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Taxonomy and palaeobiogeography of the Cenozoic Euro-Mediterranean rissoid gastropod *Galeodinopsis* and its relationship with close genera

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The investigation of the Late Paleogene to Late Neogene species of rissoid gastropod *Galeodinopsis* in the Euro-Mediterranean area has supported the hypothesis that this genus is an intermediate form between two well-known rissoids, *Alvinia* and *Manzonia*. We recognized four species of *Galeodinopsis*: *G. biangulata*, *G. germanica* sp. nov., *G. semperi* (new name for *Rissoa duboisii*), and *G. tiberiana*. The oldest (very Late Eocene/Oligocene) representatives of *Galeodinopsis*, *G. biangulata*, and *G. semperi*, share similar shell shape and microsculpture with *Alvinia*. This suggests that *Galeodinopsis* originated from some Eocene species related to *Alvinia*. The new species represents the first occurrence within *Galeodinopsis* of a combination of characters very close to those of *Manzonia*, above all the typical pitted microsculpture. We hypothesize that *Manzonia* evolved from *Galeodinopsis* rather than from the genera *Alvania* or *Alvinia*, as previously supposed. *Galeodinopsis* originated during the very Late Eocene/Oligocene in the North Sea Basin. Afterwards it underwent a strong southward shift to the mid-high east Atlantic and the Mediterranean area, during the Mio-Pliocene, and to the Recent tropical eastern Atlantic coasts, where the type species *G. tiberiana* still lives. The shift likely was due to a combination of climate cooling and palaeogeographical changes. The distribution of *G. biangulata* suggests that connections between the North Sea Basin and the Atlantic domain opened through the Channel area at least during the Early Oligocene, earlier than indicated previously. The distribution of *Manzonia moulinsi* supports the idea of a southern connection to the Atlantic Aquitaine Basin via the Rhine Graben during the Late Oligocene. From a palaeoecological point of view, *Galeodinopsis* includes warm species with planktotrophic larval development that are typical of the shelf environment in fully marine conditions.

Key words: Gastropoda, Rissoidae, taxonomy, palaeogeography, biogeography, Cenozoic, North Sea, Atlantic connection, Europe.

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Introduction

The family Rissoidae includes some of the most diverse gastropod groups, with numerous genera inhabiting a great variety of environments, from shallow to bathyal depth, in the Mediterranean, Atlantic, Indo-Pacific, and the temperate Australian and New Zealand coasts (Ponder 1985). The first record of this family dates back to the late Lower Jurassic of Europe, with a discrete differentiation in Middle Jurassic (Ponder 1985; Conti et al. 1992; Kaim 2004; Schulbert and Nützel 2009). Strong diversification occurred during the Tertiary, particularly in the Euro-Mediterranean area (Sacco 1895; Seguenza 1903; Cossmann 1921; Lozouet 1998; Kowalke and Harzhauser 2004; Landau et al. 2004; Chirli 2006).

As with other small gastropods, most fossil rissoid shells preserve the larval shell (protoconch), which provides information on the larval biology of their respective species (Shuto 1974; Jablonski and Lutz 1983) and, in several cases, provides a helpful taxonomic tool for separating taxa (Ponder 1985). However, because of the high degree of diversification and confusion caused by convergence in shell characters, most of these gastropods are difficult to classify, particularly at the genus and species level. As a consequence, several attempts to separate groups at genus-subgenus level,

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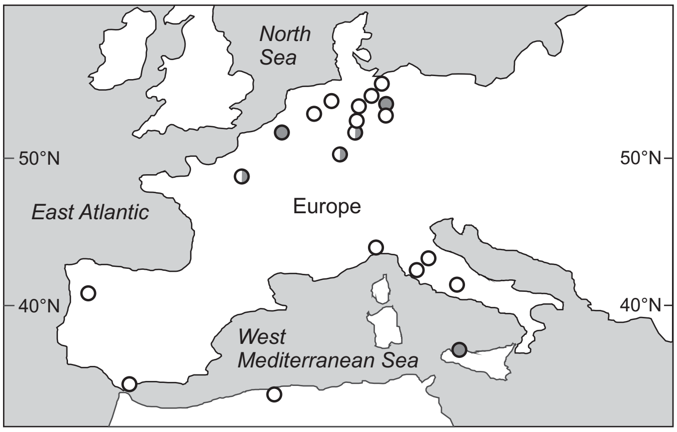


Fig. 1. Location of the study sites in the Euro-Mediterranean area. Open circles, studied from bibliographic sources; shaded circles, studied from museum/private collections.

especially within the very polymorph genus *Alvania* Risso, 1826 and closely related nominal genera, failed or simply showed the differences to be inconsistent (Ponder 1985; Garilli 2008; Garilli and Parrinello 2010). Conversely, successful results have been achieved in the Late Paleocene–Late Neogene genus *Galeodinopsis* Sacco, 1895 on the basis of an accurate taxonomic approach involving a detailed morphological study of protoconch and teleoconch characters, with special regard to teleoconch microsculpture (Garilli 2008). Notwithstanding this, the actual number of species within *Galeodinospis* is not at all defined, mainly due to the lack of a complete taxonomic setting. Actually several taxa, such as *Alvania*, *Alvinia* Monterosato, 1884, *Arsenia* Monterosato, 1891, *Flemellia* Nordsieck, 1972, and *Manzonia* Brusina, 1870, have been or could be related to *Galeodinopsis* but without the support of taxonomical comparative analyses based on in depth studies of teleoconch and protoconch features involving type species. Consequently the origin of *Galeodinospsis* and its possible phyletic relationships with close genera are still to be defined.

The main aim of this study is to provide an exhaustive taxonomic data set of *Galeodinopsis* allowing a rediscussion of its phyletic link to the other closely related rissoid taxa. We therefore describe in detail protoconch and teleoconch features of *Galeodinopsis* species from the Tertiary of central Europe and the eastern Atlantic-Mediterranean area (Fig. 1). Comparative studies between *Galeodinopsis* and type species of related genera are also provided. The palaeoecological and paleogeographical occurrences of *Galeodinopsis* is discussed. A new species of this genus from the Cenozoic of north-central Europe is also described.

Institutional abbreviations.—BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MGUP, Museo Geologico G.G. Gemmellaro, Università di Palermo, Italy; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MNHU, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MPOB, Museo di Paleobiologia e dell'Orto Botanico, Università di Modena and Reggio Emilia, Modena, Italy; MZB, Museo di Zoologia dell'Università di Bologna, Italy; MZPD, Museo di Zoologia P. Doderlein, Università di Palermo, Italy; SMF, Senckenberg Forschungsinstitut und Naturmuseum, Malakologie, Frankfurt am Main, Germany; UCBL, Université Claude Bernard Lyon 1, Lyon, France.

Other abbreviations.—AR, Agatino Reitano collection (Tremestieri Etneo, Catania, Italy); Coll(s)., collection(s); Ht, total shell height; EM, collection Ecole Nationale Supérieure des Mines de Paris; MF, Maurizio Forli collection (Prato, Italy) ex Stefano Palazzi collection (Milo, Catania, Italy); VG, Vittorio Garilli collection; W, shell width.

Historical background

Sacco (1895) described *Galeodinopsis* as a subgenus of *Alvania*, but Ponder (1985) did not follow this separation and considered *Galeodinopsis* to be a synonym of *Alvania*. Recently, *Galeodinopsis* has been re-evaluated as a distinct genus representing shells with characters shared by the genera *Alvania* and *Manzonia* Brusina, 1870 (Garilli 2008). In particular, mainly on the basis of the characters of the type species, the Miocene to Recent species *Rissoa tiberiana* Coppi, 1876 (Fig. 2), *Galeodinopsis* is characterized by an *Alvania*-like shape, with an inflated last whorl usually bearing varices and a large aperture resembling that of *Galeodina* Monterosato, 1884 (= *Alvania* according to Garilli 2008), and a *Manzonia*-like combination (see also below) of characters such as the double-rimmed outer lip, the teleoconch pitted microsculpture, and the netted protoconch 1 (Garilli 2008). Apart from the type species, only the Oligocene species "*Rissoa Duboisii* Nyst, 1845" has been included in *Galeodinopsis*, whereas the Recent Macaronesian species *R. spreta* Watson, 1873 was doubtfully considered a close species (Garilli 2008). The fossil species *R. multicostata* Speyer, 1864, compared with *G. tiberiana* by the same author, was tentatively placed in *Alvinia*, but without an in-depth critical review.

The genus *Manzonia* (Fig. 3), type species *Turbo crassus* Kanmacher in Adams, 1798, includes species most of which are characterized by ovate-conic-elongate shells bearing robust axial sculpture, formed by strongly curved to sinuous, opisthocline ribs in *Manzonia* s. s., and strong, smooth spiral cords on the base of the shell. Other relevant characters are the markedly duplicated peristome, the netted sculpture of protoconch 1 (in multispiral protoconchs assumed to indicate planktotrophic larval development; Fig. $3G_2$) and a characteristic teleoconch microsculpture, consisted of a pitted surface on flat spiral cords (Ponder 1985; Moolenbeek and Faber 1987a) and roughly prismatic elements forming numerous, very fine spiral threads in the interspaces between primary cords (Garilli 2008; see Fig. $3A_2$, B_2, G_4). *Manzonia* shells do not bear varices (apart from that surrounding the outer lip); to our knowledge the sole specimen

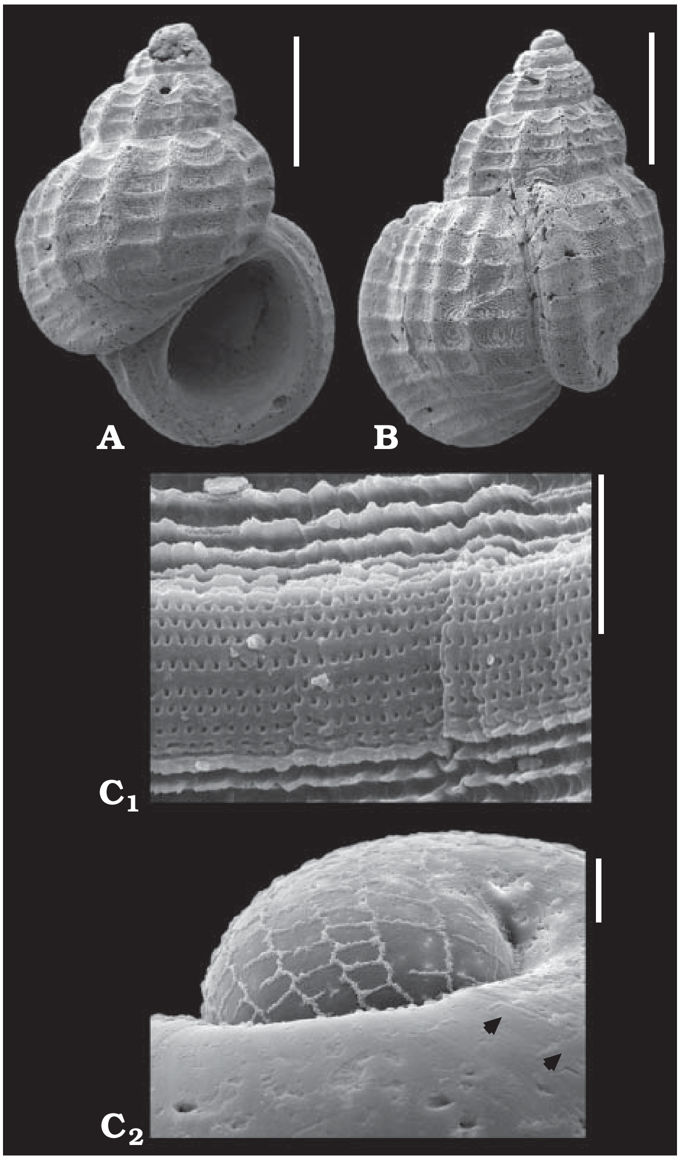


Fig. 2. Rissoid gastropod *Galeodinopsis tiberiana* (Coppi, 1876), type species of *Galeodinopsis* Sacco, 1895 from Rio Grizzaga sands, Gagliardella, Fogliano, Maranello, Modena, N Italy, type locality, Piacenzian, Pliocene. **A**. Specimen ex MF, MZPD Mal 2035a, in apertural view. **B**. Specimen ex MF, MZPD Mal 2035b, in dorsal view. **C**. Specimen ex MF, MZPD Mal 2035c showing typical Manzonia-like teleoconch microsculpture (C_1) and detail of protoconch 1 with netted sculpture (C_2). Black arrows indicate the protoconch 1/protoconch 2 boundary. Scale bars: A, B, 1 mm; C, 20 µm.

with a varix on the last whorl is a *Manzonia* sp. from the early Late Miocene of Montegibbio (Modena, northern Italy) (Fig. 3H). Subgeneric division within *Manzonia* is still debated as well its degree of affinity to *Alvania*. The classification of *Alvinia* Monterosato, 1884 (type species *Alvania weinkauffi* Weinkauff, 1868 ex Schwartz von Mohrenstern ms) as a subgenus of *Manzonia*, as proposed by Ponder (1985) and accepted by Kowalke and Harzauser (2004), was not followed by Moolenbeek and Faber (1987c). Even the consideration of *Flemellia* Nordsieck, 1972 (new name for *Seguenziella*, Sacco, 1904, new name for *Taramellia* Seguenza, 1903, new name for *Flemingia* Jeffreys, 1884; see Ponder 1985) as a *Manzonia*-linked taxon appears to be controversial, because its type species, *Turbo zetlandicus* Montagu, 1815, was only provisionally placed in *Manzonia* (*Flemellia*) by Moolenbeek and Faber (1987c), while Ponder (1985) considered it to be a species of *Manzonia* (*Alvinia*), as he considered *Flemellia* to be a synonym of *Alvinia*. Conversely, Bouchet and Warén (1993) considered *Flemellia* to be a synonym of *Alvania*. The type species of *Alvinia* has a turrited-shouldered shell lacking the typical microsculpture and the marked duplication of the peristome (Figs. 4A, B, 5B) seen in the type species of *Manzonia*, and its protoconch is paucispiral and characterized by discontinuous spiral cords of rough tubercles. *Alvania,* type species *Turbo cimex* Linnaeus, 1758, and *Arsenia*, type *Turbo punctura* Montagu, 1803, have a conical-ovate shell without a shoulder, but with a simple outer lip; protoconch 1 in *Alvania* and *Arsenia* is characterized by spiral elements and very fine dots, and the microsculpture is weak to obsolete (Figs. 6, 7C–E). Some *Alvania* species bear stronger microsculpture with discontinuous fine threads representing a sort of *Alvinia*-impoverished pattern (Garilli 2008; Garilli and Parrinello 2010). The taxonomical state of the art is also complicated by the features of species such as *T. zetlandicus* and *Rissoa testae* Aradas and Maggiore, 1844 (type species of *Actonia* Monterosato, 1884, regarded as synonym of *Alvania* by Ponder [1985] and Bouchet and Warén [1993]): *T. zetlandicus* has a shell shape and microsculptural pattern (Figs. 4C_1, C_2, D, 5A) similar to those seen in the type species of *Alvinia*, and shares the netted pattern of protoconch 1 and the duplicated peristome (Fig. 4C_1, C_3, C_4) with *Manzonia* s.s.; *R. testae* (Fig. 8) has shell shape and protoconch characters comparable to those of *Manzonia,* but has a microsculpture similar to that of *Alvinia* and *Flemellia*. All this makes the relationship between *Alvania, Alvinia* and *Manzonia* yet to be established, despite Gofas (2010), supporting Ponder's (1985) view, emphasizing that even species lacking the pitted microsculpture may be regarded as closer to *Manzonia* than to *Alvania*. Ponder (1985) also suggested that *Manzonia* (*Alvinia*) may have diverged from *Alvania* early in the Tertiary.

