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

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Early Jurassic aragonitic foraminifera 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 the test surface is not random and probably related to a biological function. We here propose that the papillose lamellae and tube infoldings that characterize representatives of the genus were rudimentary features for light catching and symbiont positioning, respectively.

Key words: Foraminifera, Involutinidae, *Aulotortus* model, papillae, symbiosis, Jurassic, Austria.

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Introduction

Representatives of the suborder Involutinina are a significant constituent of early–middle Mesozoic communities of carbonate platforms and have a strong potential as paleontological tools. Globally distributed, they have shown a rapid diversification and dispersion during the Triassic. Their distribution throughout carbonate platforms is wide, from restricted, lagoonal, shallow water deposits up to deeper, “basinal-like” environments (Piller 1978). The Involutinina are, however, usually strongly affected by diagenetic alterations and are thus only occasionally preserved in the fossil record. Their poor preservation introduces significant difficulties for their description, classification and use in paleoecologic, stratigraphic, and phylogenetic studies.

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*.

Institutional abbreviations.—MHNG, Muséum d’Histoire Naturelle de la ville de Genève, Genève, Suisse.

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,

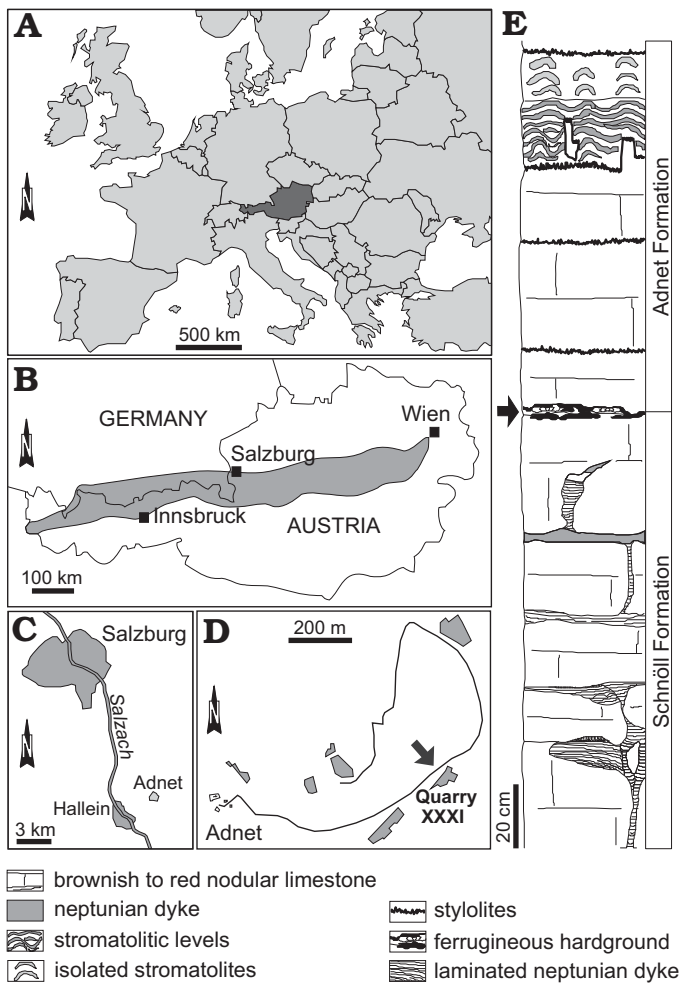


Fig. 1. **A.** Map of Europe locating Austria (dark gray). **B.** Map showing the location of the Northern Calcareous Alps in the territories of Austria and Germany (grey). **C.** Enlargement of the area of Salzburg showing the Adnet locality. **D.** Location of the sampled quarry (Quarry XXXI). The quarry numbering follows that of Kieslinger (1964). **E.** Lithologic section of the quarry XXXI and samples location within the “marmorea-crust” (arrow).

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 involutinids 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 involutinids 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 microspheric forms but, as for other involutinids (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 lami-

nar 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 (= now *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 formed either by a complete or a semi tube (see Piller 1978 for definition) (Fig. 2A–F). Therefore, the validity of *I. turgida* 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; Kristan 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* (Kristan 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 Involutinina 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 Bütschli, 1880

Family Involutinidae Bütschli, 1880

Subfamily Involutininae Bütschli, 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.

?1974 *Hensonina* Moullade and Peybernès; Moullade and Peybernès 1974: pl. 3: 6–9; type species misidentified as *Trocholina lenticularis* Henson, 1947.

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 repartition, and perforation size and connection. Herein we consider that *I. liassica* (Jones in Brodie, 1853) (Rhaetian–early Middle Jurassic) and *I. hungarica* (Sidó, 1952) (Aptian–Albian) are the only described species presenting distinct mor-

phological 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).

