

A whole revision of the species classified in these two genera is required. In both genera, specific determination should be based on steady, reliable criteria or on the combination of several unstable characters. According to our observations, only few forms show steady patterns but the combination of criteria such as the lamellae thickness, the shape of the test, and the perforation size has proved to be useful for specific identification. The recognition of a direct phylogenetic link between Aulotortus and Involutina may also facilitate the distinction between factual and artificial species. From Aulotortus to Involutina, only one morphological acquisition is required (the development of papillose lamellae) and it is likely to suppose that involutins kept the characteristics of their ancestors. Comparisons between the two genera at the specific level have emphasized strong morphological resemblances between the specimens illustrated by He and Yue (1987: pl 5: 21–23) as “Aulotortus columnaris” and Involutina liassica, and between Aulotortus minitus and the few discoidal specimens found in our material (Fig. 2H, I). Hence, as already stated by Koehn-Zaninetti (1969: fig. 21), it is probable that Aulotortus representatives have shown a
parallel evolution leading to the appearance of several involutins. As a consequence of this parallel evolution, it is now possible to confirm that in both genera neither irregularities or little oscillations in the mode of coiling nor slight modifications of the tubular chamber morphology are consistent for specific differentiation and establishment.

Pending further studies on the taxonomy of the two groups, we would advise a cautious use of Aulotortus and Involutina in biostratigraphic studies.

Hypothesis on functional morphology and related discussion

The emergence of Involutina in the Late Triassic has recorded the acquisition of papillose lamellae in planispirally coiled Involutinina. As previously mentioned, the shape of the test is controlled by the laminar deposits thickness (subglobular forms show protuberant umbilical masses with thick laminar deposits whereas discoidal forms display thin laminar deposits). In the Adnet material, the papillae size of Involutina liassica varies considerably from specimen to specimen, even in the same thin section. The thicker the test is, the more prominent the papillae are (Fig. 2A–F). This observation has already been mentioned by Moullade and Peybernès (1974) and Schlagintweit and Piller (1990) for Involutina hungarica. The same correlation is observable from species to species. Discoidal forms show less prominent papillae than lenticular forms (Fig. 2A–F, H, I). It is noteworthy that the number of papillae is also reduced in discoidal forms. Moreover, in discoidal forms, the papillae repartition is not arbitrary (e.g., see Kristan 1957: pl. 22: 2). The papillae form a spiral on the test surface that follows the tubular chamber progression. This peculiar repartition (straight above the tube), the convergent evolution (appearance of papillae) in aragonitic forms at the end of the Triassic, and the correlation existing between the test shape/thickness and the papillae size/quantity strongly suggests that papillose lamellae have a biological role.

The biological role of papillae in the Involutinina has been discussed by Piller (1977). As Involutina is usually found in deeper deposits than Aulotortus, Piller (1978) concluded that papillae are a probable reinforcement of the test structure related to higher hydrostatic pressure. Although it is widely thought that Involutina is indicative of slope to basin depositional settings (Piller 1978), no occurrence of the genus in deep basinal settings (e.g., co-occurring with thin-shelled bivalves and/or radiolarians limestones) have been mentioned. Involutina has been mostly found associated with an abundant and diversified fauna, in deposits showing a high affinity with the platform, suggesting an occurrence in the photic area. In the Late Triassic, Involutina occurs together with sponges, gastropods, ammonites, echinoderms, ostracods, crustaceans, bryozoans, brachiopods, and other foraminifers (Kristan 1957). In Early Jurassic deposits, Involutina is particularly abundant on the top of drowned Triassic carbonate platforms and is also found associated with abundant and diversified bioclasts. In the Adnet area, for instance, Involutina liassica is found together with echinoderms, ostracods, oncocids, other foraminifers, gastropods, bivalves, holothurians, crustacean debris, serpulids, ammonites, brachiopods, and globochaetes (Böhm et al. 1999 and personal observations). The oncocids and possibly the globochaetes (Skompski 1982) attest to the presence of Involutina liassica in the photic area. Furthermore, most involutinins associated with Involutina show a relatively thin wall on one or both sides of the test (e.g., Trocholina, Coronaserra, Coronipora, Kristanottmana), attesting that their test does not necessitate any reinforcement to face the local hydrostatic pressure, as expected for foraminifers.

Conversely, the lamellae thinning may document a slow-down of the biomineralization process with depth increase (Hottinger 1997) and the presence of papillae, may help to maximize the amount of light penetrating the wall (Hottinger 2006). The assumption that papillose lamellae express a paleoecological adaptation to deeper environments for light catching is consistent with our data (for the same depth, thicker tests require a more prominent relief) and supports the hypothesis that the Involutinina may have held symbiont-bearing representatives (Rigaud et al. 2013b).

Accordingly, in Involutina, the “plaits or infoldings of the outer shell” interpreted as “septa” by Brady (1864) can be reinterpreted. These features, named “ demi-cloisons” by Terquem (1862), are well-visible in equatorial section. They form small compartments on the tubular chamber periphery (Fig. 2G). We propose that they have served as rudimentary eggholders (see Hottinger 1977), adaptive features for symbiont positioning immediately beneath the test wall.

Concluding remarks

Prior to this study, the structure of Involutina was inadequately defined. The recognition of a direct phylogenetic link between Aulotortus and Involutina has highlighted inaccuracies in the classification, phylogeny, and possibly the stratigraphic range of planispirally coiled involutinids. An entire revision of the group is required. Pending this revision, a cautious use of Aulotortus and Involutina in biostratigraphic studies is recommended.

The evolutive acquisition of papillose lamellae is most likely a clue that Involutina had a symbiotic life. Such a mode of life implies that the involutinins can be used as depth bioindicators within the photic area. In papillose Involutinina, the papillae (number and size) might thus become relevant paleobathymetric tools.
The earliest Jurassic has been characterized by a global sea-level rise. In *Involutina*, the acquisition of evolutive features such as papillae and rudimentary egg-holders was most probably a significant advantage over *Aulotortus* to face the Triassic–Jurassic extinction event.

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