An exhaustive palaeontological dataset on these arguments, with emphasis on possible transitional steps between most of these taxa, has never been provided. The only well-established *Manzonia* species from the Paleogene of Europe are *Alvania foraminata* Lozouet, 1998, from the French Late Oligocene, Chattian, and *Rissoa moulinsi* d'Orbigny, 1852 known from the Chattian and Miocene of central-western Europe, both showing all the main distinctive characters mentioned above (see Lozouet 1998: fig. 9f–j; Garilli 2008). More species occurred during the European Neogene (Kowalke and Harzhauser 2004; Garilli 2008 and references therein), where diversification involved several indisputable *Manzonia* taxa such as *Rissoa* (*M.*) *falunica* Morgan, 1915, *R.* (*M.*) *pontileviensis* Morgan, 1915, *Cyclostoma scalare* Dubois, 1831, *Flemingia subzetlandica* Boettger, 1907 (possibly = *M. zetlandica* var. *miocrassicosta* Sacco, 1895; see

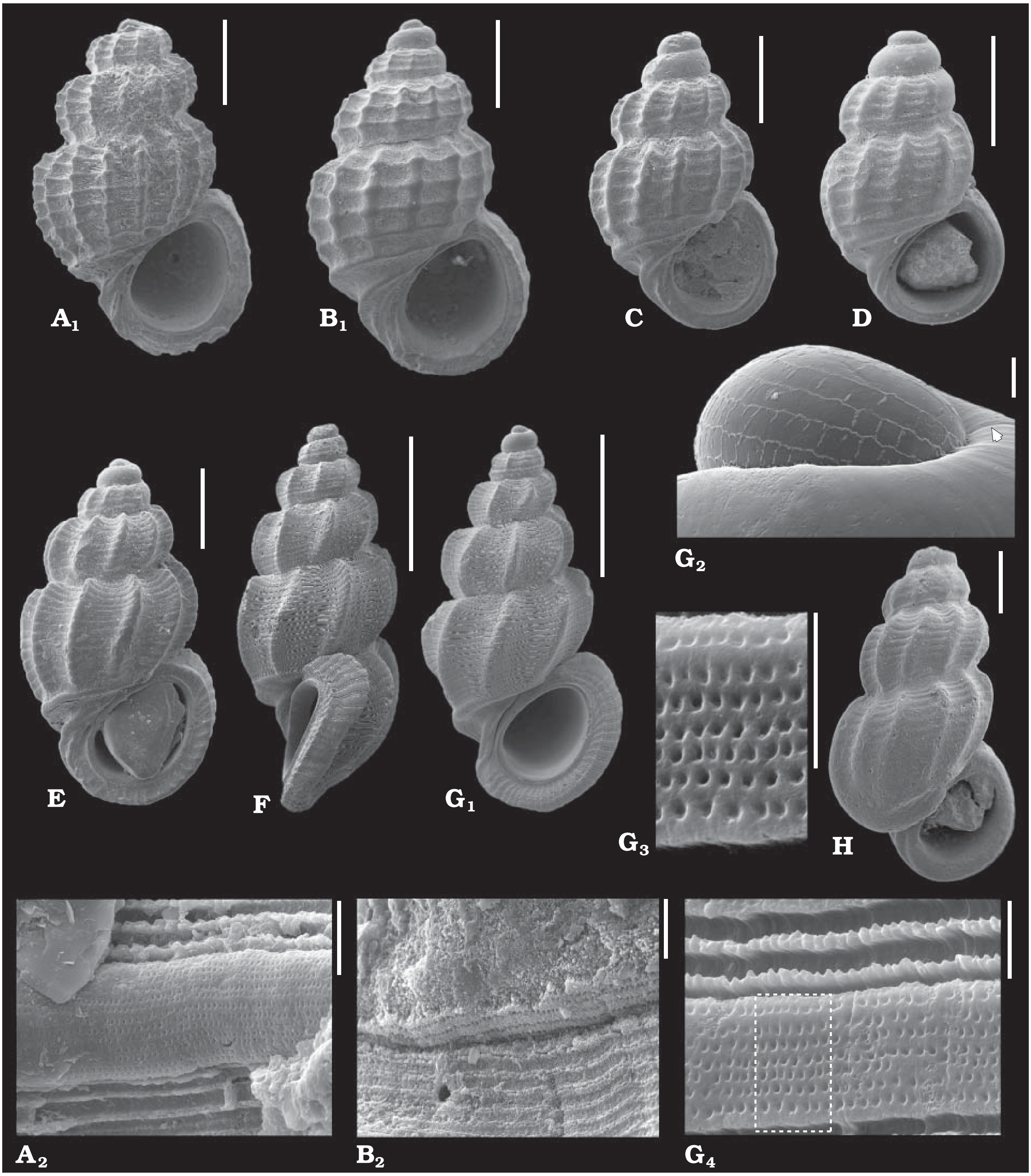


Fig. 3. Species of rissoid gastropod *Manzonia* Brusina, 1870. **A**. Manzonia scalaris (Dubois, 1831); specimen ex MF, MZPD Mal 2039 from Valea Cosului, Lapugy, Banat, Romania, Badenian, Miocene, in apertural view (A_1); microsculpture (A_2). **B**. *Manzonia subzetlandica* (Boettger, 1907); specimen ex MF, MZPD Mal 2038 from the same site as in A, in apertural view (B_1); microsculpture (B_2). **C**. *Manzonia moulinsi* (d'Orbigny, 1852), specimen ex MF, MZPD Mal 2037 from Albig, Alzey, Worms, W Germany, Rupelian, Oligocene, in apertural view. **D**. *Manzonia pontileviensis* (Morgan, 1915), specimen ex MF, MZDP Mal 2041 from Moulin de Charenton, Pontlevoy, Loire Basin, France, Middle Miocene, in apertural view. **E**. *Manzonia falunica* (Morgan, 1915), specimen ex MF, MZPD Mal 2040 from Ferriere-Larcon, Loire Basin, Middle Miocene, in apertural view. **F**, **G**. *Manzonia crassa* (Kanmacher in Adams, 1798), type of *Manzonia*; from N2 layer of Garilli (2011), Kyllini, Elea, NW Peloponnesus, Greece, Late Pleistocene. →

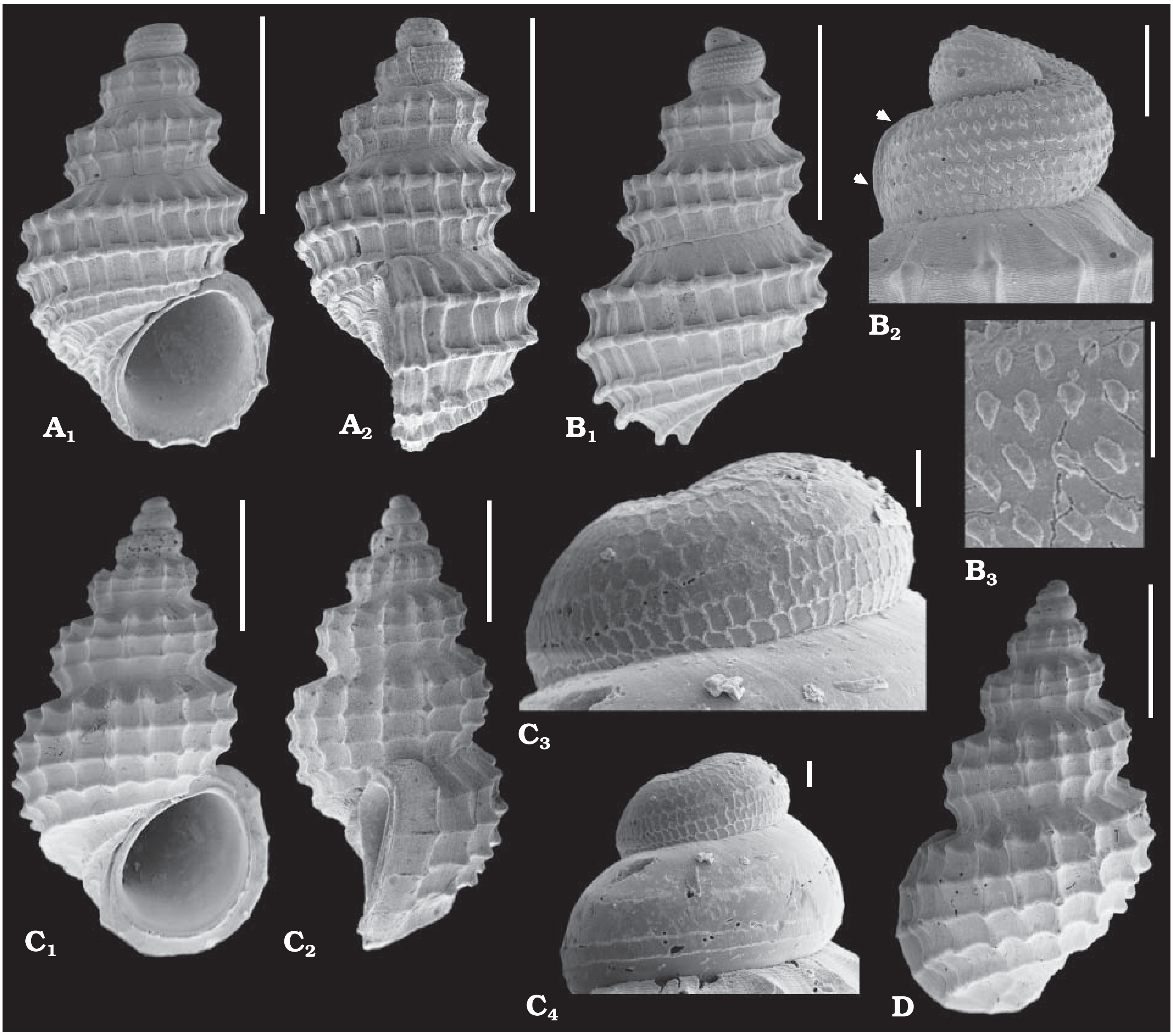


Fig. 4. Rissoid gastropod *Alvinia weinkauffi* (Weinkauff, 1868 ex Schwartz von Mohrenstern ms), type species of *Alvinia* Monterosato, 1884, matching Weinkauff's illustration (1885: pl. 21: 14, 15), and *Alvinia zetlandica* (Montagu, 1815), type species of *Flemellia* Nordsieck, 1972. **A**, **B**. *Alvinia weinkauffi*. **A**. Specimen ex VG, MZPD Mal 2047, Recent, infralittoral bottom off Capo Gallo, Palermo NW Sicily, in apertural (A_1) and profile (A_2) views. **B**. Specimen ex VG, MZPD Mal 2048, Recent, infralittoral bottom (37 m deep) off Formica Island, W Sicily, in dorsal view (B_1), protoconch in dorsal view (B_2), and close-up of sculpture (B_3). **C**, **D**. *Alvinia zetlandica*, Calabrian, Early Pleistocene, Lazzaro, Vallone Catrica, Reggio Calabria, S Italy. **C**. Specimen ex MF, MZPD Mal 2046a, in apertural (C_1) and profile (C_2) views, protoconch in dorsal view (C_4) and close-up showing the netted sculpture of protoconch 1 (C_3). **D**. Specimen ex MF, MZPD Mal 2046b, in dorsal view. White arrows indicate protoconch/teleoconch demarcation. Scale bars: A, B_1, C_1, C_2, D, 1 mm; B_2, 150 µm; B_3, 75 µm; C_3, C_4, 30 µm.

F. Specimen ex VG, MZPD Mal 2043a in profile view. **G**. Specimen ex VG, MZPD Mal 2043b, in apertural view (G_1); netted sculpture of protoconch 1 (G_2), white arrow indicates the protoconch 1/protoconch 2 boundary; teleoconch microsculpture (G_4), detail showing the typical pitted pattern formed by very short axial bridges (G_3). **H**. *Manzonia* sp., specimen ex MF, MZPD Mal 2042 from Rio delle Bagole, Montegibbio, Modena, N Italy, Tortonian, Late Miocene, in apertural view showing a varix on the last whorl. Scale bars: F, G_1, 1 mm; A_1, B_1, C_1, D, E, H, 500 µm; A_2, B_2, G_2–G_4, 20 µm; C_2, 10 µm.