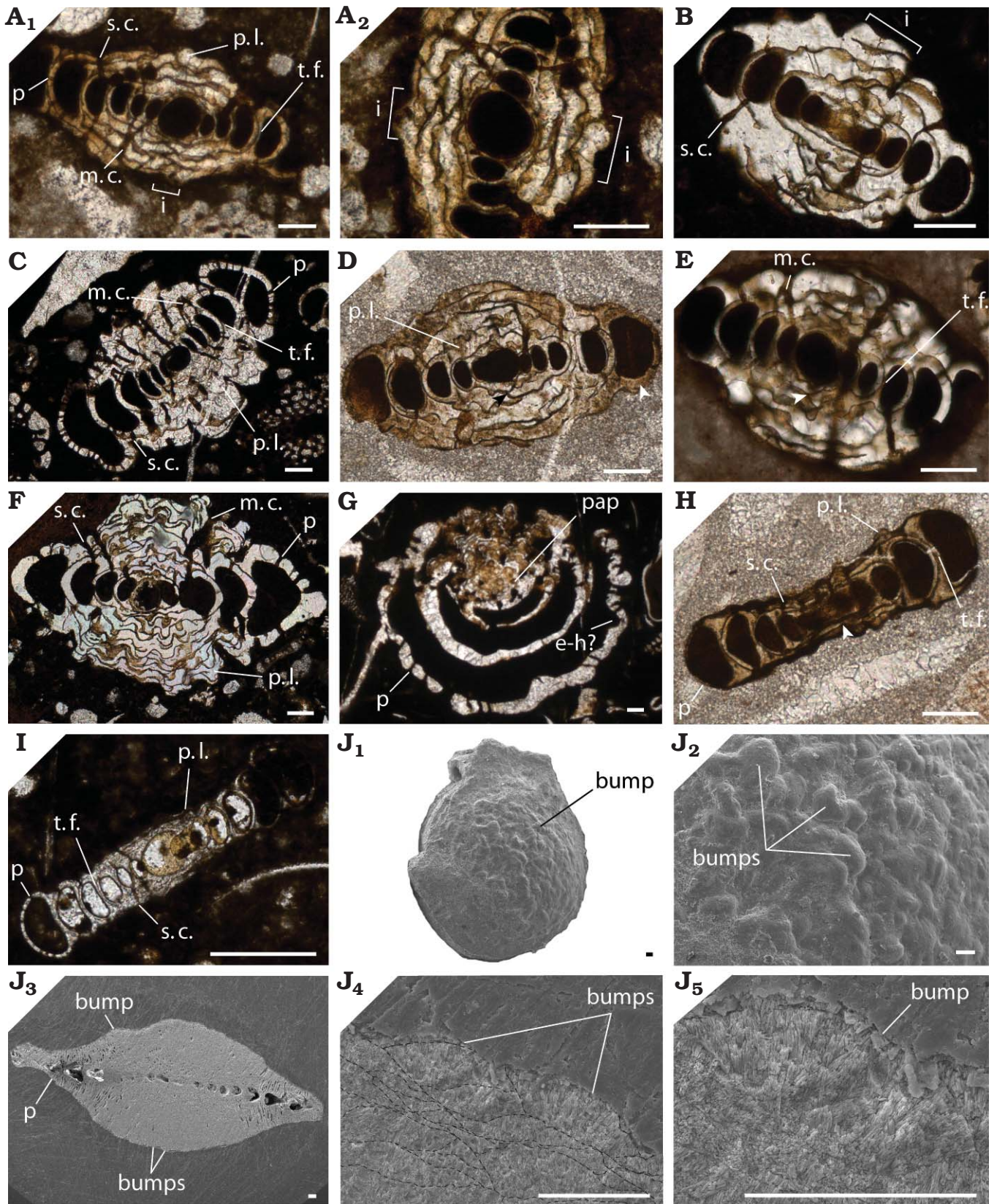
Emended diagnosis.—Test free, discoid, lenticular, to subglobular. Globular proloculus followed by a planispirally enrolled and undivided tubular chamber with successive coils possibly showing irregularities or oscillations. Well-developed, at least in the juvenile part and on both sides of the tubular 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 Kristan (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 homeomorph 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.

Fig. 2. Ornamented involutinins. **A–G.** *Involutina liassica* (Jones in Brodie, 1853), Early Jurassic, Adnet area, Austria, collection MHNG-75631, thin sections 402, 4a1, 4a2. Specimens with a structure partly preserved from diagenesis by a ferromanganese impregnation. Note the large intraspecific morphological variability. **A.** MHNG-75631-40a; A₁, axial section, specimen with merged canals and relatively well-developed tube floors. Note the lamellae interfingering; A₂, enlarged view of A₁. **B.** MHNG-75631-40b. Transverse, sub-axial section of a specimen without tube floor. **C.** MHNG-75631-40c. Axial section of a specimen with merged canals. **D.** MHNG-75631-42a. Axial section. Note relics of the fibrous wall structure (white arrow) and the lamellae interfingering (black arrow). **E.** MHNG-75631-42b. Axial section of a specimen presenting a tube floor in its juvenile part only. Arrows point interfingering lamellae. **F.** MHNG-75631-41a. Axial section of a specimen with thick umbilical masses and well-developed papillose lamellae. Note that papillae are the expression of local lamellae thickenings. **G.** MHNG-75631-41b. Transverse, sub-equatorial section showing transversely sectioned papillae. Note the folding of the tube wall, possibly delimiting rudimentary eggholders-like structures. **H, I.** *Involutina* sp. (Early Jurassic, Adnet area, collection MHNG-75631, thin sections 4a2, 402). Discoidal specimens partly preserved from diagenesis by a ferromanganese impregnation. **H.** MHNG-75631-42c. Transverse section. Note the presence of interfingering papillose lamellae (arrow). **I.** MHNG-75631-40d. Axial section. Straight canals perforate the umbilical masses. **J.** *Triadodiscus inceptus* di Bari and Laghi 1994 (Carnian, Late Triassic, Italy, di Bari and Laghi material, SEM images), →