Kowalke and Harzhauser 2004: fig. 8A; Fig. 3). Today, one of the most *Manzonia* species-rich provinces is represented by the northeastern Atlantic seamounts and the Macaronesian archipelago (Moolenbeek and Faber 1987a–c; Gofas 2007), where the high diversification is testified to by species somewhat morphologically distant from the type species, but showing some typical characters. Apart from doubtful Late Cretaceous records (Ponder 1985), the earliest occurrence of *Alvania* is from the Eocene of Europe (Le Renard 1990;

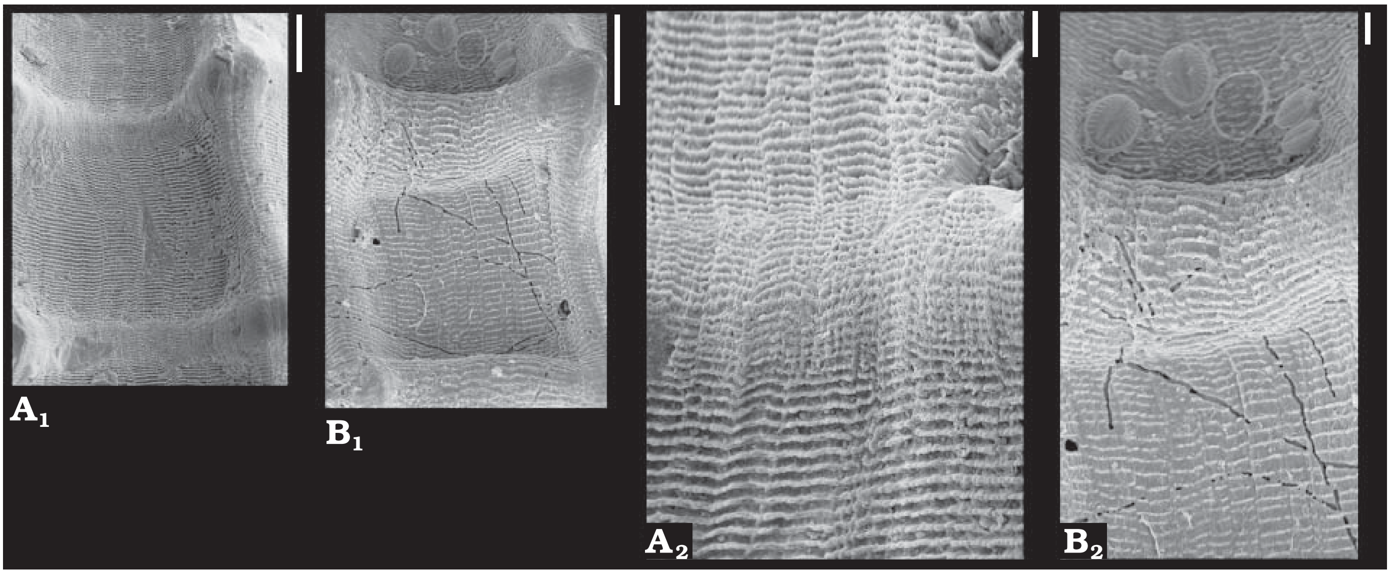


Fig. 5. Teleoconch microsculpture in the type species of rissoid gastropods *Alvinia* Monterosato, 1884 and *Flemellia* Nordsieck, 1972. **A**. *Alvinia zetlandica* (Montagu, 1815), type species of *Flemellia*, ex MF, MZPD Mal 2046a (same specimen as in Fig. 4C), Calabrian, Early Pleistocene of Lazzaro, Vallone Catrica, Reggio Calabria, S Italy, showing closely spaced spiral threads on shell surface at different magnifications. **B**. *Alvinia weinkauffi* (Weinkauff, 1868 ex Schwartz von Mohrenstern ms), type species of *Alvinia*, ex VG, MZPD Mal 2048 (same specimen as in Fig. 4B), Recent, infralittoral bottom (37 m deep) off Formica Island, W Sicily, showing narrow spiral threads on shell surface at different magnifications. Scale bars: A_1, B_1, 50 µm; A_2, B_2, 10 µm.

MNHN Fossil Database of Tertiary shells and references therein), where this genus underwent strong diversification during Neogene–Recent time (e.g., Sacco 1895; Bouchet and Warén 1993; Giannuzzi-Savelli et al. 1996; Chirli 2006). As for *Alvinia*, less is known about the palaeontological record, although it is clear enough that species resembling the type species occurred earliest in the Eocene, Lutetian, of France (Le Renard 1990; MNHN Fossil Database of Tertiary shells, with references), also with shells not at all distant from *Alvania*. It assumed the characteristic turrited shape in the Miocene of the central Paratethys and of the North Sea Basin (see Bałuk 1975, as *Alvania* (*Taramellia*); Kowalke and Harzhauser 2004, with references).

Material and methods

The examined material is housed in several European institutions. Part of this material was provided by private collectors or collected by the first author, and is now housed in MZPD. Another part, used for comparison, comes from samples collected during the oceanographic field trip CS'96 in the Strait of Sicily (vessel "Urania", Chief Scientist Marco Taviani) and is now housed in MZB.

In the parts dedicated to each species of *Galeodinopsis*, a list of the material is provided with all information given on the original labels. An abbreviated list of essential synonymy and/or chresonymy is also provided. For all the discussed species, four to five shells were studied by SEM, using LEO 420 SEM and Philips XL30 ESEM. SEM pictures of the type specimen of *Rissoa duboisii* from Nyst coll. were provided by IRSNB. Those of material at UCBL were provided by Arlette Armand (U.F.R. Sciences de la Terre, Lyon, France). With the exception of material loaned by public institutions, specimens examined by SEM were cleaned in a Bransonic 5 ultrasonic machine using distilled water. Specimens from public institutions were cleaned using a very fine brush wet with distilled water. Particular attention was given to the protoconch and teleoconch microsculpture as sources of taxonomic characters at species and genus level. The number of protoconch whorls was counted according to Verduin's (1977) method. Shells were measured using a stereomicroscope provided with a cross-line micrometer eyepiece and/or by SEM micrometer tool. The type specimen of *Rissoa duboisii* was measured on the SEM images. All the shells contained in each studied lot were measured with the exception of *Galeodinopsis tiberiana* from MF (with more than 200 shells), for which only selected specimens were measured, in particular those assumed to be at terminal growth. Dimensions of the shell at MNHU (catalogue number MB.Ga.43) are from Tembrock (1964: pl. 7: 6). For lots containing numerous shells, measurements are given for selected specimens together with average value and standard deviation. Measurements are shown in Supplementary Online Material at http://app.pan.pl/SOM/app59-Garilli_Parrinello_SOM.pdf. The position of varix/varices on the last whorl is indicated in degrees of the angle formed by the plane of the varix and the outer lip. Geographical and stratigraphical distributions of each discussed species are based on the examined material and the literature. Published records were critically evaluated on the basis of good illustrations, satisfactory descriptions and cross-checked references. As for material from institutions and private collections, in general we followed the stratigraphical attribution reported by the collectors.

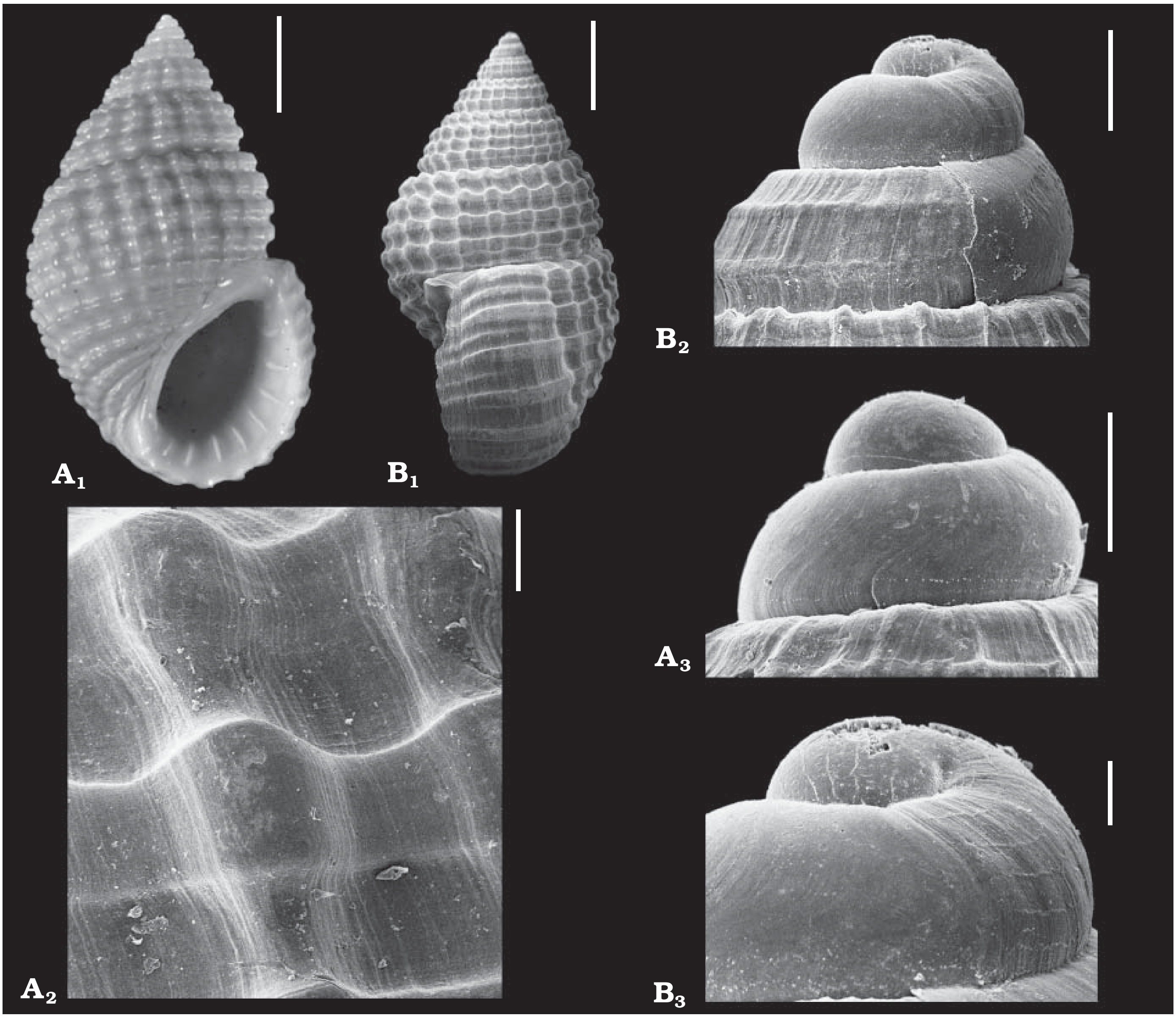


Fig. 6. Rissoid gastropod *Alvania cimex* (Linnaeus, 1758), type species of *Alvania* Risso, 1826, ex VG, MZPD Mal 2045, from N2 layer of Garilli (2011), Kyllini, Elea, NW Peloponnesus, Greece, Late Pleistocene. **A**. Specimen ex VG, MZPD Mal 2045a; shell in apertural view (A$_1$), protoconch in dorsal view (A$_3$), and a close-up of teleoconch surface (A$_2$) illustrating the very obsolete spiral elements and the incremental scars. **B**. Specimen ex VG, MZPD 2045b, shell (B$_1$) and protoconch (B$_2$) in profile view, and fine spiral threads on protoconch 1 (B$_3$). Scale bars: A$_1$, B$_1$, 1 mm; A$_2$, A$_3$, B$_2$, 100 μm; B$_3$, 30 μm.

Stratigraphical notes on some recovery areas

Agatino Reitano provided part of the analysed shells as coming from unspecified sandy layers cropping out between the ORTO 1 and KYLA3a samples of Dell'Angelo et al. (2012) in the Altavilla succession (Altavilla Milicia, NW Sicily, Italy). The age of these samples, presumably Late Zanclean–early Late Piacenzian, is from Dell'Angelo et al. (2012).

The "Middle Pliocene" age indicated by the respective collectors for some sites, following the three-fold Zanclean–Piacenzian–Gelasian division, is intended to be Piacenzian, according to the recently ratified, two-fold Pliocene stratigraphy (Gibbard et al. 2010).

Most of the species discussed here are from the Late Paleogene of Europe (mostly Germany and France), where the stratigraphy of the Eocene/Oligocene boundary has been debated (see Snyder et al. 1985 for a synthetic overview). As a consequence, the attribution of the Latdorfian Stage (partially corresponding to the Late Eocene/Early Oligocene Tongrian) (Müller 2011 with references) to the Eocene or to the Oligocene Series is still controversial. In the first case, involving a two-fold Oligocene (Rupelian–Chattian), the Latdorfian, as well as at least part of the Tongrian, should be included in the Late Eocene (Priabonian). In the second case, the Lat-

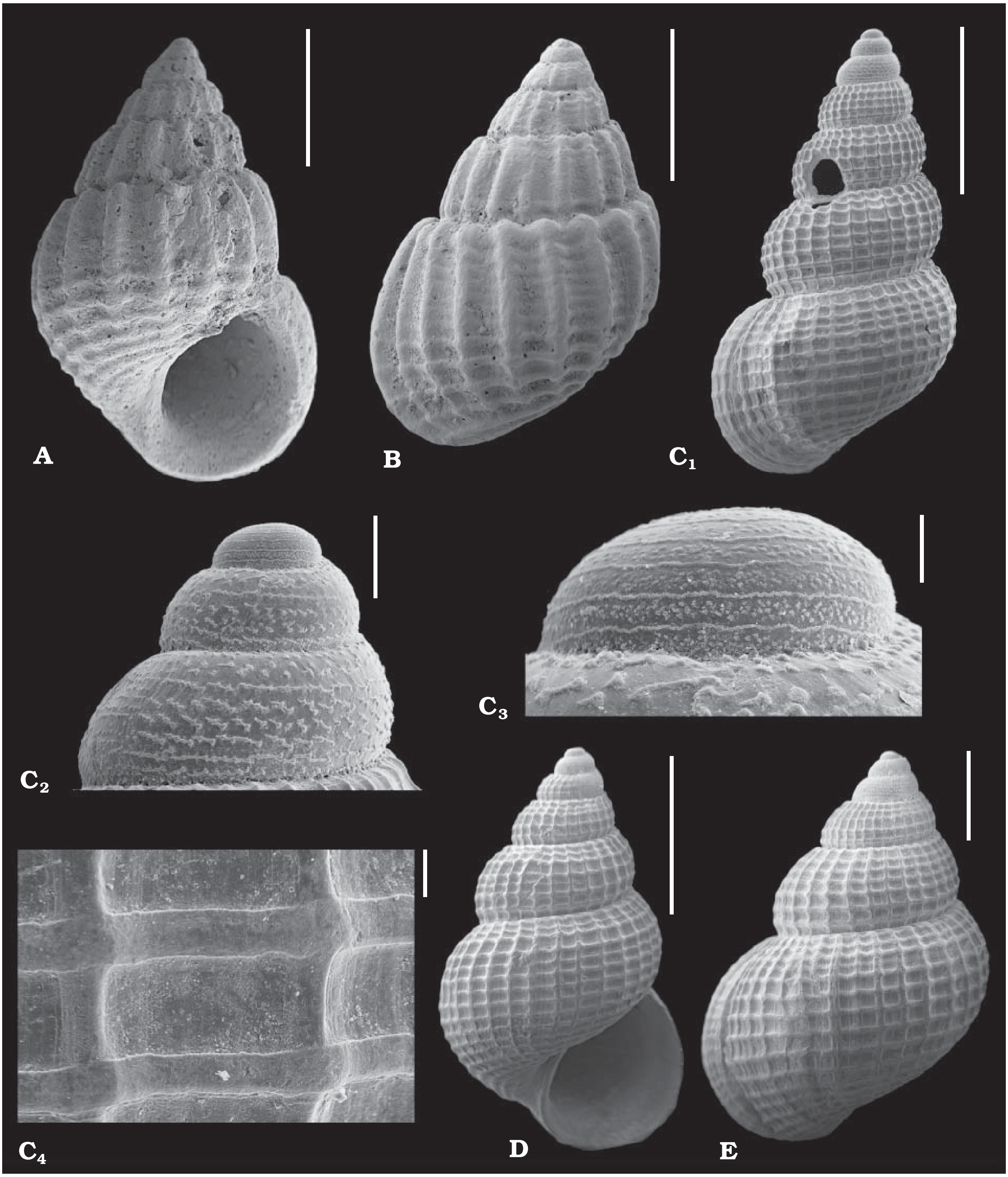


Fig. 7. Rissoid gastropods *Alvania areolifera* (Sandberger, 1863) (**A**, **B**) and *Alvania punctura* (Montagu, 1803), type species of *Arsenia* Monterosato, 1891 (**C**–**E**). **A**. Specimen MNHU MB.Ga.7749.1, Waldböckelheim, Rheinland-Pfalz, W Germany, Rupelian, Oligocene, in apertural view. **B**. Specimen MNHU MB.Ga.7749.2, same site as in A, in dorsal view. **C**. Slender specimen ex VG, MZB 49971, Recent, station CS'96/54, 135 m deep, Graham Bank, Strait of Sicily, in dorsal view (C_1), protoconch (C_2), sculpture of protoconch 1 (C_3), detail of teleoconch microsculpture (C_4). **D**. Specimen ex VG, MZPD Mal 2044a, Sicilian, Early Pleistocene, Acqua dei Corsari, Ficarazzi, Palermo, NW Sicily, in apertural view. **E**. Specimen ex VG, MZPD Mal 2044b, with inflated last whorl, same site as in D, in dorsal view. Scale bars: A, B, C_1, D, 1 mm; E, 500 μm; C_2, 100 μm; C_3, C_4, 25 μm.

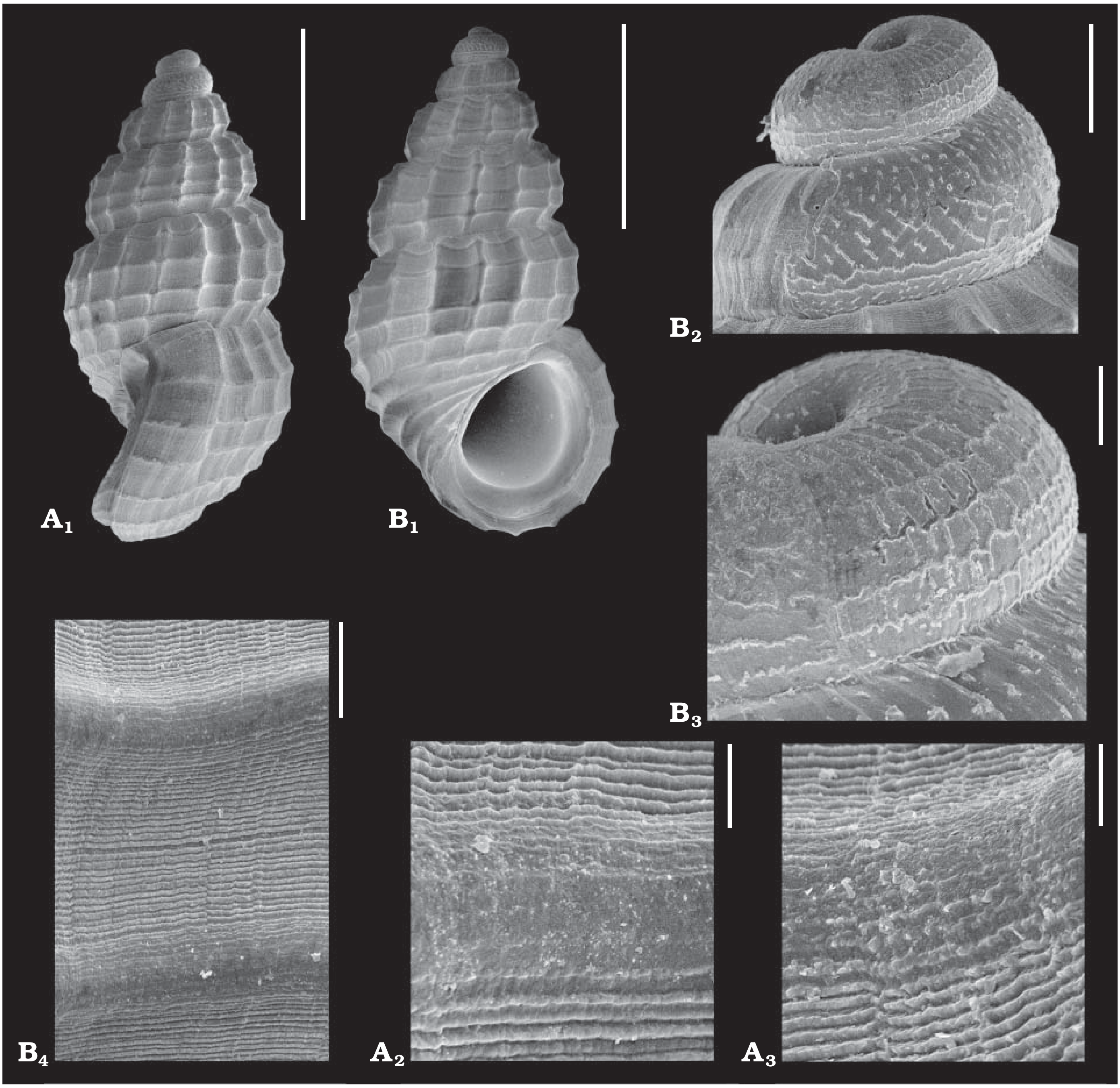


Fig. 8. Rissoid gastropod *Alvinia*? *testae* (Aradas and Maggiore, 1844), type species of *Actonia* Monterosato, 1884, ex VG, MZB 49972, Recent, station CS'96/71, 118.9 m deep, Graham Bank, Strait of Sicily. **A**. Specimen ex VG, MZB 49972a, in profile view (A_1), note the profile of the outer lip comparable to that of *Manzonia* Brusina, 1870 and *Flemellia* Nordsieck, 1972; teleoconch microsculptural pattern (A_2, A_3) comparable to that of *Alvinia* and *Flemellia*. **B**. Specimen ex VG, MZB 49972b, in apertural view (B_1), showing the double-rimmed aperture comparable to that of Manzonia and Flemellia; protoconch in profile view (B_2), the netted sculpture of protoconch 1 (B_3), and a panoramic view of microsculpture (B_4). Scale bars: A_1, B_1, 1 mm; B2, 100 µm; B_3, B_4, 30 µm; A_2, A_3, 10 µm.

dorfian would be the lower part of a three-fold Oligocene, as presumably intended by several 19th century and later authors (e.g., Speyer 1864; Koenen 1867; Wiechmann 1871; Görges 1957; Anderson 1960), who discussed some of the species here studied. This matter is made harder by the gap in many Late Paleogene successions due to the marked regression recorded at the Eocene/Oligocene boundary (Cavalier et al. 1981). The International Commission on Stratigraphy (see the International Stratigraphic Chart, available at http://www.stratigraphy.org/index.php/ics-chart-timescale) has ratified a two-fold Oligocene (Rupelian–Chattian) subdivision. This stratigraphical issue is beyond the scope of the present article, for which we have considered material indicated as from Latdorf (or Latdorfian/Lattorfian) as older than that reported from

Rupelian or Chattian. Material referred to middle Oligocene, following the three-fold division, therefore is Rupelian in age.

An (Early) Chattian age is indicated for the deposit at Söllingen (Janssen, 1978a, 1979 and personal communication, 2014).

As for most of the material from the Paris Basin, the collecting sites (Jeure and other localities cited by Deshayes 1864) are from the "Sables supérieurs", therefore from the Late Tongrian, actually (Early) Rupelian (Harris and Burrows 1891; Keen 1972). The material collected at (Château) Brunehaut (locality not cited by Deshayes 1864) is from the same age/formation (Harris and Burrows 1891). The Late Tongrian material from Klein-Spauwen "Tongrien ass. sup. Tg2b" (type locality of *Rissoa duboisii* Nyst, 1845) is also of Early Rupelian age (see also Anderson 1960: 25).

Systematic palaeontology

Class Gastropoda Cuvier, 1797

Subclass Caenogastropoda Cox, 1959

Order Littorinimorpha Golikov and Starobogatov, 1975

Family Rissoidae Gray, 1847

Subfamily Rissoinae Gray, 1847

Genus *Galeodinopsis* Sacco, 1895

Type species: *Rissoa tiberiana* Coppi, 1876, by original designation, Pliocene of N Italy, Emilia Romagna, Modena, Maranello, Gagliardella, "Tagliata" (see Garilli 2008: 43).

Galeodinopsis biangulata (Deshayes, 1864)

Figs. 9, 10.

1863 *Rissoa Duboisii* Nyst; Sandberger 1863: 131–132, pl. 10: 10–10a, as *Rissoa succincta* Nyst in pl. 10 (lapsus calami).

1864 *Rissoa biangulata* nov. sp.; Deshayes 1864: 407–408, pl. 24: 29–30 (figures in separate volume, 1866).

1867 *Rissoa Duboisii* Nyst; Koenen 1867: 113.

1921 *Manzonia* (*Taramellia*) *areolifera* Sandberger; Cossmann 1921: 31, pl. 2: 11, 12.

1960 *Alvania* (*Taramellia*) *duboisi* (Nyst, 1843); Anderson 1960: 25, pl. 3: 3.

1985 *Manzonia* (*Manzonia*) *duboisi* (Nyst, 1843); Ponder 1985: 48, fig. 100C.

2008 *Galeodinopsis duboisi* (Nyst, 1843); Garilli 2008: figs. 100–103.

2011 *Taramellia duboisi* (Nyst, 1845); Müller 2011: 24–25, pl. 5: 22a, b.

Type material: One possible syntype in UCBL provided with original label by Deshayes (Fig. 10A, B), with catalogue number EM 31000.

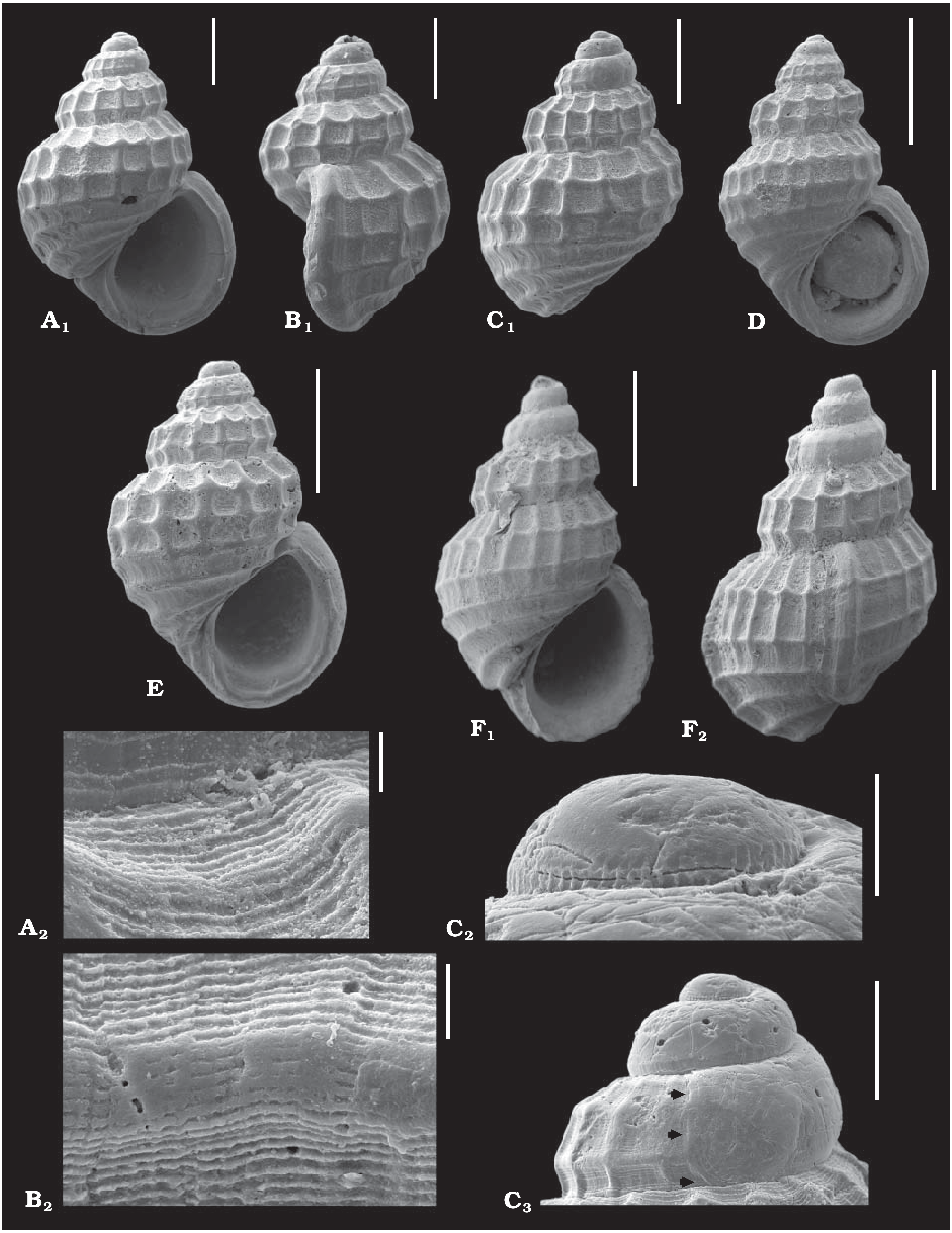
Type locality: Deshayes (1864: 407) reported Jeure, Montmorency, Versailles (Paris Basin, France) and Weinheim (Mainz Basin, Germany). This last locality is with reference to the material published in Sandberger (1863: 131, pl. 10: 10–10a).

Type horizon: Deshayes (1864: 407) reported "Sables supérieurs" (upper sands), from the Paris Basin, which are Early Rupelian in age.

Material studied.—10 shells in MNHU, MB.Ga.7744, as *Rissoa duboisi* Nyst, Waldböckelheim, Rheinland-Pfalz, W Germany, middle Oligocene marine sand; 5 shells, MZPD Mal 2036, originally in MF, FE15A, in two separate lots as *Alvania duboisi* and *Manzonia duboisi*, Hessen, SE of Kassel, Hessisch-Lichtenau, Glimmerode, central Germany, Late Oligocene (Chattian); 28 shells in UCBL, Deshayes coll. (one of them with original label), Tertiary of the Paris Basin, France; 10 shells in UCBL, Paris Basin coll., Brunehaut, France; 18 shells, in UCBL, Paris Basin coll., Jeures, France.