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 μ m.

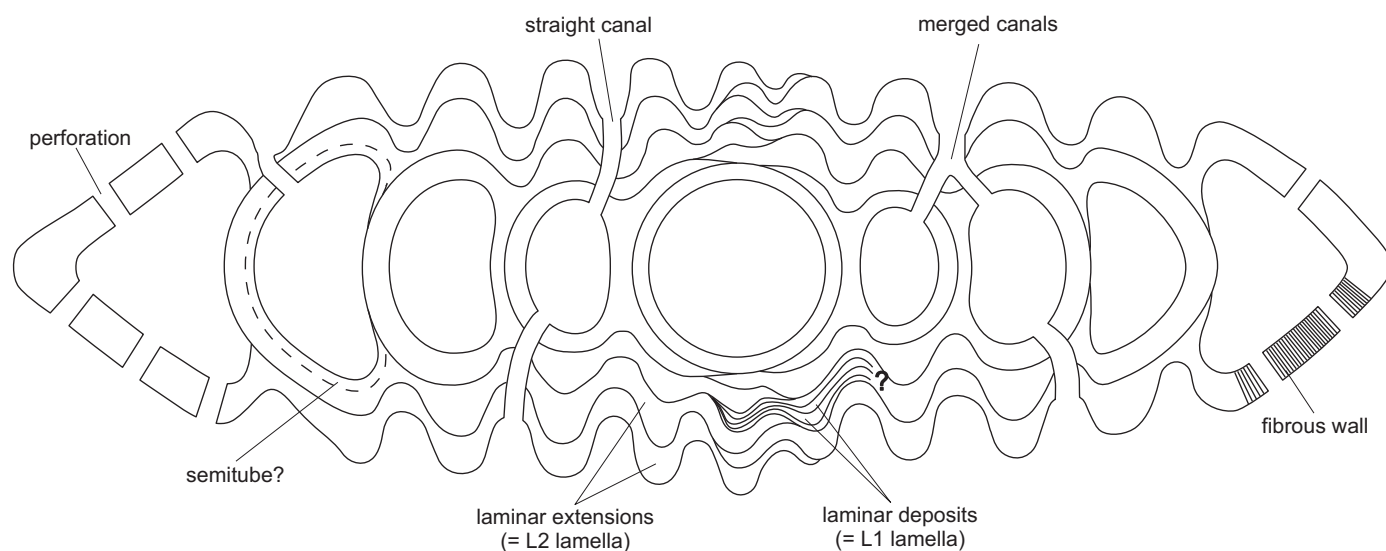


Fig. 3. Structural model of *Involutina* (in axial section). The presence of a semitube, as defined by Piller (1978), is only barely discernible in few of our specimens.

Among Involutinina, *Involutina* shows affinities with the genus *Planispirillina* Bermúdez, 1952 but contrary to *Involutina*, *Planispirillina* presents an asymmetric test with a spiral side devoid of papillose lamellae. In isolated specimens, *Involutina* may be confused with *Papillaconus* Rigaud, Blau, Martini, and Rettori, 2013a. The mode of coiling, trochospiral in *Papillaconus* allows their distinction. From *Aulotortus* Weynschenk, 1956, *Involutina* only differs in the presence of papillose lamellae.

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 monocrystalline Spirillinidae 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 homeomorphic 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 monocrystalline 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 specimen 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, Rigaud, and Wilmssen, 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 involutinins (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), Gaździcki (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 (interfingering 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 interfingering 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 involutinins 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. 2J).

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 tenuis*). 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 diagnostic 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 unevenness, 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 involutinins 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 minutus* 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 involutinins. 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. At this time, papillae are also documented in both tubular (i.e., *Trocholina*, *Semiinvoluta*, *Frentzenella*) and multichambered (i.e., *Cassianopapillaria*) trochospirally coiled aragonitic forms. In *Involutina*, a strong correlation between the shape of the test and the papillae size is observed. 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 (1978). 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 basinal 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, oncoids, other foraminifers, gastropods, bivalves, holothurians, crustacean debris, serpulids, ammonites, brachiopods, and globochaetes (Böhm et al. 1999 and personal observations). The oncoids 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*, *Kristantollmanna*), 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 slowdown 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 bio-indicators 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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