Description.—Shell small, conical-ovate to conical-turrited, reaching 4.95 mm in height and 3.15 mm in width; Ht/W quite variable, also depending on occurrence and position of varices on last whorl, from 1.4 to 2 in shells over 3 mm in height, average value 1.62. Protoconch multispiral, conical with 2.2 to 2.3 rounded whorls and a rather immersed nucleus. Protoconch 1 of about 0.7 whorls with netted sculpture consisting of 6–7 very thin spiral lirae and numerous, irregular, short, very narrow axial segments occurring in interspaces between lirae. Protoconch 2 sculptured with microscopic dots roughly forming one adapical and two abapical discontinuous fine spiral threads, particularly next to protoconch/teleoconch boundary. Protoconch/teleoconch boundary well-marked by thin, sinuous lip. Teleoconch with up to 4.5 convex whorls. Whorls sculptured with axial and spiral elements forming more-or-less strong clathrate, almost bicarinate pattern and acute knobs at their intersections. Axial ribs slightly curved, opisthocline to almost straight, most more prominent than spirals; 13–16 (rarely 17–18) on the penultimate whorl; lacking on shell base. Main spiral sculpture of cords overriding axial ribs; 2 on early and penultimate whorls; 6–8 and 3–6 on last whorl and on shell base, respectively. A very weak to obsolete subsutural cord occurs next to suture in some specimens. Teleoconch microsculpture on spiral cords of fine, rather flat, closely spaced spiral threads, joined by very low, short axial elements in a few specimens. Last whorl well expanded, making up 0.6 to 0.75 of total shell height, some shells bearing one varix at angles of 65° to 340°. Aperture wide, ovate, very rounded anteriorly, with acute angle posteriorly, making up about 0.4–0.55 and about 0.6–0.75 of total shell and of last whorl height, respectively. Outer lip sinuous, weakly opisthocline, double-rimmed; internally smooth, with thin rim on its edge; externally with

Fig. 9. Rissoid gastropod *Galeodinopsis biangulata* (Deshayes, 1864) from Glimmerode, Hessisch-Lichtenau, SE of Kassel, Hessen, Late Oligocene, Chattian (**A**–**E**), Waldböckelheim, Rheinland-Pfalz, Rupelian sands (**F**). **A**. Specimen ex MF, MZPD Mal 2036a, in apertural view (A_1); detail of a subsutural cord (A_2). **B**. Specimen ex MF, MZPD Mal 2036b, in profile view (B_1), teleoconch microscultpure (B_2). **C**. Specimen ex MF, MZPD Mal 2036c, in dorsal view (C_1); detail of protoconch showing traces of the netted sculpture on protoconch 1 (C_2); protoconch in dorsal view (C_3), black arrows indicate the protoconch/teleoconch boundary. **D**. Slender specimen ex MF, MZPD Mal 2036d in apertural view. **E**. Specimen ex MF, MZPD Mal 2036e with strong sculpture, in apertural view. **F**. Slender specimen MNHU MB.Ga.7744 with weaker sculpture resembling *Manzonia areolifera* sensu Cossmann (1921), in apertural (F_1) and dorsal (F_2) views. Scale bars: D–F, 1 mm; A1, B1, C1, 500 μm; C3 200 μm; C2, 50 μm; A2, B2, 20 μm. →


A1
B1
C1
D
E
F1
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A2
C2
B2
C3

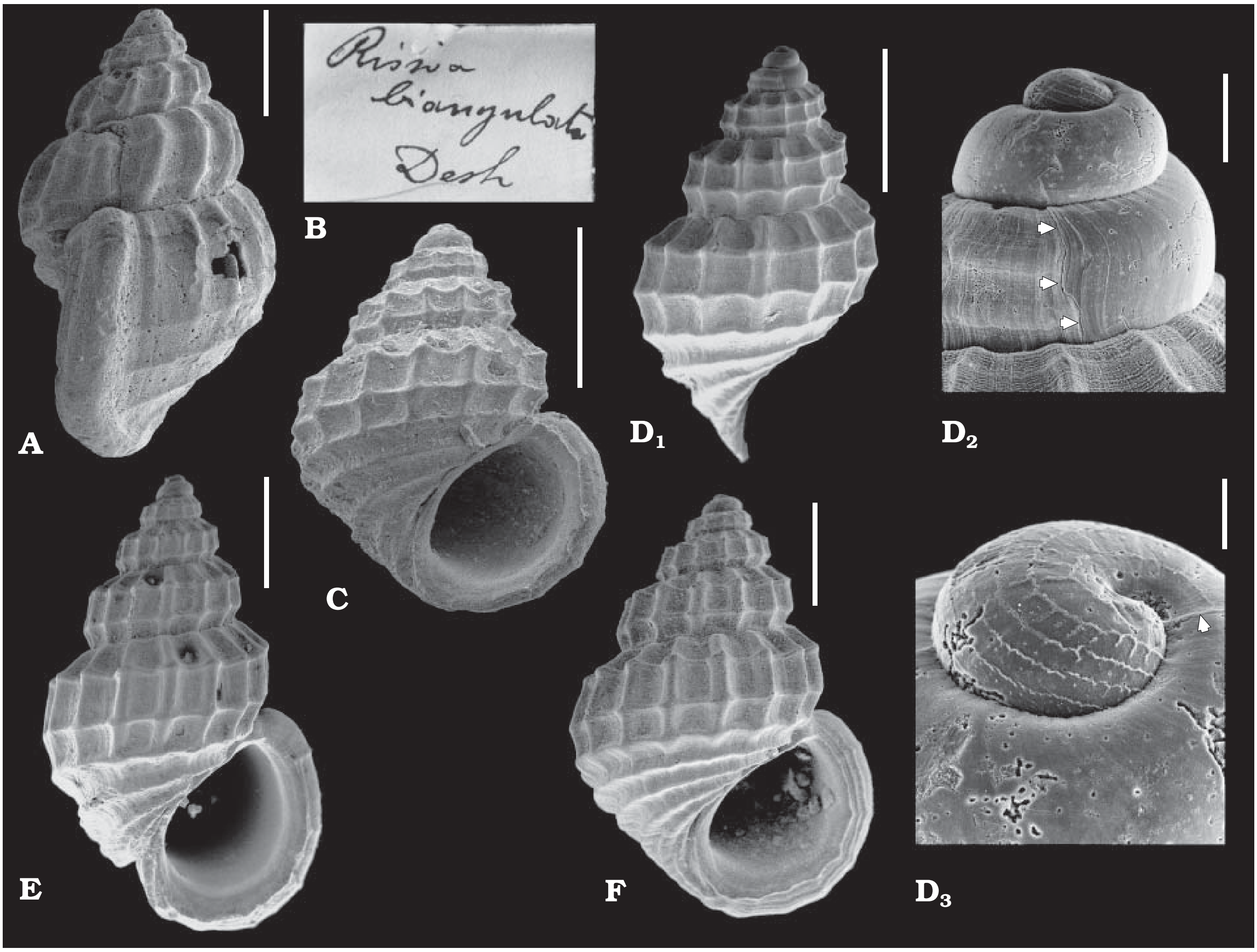


Fig. 10. Rissoid gastropod *Galeodinopsis biangulata* (Deshayes, 1864) from the Oligocene of the Paris Basin. **A**. Possible syntype specimen UCBL EM 31000, Deshayes collection, in profile view, resembling Deshayes' illustration (1866: pl. 24: 30). **B**. Original label of the same specimen. **C**. Specimen UCBL, EM 30996, Paris Basin collection from Jeures, in apertural view. **D**. Specimen UCBL, EM 30997, Deshayes collection, in profile view (D_1); protoconch in profile view (D_2), white arrows indicate the protoconch/teleoconch boundary; detail of protoconch showing trace of the netted sculpture on protoconch 1 (D_3), white arrow indicates the protoconch 1/protoconch 2 boundary. **E**. Specimen UCBL, EM 30998, Deshayes collection, in apertural view, matching Deshayes' illustration (1866: pl. 24: 29) and resembling *Manzonia areolifera* sensu Cossmann (1921). **F**. Specimen UCBL, EM 30999, Deshayes collection, in apertural view. Scale bars: A, C, D_1, E, F, 1 mm; D_2, 100 µm; D_3, 30 µm.

very marked varicose swelling. Inner lip curved, weakly expanded in columellar part, forming very narrow to obsolete umbilical chink.

Remarks.—Often misidentified as *Rissoa duboisii* Nyst, 1845, above all because of the low-quality original illustration and the inadequate description by Nyst (1845: pl. 37: 19), *Galeodinopsis biangulata* is characterized by having 2 spiral cords on all teleoconch whorls with the exception of the last. It shows marked variability in Ht/W ratio and in the robustness of spiral and axial elements. The morph with delicate sculpture (Figs. 9F and 10E) matches that illustrated by Cossmann (1921: pl. 2: 11, 12) as "*Manzonia* (*Taramellia*) *areolifera* (Sandb.)", a determination probably due to a lapsus calami in Sandberger (1863). Actually, *Rissoa areolifera* Sandberger, 1863 is a quite different species attributed to *Alvania*, as shown by material from the type locality (catalogue number MB.Ga.7749 at MNHU) matching the original illustration in Sandberger (1863: pl. 10: 11–11a as "*Rissoa Duboisi*", lapsus calami). In fact, this species is represented by conical shells lacking varices, and with a smaller aperture without a double-rimmed outer lip (see Fig. 7A, B).

The type specimen illustrated by Deshayes (1866: pl. 24: 29, 30) was not found in his coll. from the Paris Basin at UCBL. However, indisputable conspecific specimens in the same institution are in this and other colls. from the same geological formation. Among them one specimen (EM 31000) with an original label from Deshayes (Fig. 10A, B) could be regarded as a syntype. It has all of the main characterizing characters as illustrated by Deshayes (1866: pl. 24: 30). Another specimen from the same collection (Fig. 10E) matches well that illustrated by the same author (Deshayes

1866: pl. 24: 29). Conspecific shells (Fig. 10C) in UCBL, from "Jeures", near Fontenay (Paris Basin coll.), could be regarded as topotype material as this locality is the same as cited in the original description ("Jeure", see Deshayes 1864: 407). This locality is also known as "Jeurre" (Harris and Burrows 1891).

The microsculpture of *Galeodinopsis biangulata* is different from that shown by the type species (see below), having a sort of pseudopitted pattern. This consists of fine, rather flat, closely spaced threads covering the main spiral cords (Fig. $9B_2$). The pseudopitted character is due to the very obsolete or absent narrow axial bridge that form the typical pitted surface in *Manzonia*. Other very narrow, raised spiral threads are present in the interspaces between the main spiral cords and on the subsutural one (Fig. $9A_2$). Comparable microsculpture occurs in *G. semperi* (Wiechmann, 1871) (see the section dedicated to this species) and in rissoid species linked to *Alvinia*, such as *Turbo zetlandicus* (Fig. 5A), with which *G. biangulata* shares the turrited-shouldered shell shape. However, a relevant combination of characters justifies the placement of this species within *Galeodinopsis*: the ornamentation of the protoconch, particularly the netted protoconch 1 (Fig. $9C_2$), the common occurrence of varices on the last whorl, the large aperture with a double-rimmed outer lip, and the quite inflated last whorl. Therefore, the placement in *Taramellia* Seguenza, 1903 (Müller 2011 as *T. duboisi*) also should not be accepted, as this genus is a synonym of *Alvinia* (Ponder 1985).

Stratigraphic and geographic range.—Late Eocene/very Early Oligocene at Latdorf (Latdorfian Stage) and Magderburg, central Germany (Koenen 1867, as *Rissoa Duboisii*; Müller 2011, as *Taramellia duboisi*); Rupelian of northern France (Paris Basin) and western Germany (Mainzer Basin), at Waldböckelheim; Chattian of central, at Glimmerode, and north-central Germany, at Söllingen (Koenen 1867).

Galeodinopsis germanica sp. nov.

Fig. 11.

1960 *Alvania* (*Alvinia*) *multicostata* (Speyer, 1864); Anderson 1960: 24, pl. 3: 1.

1978 *Alvania* (*Arsenia*) *semperi* Wiechmann, 1871; Janssen 1978a: pl. 11: 31.

Etymology: From Latin *germanicus*, German.

Type material: The holotype (SMF 335576), represented by a presumably fully grown shell preserving protoconch and provided with two varices on the last whorl, and 6 paratypes (SMF 336787, 336788, 336789, 336790, 336791a, 336791b), originally labelled as "*Alvania semperi* Wiechmann".

Type locality: Abandoned mine-pit Höllkopf, Glimmerode, south of Hessisch-Lichtenau, Hessen, Germany.

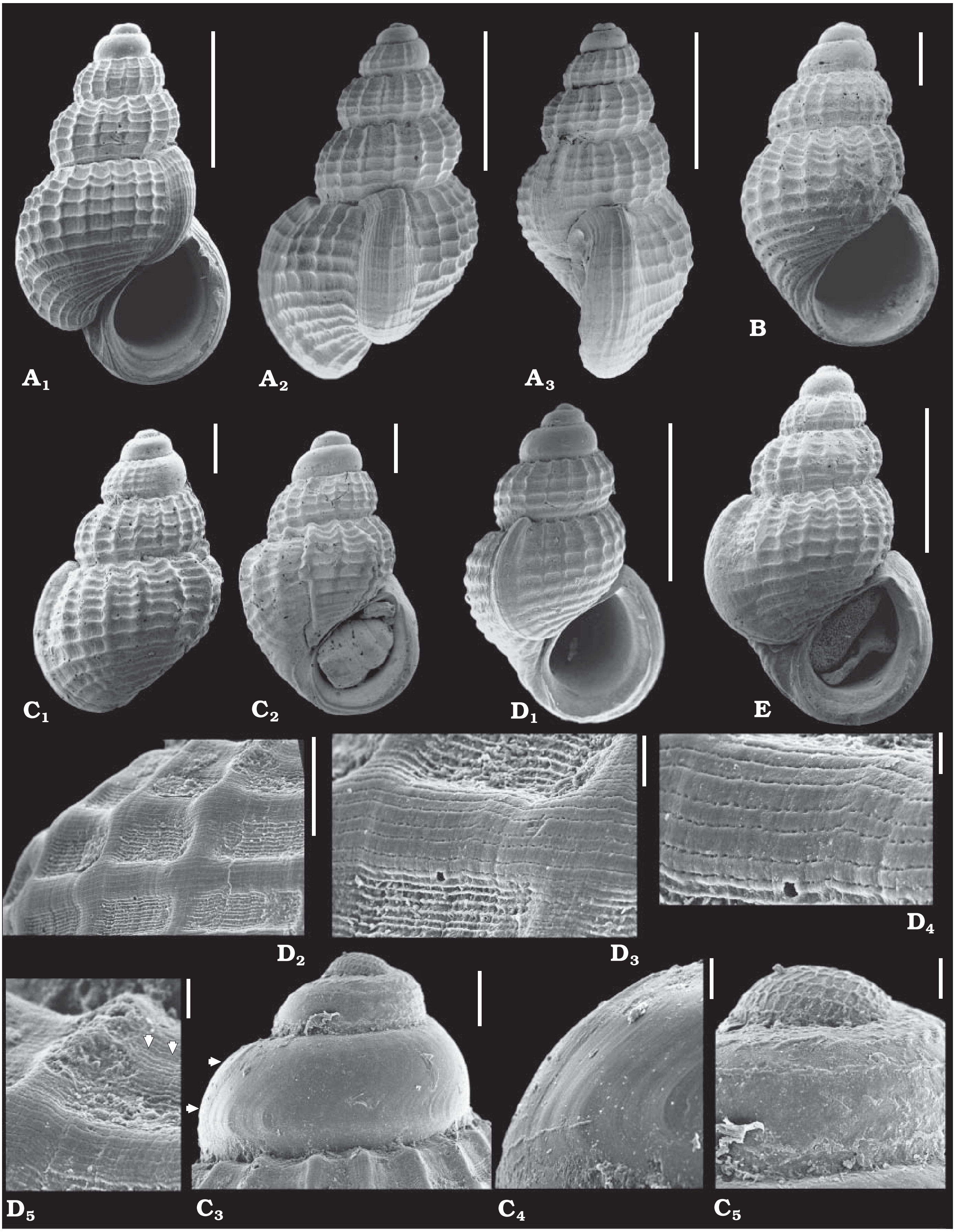
Type horizon: Early Chattian (Late Oligocene) Kasseler Meeressand.

Material.—Type material only.

Diagnosis.—Shell small, conical-ovate. Protoconch multispiral with up to 2.5 rounded whorls. Protoconch 1 with netted sculpture; protoconch 2 sculptured with fine lirae and axial segments between lirae. Teleoconch with up to 3.3 convex whorls sculptured with axial and spiral elements forming a clathrate pattern. Axial ribs slightly curved, prevailing over spirals in most specimens. Microsculpture characterized by *Manzonia*-like pattern, with numerous lines of pits on spiral cords. Last whorl well expanded, with one or two varices. Aperture wide, ovate, with double-rimmed outer lip. Inner lip curved, forming very small umbilical chink.

Description.—Shell small, conical-ovate, reaching 2.6 mm in height and 1.5 in width; average Ht/W of 1.65, about 1.7 in shells higher than 2 mm. Protoconch multispiral, conical, with 2.2 to 2.5 rounded whorls, nucleus rather immersed. Protoconch 1 of about 0.7 whorls with netted sculpture consisting of 5–6 very thin spiral lirae and numerous, irregular, short, very narrow axial segments in interspaces. Early protoconch 2 sculptured with 2 more-or-less discontinuous fine spiral threads in subcentral and abapical position, and very narrow, opisthocline plicae in subsutural position. Close to protoconch/teleoconch boundary only one irregular, strongly discontinuous thread formed by merged microscopic dots. Protoconch/teleoconch boundary well marked by thin, sinuous lip. Teleoconch with up to 3.3 evenly convex whorls sculptured with axial and spiral elements, forming clathrate pattern. Axial ribs slightly curved, more-or-less markedly opisthocline, more prominent than spirals; 17–22 on penultimate whorl; lacking on shell base. Spiral sculpture of almost flat cords overriding axial ribs; 4 cords close to protoconch/teleoconch boundary, rapidly increasing to 5–6; 6–7 on penultimate whorl of shells with height over 2 mm; 11–14 on last whorl, of which 5–7 on base. Subsutural and suprasutural cords usually weaker and/or discontinuous. Microsculpture on main spiral cords of flat ridges delimited by at least 7 spiral alignments of microscopic, subcircular pores forming pitted pattern. Pores formed by extremely short axial elements in very narrow interspaces between ridges. Narrow, raised spiral ridges cover interspaces between primary spiral sculpture, formed by discontinuous, tooth-like elements, extending perpendicularly from shell surface. Microsculpture of subsutural cord lacking pitted pattern, consisting of weakly raised spiral ridges with flat centres. Last whorl well expanded, making up 0.6 to 0.72 of total shell height; some shells with one or two varices forming angles of about 100°, 180°, 250°, and 340° to plain of peristome. Aperture wide, ovate, very rounded anteriorly, with acute angle posteriorly, making up 0.4–0.5 and about 0.6–0.75 of total shell and last whorl height, respectively. Outer lip double-rimmed, slightly sinuous, weakly opisthocline, internally smooth, externally with varicose swelling covered by incremental scars and spiral sculpture. Inner lip curved, weakly expanded in columellar area, forming very narrow to obsolete umbilical chink.

Remarks.—*Galeodinopsis germanica* sp. nov. is easily separable from other congeners by its slender shell shape resembling some *Manzonia* species, with which it shares the microsculptural pattern and the sculpture with axial elements more prominent than spirals. The most similar *Manzonia* species is *M. foraminata* (Lozouet, 1998), from the French


A1
A2
A3
B
C1
C2
D1
E
D2
D3
D4
D5
C3
C4
C5

Late Oligocene (Chattian) of the Aquitaine Basin. There are, however, significant differences allowing separation between *G. germanica* sp. nov. and *Manzonia* species: the occurrence in *G. germanica* sp. nov. of 1 or 2 varices on the last whorl, the absence of strongly raised cords on the shell base and the less rounded and proportionally larger aperture. These are typical *Galeodinopsis* characters. *G. germanica* sp. nov. is comparable with weakly sculptured morphs of *G. semperi* (hereafter described), from which it differs mainly by having different sculpture, consisting of more prominent, markedly curved ribs. *G. germanica* sp. nov. can also be distinguished by its more rounded teleoconch whorl profile (lacking the characteristic marked subsutural ramp of *G. semperi*) and by the typical pitted microsculptural pattern, as in the *Galeodinopsis* type species, *G. tiberiana* (compare Figs. 2C$_1$ and 11D$_4$). Also it bears more spiral cords: 6–7 vs. 3–5 and 11–14 vs. 7–10 on the penultimate and last whorl, respectively. The shells illustrated by Anderson (1960: pl. 3: 1, as *Alvania multicostata*) and Janssen (1978a: pl. 11: 31, as *Alvania semperi*) possibly are *G. germanica* nov. sp., having convex, rounded whorls, with no or obsolete subsutural ramp, and provided with axial elements more prominent than spirals. Due to this confusion, most of the Oligocene occurrences/material reported by these authors as "*A. multicostata*"/"*A. semperi*" possibly include both *G. germanica* nov. sp and *G. semperi* (see the next section for description of this species). Unfortunately, we were unable to study this material.

Galeodinopsis germanica sp. nov. shows a sculptural pattern of protoconch 2 very similar to that observed in other *Galeodinospis* species, except for the occurrence of subsutural plicae (Fig. 11C$_3$–C$_5$). It is remarkable that the microsculpture of the very weak subsutural cords (Fig. 11D$_5$) is similar to the microsculptural pattern seen in *G. biangulata*, *G. semperi* and other species related to *Alvinia*.

Stratigraphic and geographic range.—Chattian of central Germany, at Glimmerode (type locality) and Freden (Anderson 1960, as *Alvania muticostata*), and of western Germany, at Moers (Janssen 1978a, as *Alvania semperi*).

Galeodinopsis semperi (Wiechmann, 1871)

Figs. 12, 13.

1845 *Rissoa Duboisii* nov. sp.; Nyst 1845: 418, n° 358, pl. 37: 19.
1864 *Rissoa multicostata* nov. sp.; Speyer 1864: 290, pl. 41: 3–5, non *R. multicostata* Adams, 1850 nec *R. multicostata* Garrett, 1857, which belong to *Rissoina* d'Orbigny, 1840.
1871 *Alvania Semperi* nov. sp.; Schwartz v. Mohrenstern (in litt.) Wiechmann 1871: 58–60.
1954 *Alvania duboisi* (Nyst); Glibert and Heinzelin 1954: 351, pl. 5: 13.
1964 *Alvania* (*Arsenia*?) *multicostata* (Speyer, 1864) var.?; Tembrock 1964: pl. 7: 6, 7.
2008 *Alvania* (*Alvania*) *multicostata* (Speyer); Müller 2008: pl. 4: 10a, b.
2011 *Alvania* (*Alvania*) *multicostata* (Speyer, 1864); Müller 2011: pl. 5: 18a, b, 19a, b, 20, 21, 23a, b, and 24a, b.

Type material: Repository of Wiechmann (1871) types unknown.

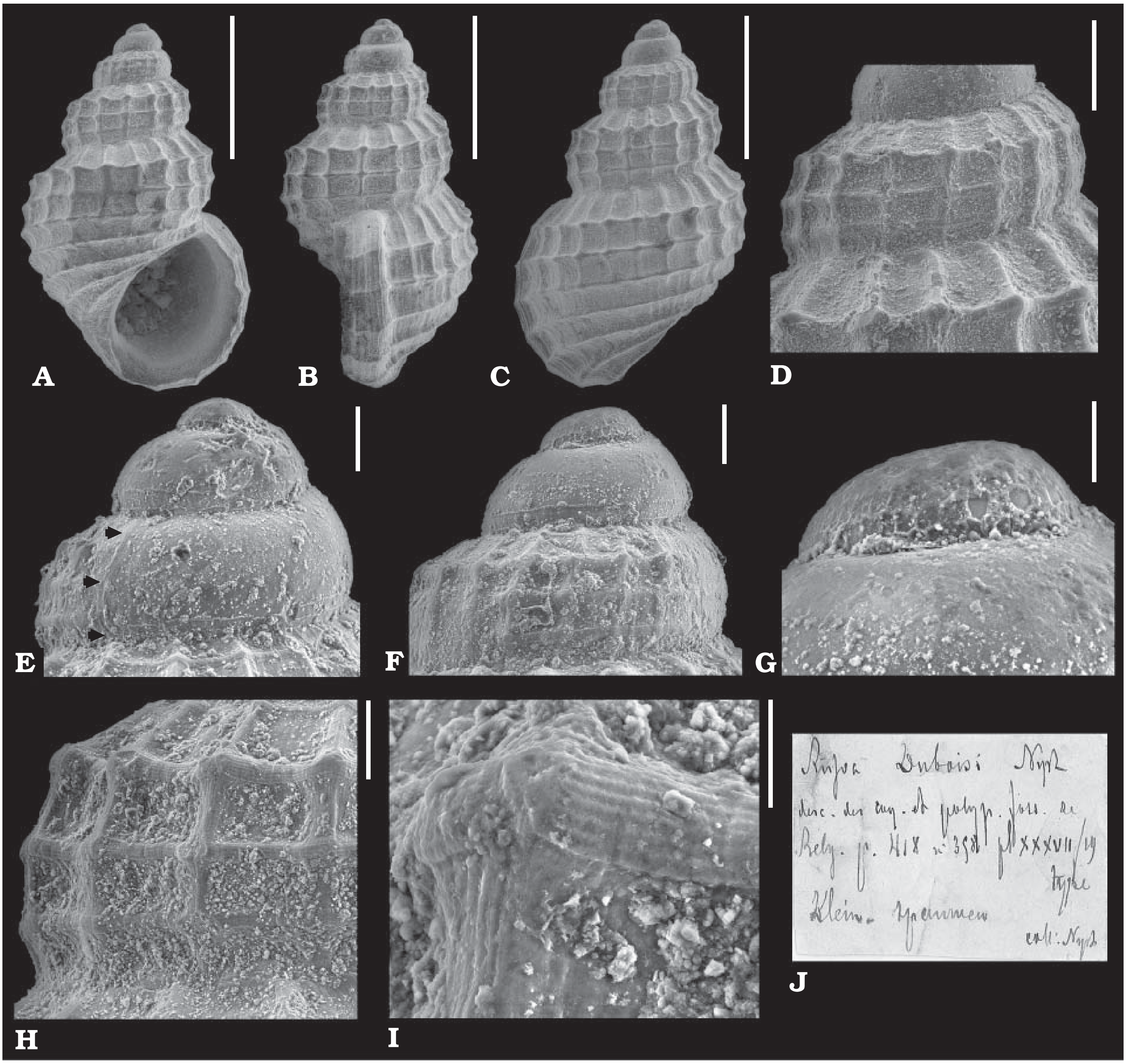
Type locality: Wiechmann (1871: 58–59) based his species on shells from Söllingen (type locality of *Rissoa multicostata* Speyer, 1864) and also cited conspecific specimens from Crefeld (also known as Krefeld), Doberg and Sternberg. All these localities, which are Chattian in age, are in N Germany.

Type horizon: Oligocene marine sand, as for Söllingen (see Anderson 1960: 24).

Material studied.—The type specimen (Fig. 12) of *Rissoa duboisii* Nyst, 1845 in IRSNB, 3956, Tg2b layer of Klein-Spauwen, Belgium, Tongrian; 3 shells in MNHU, MB.Ga.7745, as *Rissoa multicostata* Speyer, Magdeburg?, Sachsen-Anhalt, Germany, Middle Oligocene; 1 shell in MNHU, MB.Ga.43, illustrated by Tembrock (1964: pl. 7: 6) as *Alvania* (*Arsenia*?) *multicostata* (Speyer, 1964) var.?, from Latdorfian bed, Latdorf, Germany; 1 shell in BGR, X1239, illustrated by Tembrock (1964: pl. 7: 7) as *Alvania* (*Arsenia*?) *multicostata* (Speyer, 1964) var.?, drill hole Drehna 5/1960, Lusatia/Brandenburg, Germany, Late Oligocene; 1 incomplete shell in BGR, X9909, illustrated by Gründel (1997: fig. 2) as *Alvania* (*Arsenia*) *semperi* Wiechmann, 1871.

Description.—Shell small, conical-turrited, reaching about 4.1 mm in height and 2.6 mm in width (about 2.55 × 1.6 in type specimen of *Rissoa duboisii*); Ht/W variable, mainly depending on occurrence and position of varices on last whorl, from 1.4 to about 1.7. Protoconch multispiral, conical, with 2.3 to 2.7 rounded whorls and rather immersed nucleus. Protoconch 1 of about 0.7 whorls with netted sculpture consisting of at least 6 very thin spiral lirae and numerous, irregular, short, very narrow axial segments occurring in interspaces between lirae. Intersection of spiral and axial forming rough hexagons or squares. Protoconch 2 sculptured with very few microscopic dots roughly forming one or two discontinuous fine spiral threads in suprasutural position. Protoconch/teleoconch boundary marked by weakly sinuous, very thin lip. Teleoconch with up to at least 3.5 convex whorls. Whorls sculptured with equal axial and spiral elements forming clathrate pattern of acute nodules at their intersections. Axial ribs slightly curved, opisthocline to almost straight; 18–24 on penultimate whorl; lacking on shell base. Main spiral sculpture of cords overriding axial ribs. Cords 3–4 on early teleoconch and on penultimate whorl; 7–10 and 3–7 (depending on shell height) on last whorl and shell base, respectively. A further, much weaker, almost flat subsutural cord occurs on

← Fig. 11. Rissoid gastropod *Galeodinopsis germanica* sp. nov., abandoned mine-pit Höllkopf, Glimmerode, south of Hessisch-Lichtenau, Hessen, Germany, Chattian (Late Oligocene) Kasseler Meeressand. **A**. Holotype SMF 335576, in apertural (A$_1$), dorsal (A$_2$), and profile (A$_3$) views. **B**. Paratype SMF 336790, in apertural view. **C**. Paratype SMF 336789, in apertural (C$_1$) and dorsal (C$_2$) views; protoconch in dorsal view (C$_3$), white arrows indicate approximate position of the protoconch/teleoconch boundary; details of protoconch showing sculpture on late protoconch 2 (C$_4$), protoconch 1 and early protoconch 2 (C$_5$). **D**. Paratype SMF 336788, in apertural view (D$_1$), teleoconch sculpture (D$_2$), details of microsculpture showing the typical *Manzonia*-like pitted pattern (D$_3$, D$_4$), and the *Alvinia*-like pattern (white arrows) on the obsolete subsutural cord (D$_5$). **E**. Paratype SMF 336787, in apertural view. Scale bars: A$_1$–A$_3$, D$_1$, E, 1 mm; B, C, 300 μm; C$_3$, D$_2$, 100 μm; C$_4$, C$_5$, 30 μm; D$_3$, D$_5$, 20 μm; D$_4$, 10 μm.



Rissoa Duboisi Nyst
desc. des coq. et polyp. foss. de
Belg. p. 418 n° 358 pl XXXVII/19
type
Klein-Spauwen
coll: Nyst

Fig. 12. **A**–**I**. Rissoid gastropod *Galeodinopsis semperi* (Wiechmann, 1871), the type specimen IRSNB 3956 (Nyst coll.) of synonymous *Rissoa duboisii* Nyst, 1845, Tg2b layer of Klein-Spauwen, Belgium, Late Tongrian. Specimen in apertural (**A**), profile (**B**), and dorsal (**C**) views; early teleoconch whorls (**D**); protoconch in profile view (**E**), black arrows indicate the protoconch/teleoconch boundary; subapertural view (**F**); detail of protoconch 1 showing trace of the netted sculpture (**G**); detail of teleoconch sculpture (**H**); microsculpture on spiral cord (**I**). **J**. Original label in Nyst's handwriting with the citation of "type" and references to the original description and illustration in Nyst, 1845. Scale bars: A–C, 1 mm; D 200 µm; E, F, H, 100 µm; G, 50 µm; I, 30 µm.

Fig. 13. Rissoid gastropod *Galeodinopsis semperi* (Wiechmann, 1871) from the Paleogene of Germany. **A**. Juvenile specimen BGR X1239, same specimen as illustrated by Tembrock (1964: pl. 7: 7) as *Alvania* (*Arsenia*?) *multicostata* (Speyer, 1864) var.?, from drill hole Drehna 5/1960, Lusatia/Brandenburg, Oligocene, Chattian, in apertural view (A_1); protoconch in profile view (A_2), white arrows indicate the protoconch/teleoconch boundary; detail of protoconch 1 showing trace of the netted sculpture (A_3); detail of teleoconch sculpture (A_4); teleoconch microsculpture showing the almost flat subsutural cord (A_5). **B**. Specimen MNHU MB.Ga.7745.1 with delicate sculpture from Magdeburg?, Sachsen-Anhalt, Oligocene, Rupelian, in apertural (B_1), dorsal (B_2), and profile (B_3) views; teleoconch microsculpture on spiral cord (B_4). **C**. Specimen MNHU MB.Ga.43, from Latdorf, Latdorfian, same specimen classified by Tembrock (1964: pl. 7: 6) as *Alvania* (*Arsenia*?) *multicostata* (Speyer, 1864) var.?, in apertural (C_1) and dorsal (C_2) views. **D**. Specimen MNHU MB.Ga.7745.2 from Magdeburg?, Sachsen-Anhalt, Oligocene, Rupelian, in apertural view, strongly resembling *Rissoa multicostata* Speyer, 1864 from the original illustration (pl. 41: 3). Scale bars: B_1–B_3, C, D, 1 mm; A_1, 200 µm; A_2, 100 µm; A_3–A_5, B_4, 20 µm.

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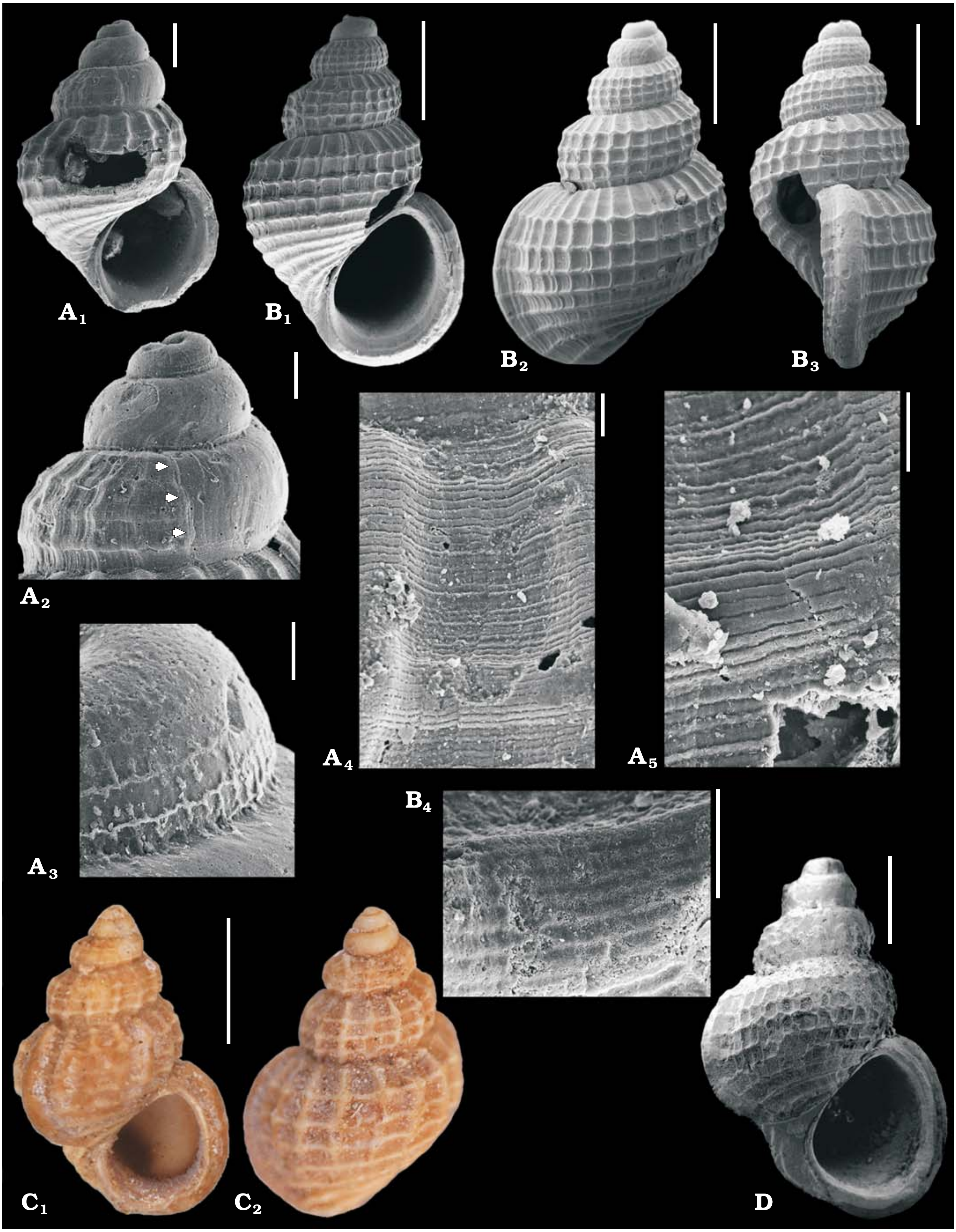
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some specimens. Teleoconch microsculpture on spiral cords of fine, raised, closely spaced spiral threads simulating a sort of pseudopitted pattern on a few specimens. Threads more raised on subsutural cord, where they do not show any trace of pitted microsculpture. Last whorl well expanded to strongly inflated, making up about 0.7 total shell height; some shells with one varix at angles of 90° to about 200°. Aperture wide, ovate, very rounded anteriorly, with acute angle posteriorly, making up about 0.5 and about 0.6–0.7 of total shell and of last whorl height, respectively. Outer lip weakly sinuous to almost straight, double-rimmed due to a thin rim on its edge; internally smooth; externally with very marked varicose swelling covered by spiral cords. Inner lip weakly curved, with very thin expansion in columellar area, forming very narrow to obsolete umbilical chink.

Remarks.—Nyst (1845) described this species under the name *Rissoa duboisii* while renaming *Cyclostoma scalare* Dubois, 1831, preoccupied by *Rissoa scalaris* Michaud, 1831. However *C. scalare* Dubois, 1831 is a different species attributed to *Manzonia* (Fig. 3A; see also Kowalke and Harzhauser 2004). Therefore, the Nyst's (1845) name should not be used, in accordance with the provisions of ICZN art. 72.7, and the available name for the species discussed here is *Alvania semperi* Wiechmann, 1871, being *Rissoa multicostata* Speyer, 1864 a primary junior homonym.

The tentative placement in *Arsenia* Monterosato, 1884 (Tembrock 1964, as *A. multicostata*) is incorrect. As we have shown (Fig. 7C–E), *Turbo punctura* Montagu, 1803, the type species of *Arsenia*, is quite distant, having a different shell shape, a single-rimmed aperture and a protoconch 1 with no netted sculpture; even its microsculpture is totally different, being almost smooth. *T. punctura* is regarded as falling within *Alvania* sensu stricto, following Ponder (1985). Therefore, the attribution to *Alvania* Risso, 1826, as indicated by Müller (2008, 2011), also is rejected. The microsculpture of *Galeodinopsis semperi* is comparable to that of rissoid species such as *Turbo zetlandicus* Montagu, 1815 (Fig. 5A_2), type of *Flemellia*, and is very similar to that observed in *G. biangulata* (compare Figs. 12I, 13A_4, A_5 with 9B_2), although only a few specimens of *G. semperi* show a trace of the narrow axial bridges that form the typical pitted surface in *Manzonia* or in the type species of *Galeodinopsis*. *Galeodinopsis semperi* can be separated from *G. biangulata* by the occurrence of at least 3 cords (vs. 2) starting from the first teleoconch whorl. Another main difference is in the number of axial ribs: 18–24 in *G. semperi*, 13–16 in most specimens of *G. biangulata*. Also, the spiral cords on the penultimate and last whorls of *G. semperi* are more numerous. As in *G. biangulata, G. semperi* is characterized by a turrited-shouldered teleoconch similar to that of *Alvinia*. The quite inflated last whorl, bearing varices on many specimens, is the main character allowing this species to be placed within *Galeodinopsis*.

Galeodinopsis semperi is quite variable, above all in teleoconch sculpture, which is strongly to gently clathrate. Morphs with marked sculpture (as in the type specimen of *Rissoa duboisii* in Nyst coll., Fig. 12A–D, H, and in a Latdorfian shell, Fig. 13C) bear fewer cords (18 on the penultimate whorl), whereas other morphs with more delicate sculpture (Fig. 13B, D), matching the original illustration of *Rissoa multicostata* Speyer (1864: pl. 41: 3–5), have more spiral cords (up to 24 in the material studied) and axial ribs (4 vs. 3 in the type specimen of *R. duboisii*). All these morphs show the same pattern of teleoconch microsculpture (compare Figs. 12I and 13B_4) and are regarded as intraspecific variability of one species. Wiechmann (1871, ex litteram from Schwartz 1864) described *Alvania semperi* as a slender form comparable to "*Alvania multicostata* Speyer" with which it shares the same reticulate sculptural pattern. This form is characterized by finer sculpture, with more numerous ribs, and by a proportionally less inflated last whorl. Koenen (1867) reported a similar form at Söllingen together with typical shells of *R. multicostata* Speyer, 1864. This form, possibly the same as illustrated by Müller (2011: pl. 5: 24a, b), is regarded as the expression of the wide intraspecific variability of *G. semperi*. Koenen (1867) and Wiechmann (1871) also noted the sculptural variability of Speyer's (1864) species, when describing a morph comparable with *Rissoa partschi* Hörnes, 1856, a species of *Alvinia* having a simple peristome (see Kowalke and Harzhauser 2004: fig. 8b). This morph, characterized by more prominent sculpture, is represented by the material described by Nyst (1845) as *R. Duboisii.*

The name "*Rissoa Semperi* Schwartz v. Mohrenstern" used by Görges (1957) with reference to Schwartz (1864, "Rissoiden, 2") is not valid, as also stated by Anderson (1960). In fact, Schwartz (1864) never described or quoted this species/name in his *Die Familien der Rissoiden*.

The specimen illustrated by Janssen (1978a: pl. 11: 30) as *Alvania* (*Arsenia*) *semperi* Wiechmann is very close to *Alvania rupeliensis* Tembrock, 1964 (pl. 7: 8). However we were not able to get shells of this last species, particularly the holotype that should be housed at BGR, and indicate whether it is a well-established taxon or simply a synonymous of *Galeodinopsis semperi*. The worn shell illustrated by Janssen (1978a, pl. 11: 32) might belong to *G. semperi*.

Stratigraphic and geographic range.—Late Eocene/very Early Oligocene at Latdorf (Latdorfian Stage) and Magderburg (Tembrock 1964; Müeller 2011, as *Alvania multicostata*), central Germany, and Klein-Spauwen, Belgium (Tongrian Stage); Early Oligocene (Rupelian) of Belgium (Late Tongrian Stage), at Klein-Spauwen, and north-central Germany, at Magderburg; Late Oligocene (Chattian) at Doberg and Crefeld, north-western Germany (Wiechmann 1871), and Söllingen (Speyer 1864; Wiechmann 1871), north-central Germany.

Galeodinopsis tiberiana (Coppi, 1876)

Figs. 2, 14A–C, F, G.

1862 *Rissoa tuba* nov. sp.; Doderlein 1862: 17 (nomen nudum).

1876 *Rissoa Tiberiana* nov. sp.; Coppi 1876: 201–202.

1990 *Manzonia fariai* nov. sp.; Rolán and Fernandes 1990: 64–65, pl. 1: 4–6.

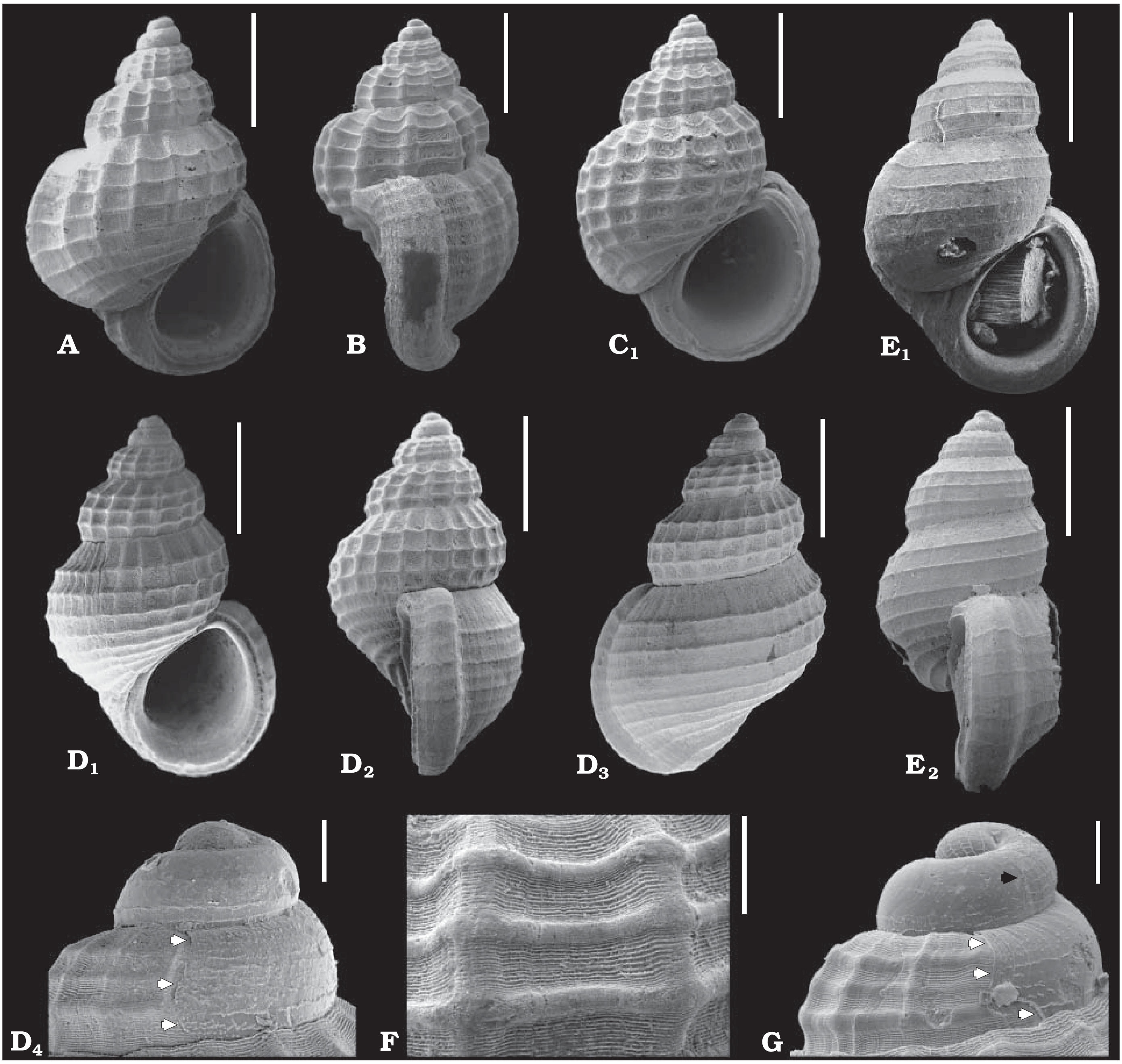


Fig. 14. Rissoid gastropods *Galeodinopsis tiberiana* (Coppi, 1876) (**A**–**C**, **F**, **G**) and *G*. cf. *tiberiana* (**D**, **E**), from the Neogene of the Mediterranean area. Altavilla Milicia, Palermo, NW Sicily, Late Zanclean–early Late Piacenzian, Pliocene (**A**, **D**, **E**); Stirone River, San Nicomede, Parma, N Italy, Pliocene (**B**); Rio Grizzaga sands, Gagliardella, Fogliano, Maranello, Modena, N Italy, Piacenzian, Pliocene (**C**, **F**, **G**). **A**. Specimen ex AR, MZPD Mal 2032, in apertural view, showing the typical *G. tiberiana*-morph. **B**. Specimen ex MF, MZPD Mal 2034 in profile view, showing the sinuous outer lip curved backwards in the lower part. **C**. Specimen ex MF, MZPD Mal 2035d, in apertural view, showing more axial and spiral elements. **D**. Specimen ex AR, MZPD Mal 2033a, in apertural (D_1), profile (D_2), and dorsal (D_3) views, somewhat transitional between specimen as in C and galeodiniform specimens as in E and in Fig. 15; protoconch in profile view (D_4). **E**. Galeodiniform specimen ex AR, MZPD Mal 2033b, in apertural (E_1) and profile (E_2) views, tentatively assigned to *G. tiberiana*. **F**. Specimen ex MF, MZPD Mal 2035e, showing detail of teleoconch sculpture with marked axial ribs. **G**. Specimen ex MF, MZPD Mal 2035f, showing protoconch in profile view. Black and white arrows indicate the protoconch 1/protoconch 2 and protoconch/teleoconch boundaries, respectively. Scale bars: A–C, D_1–D_3, E, 1 mm; D_4, F, G, 100 μm.

1994 *Alvania* (*Alvania*) *tiberiana* (Coppi, 1876); Bernasconi and Robba 1994: 79–80, pl. 4: 1, 2.

1999 *Alvania fariai* (Rolán and Fernandes, 1990); Gofas 1999: 88–89, figs. 39–42.

2004 *Alvania fariae* (Rolán and Fernandes, 1990); Landau et al. 2004: 41, pl. 7: 3, 4.

2008 *Galeodinopsis tiberiana* (Coppi, 1876); Garilli 2008: 43, figs. 90–99.

Type material: More than 100 possible syntypes (not seen) in Coppi coll., at MPOB, IPUM 13721 from the Pliocene of Emilia Romagna, N Italy.

Type locality: "Tagliata" (see Garilli 2008: 43), Gagliardella, Maranello, Modena, Emilia Romagna, N Italy.

Type horizon: Coppi (1876: 202) reported "tabiano" at "Tagliata", which may be referred to the Zanclean–Piacenzian terrigenous succession of the Emilia Romagna Apennines.

Material studied.—Those shells listed by Garilli (2008), including 31 Recent shells in MNHN, from the coasts of West Africa, originally classified as *Alvania fariai* (Rolán and Fernandes, 1990); 205 shells in MF, some at MZPD Mal 2034–2035, from different Italian Neogene sites including type locality ("La Tagliata", Maranello, Modena, N Italy), most of them originally identified as *Alvania tiberiana* (Coppi, 1876); 44 shells at MGUP, Doderlein coll., from the Mio-Pliocene of N Italy, originally identified as *Rissoa tuba* Doderlein (nomen nudum); 33 shells ex AR, as *Alvania tiberiana*, MZPD Mal 2032, from the Pliocene of Altavilla Milicia, Palermo, Sicily. For measurements of the shells housed in MNHN see Gofas (1999), who cited this species as *A. fariai* (Rolán and Fernandes, 1990).

Description.—Shell conical, sturdy, reaching 3.75 mm in height and 2.75 mm in width. Ht/W ratio 1.3–1.5. Protoconch multispiral, conical, with 2–2.2 convex whorls, nucleus rather immersed. Protoconch 1 of about 0.7–0.8 whorls, with netted sculpture, consisting of 7–8 very thin spiral lirae and numerous, irregular, short, very narrow axial segments occurring in interspaces between lirae. Protoconch 2 sculptured with very small, sparse granules, fused into 2–4 discontinuous ridges on central and abapical portions of latter part of last whorl. Some groups of granules form very short, prosocline segments on central area, mainly close to protoconch/teleoconch transition, which is marked by thin, quite sinuous lip. Teleoconch of 3–3.5 convex whorls, sculptured with a primary pattern of strong, slightly sinuous, opisthocline ribs; 12–14 (rarely 15) on penultimate whorl, becoming very weak or lacking towards base. Ribs covered with secondary spiral sculpture, formed by narrow, flat cords; 3, 4–5 and 8–10 (rarely 11–13) cords on first, penultimate and last whorls, respectively. Much weaker subsutural cord present on some specimens. Cords bear pitted microsculpture, consisting of microscopic subcircular pores forming 8–10 spiral alignments. Numerous, closely spaced, very fine spiral ridges occur between cords, formed by rough prismatic, tooth-like elements, extending perpendicularly from shell surface. At their base, each ridge has a lamella-like expansion, which covers the interspaces between two ridges. Weak subsutural cord lacking pitted surface, consisting of raised, very fine threads. Last whorl inflated, well-expanded, 0.6 to 0.75 of total shell height, many specimens bearing 1 or 2 varices with angles from about 100° to 270°, just before the outer lip on most specimens. Aperture ovate, very rounded anteriorly, weakly angulated posteriorly, comprising about 0.40–0.55 and about 0.7–0.75 (rarely about 0.6) of total shell and last whorl heights, respectively. Outer lip sinuous, weakly opisthocline; internally smooth, with thin rim on its edge; externally with very marked varicose swelling, covered with spiral sculpture, with narrow ridge on its base, towards aperture, forming double rim. Inner lip weakly curved, with very narrow columellar thickening, forming obsolete umbilical chink. Recent specimens white. After Garilli (2008), modified.

Stratigraphic and geographic range.—*Galeodinopsis tiberiana* lives in the eastern Atlantic, from Mauritania to northern Angola (see also Garilli 2008, with references). In the Mediterranean area it occurs in the Miocene (Tortonian) of northern Italy (northern Apennines) and the Pliocene of northern, central and southern Italy, of southern Spain, and of Algeria. In the Atlantic, it is recorded from the Portuguese Pliocene (Piacenzian) of the Mondego Basin (Garilli 2008, with references).

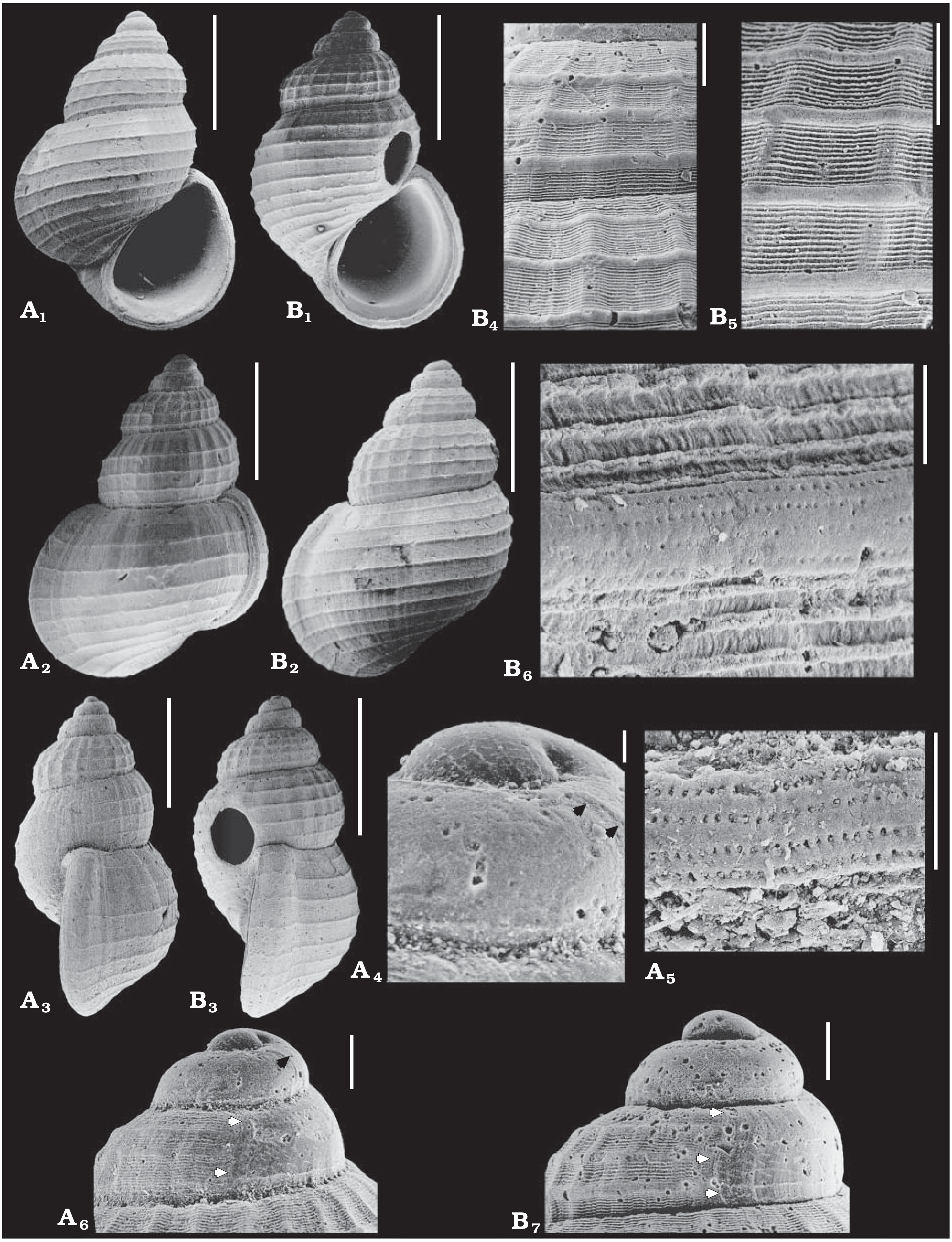
Galeodinopsis cf. *tiberiana* (Coppi, 1876)

Figs. 14D, E, 15.

Material studied.—4 shells in MZPD (Mal 2033), ex AR, as *Alvania* sp., from the Pliocene yellow fine sand cropping out in the right side of the Milicia River, Altavilla Milicia, Palermo, NW Sicily, Italy.

Description.—Shell conical, more elongate than typical *Galeodinopsis tiberiana*, reaching 3.2 mm in height and 2.05 mm in width. Ht/W ratio of about 1.5–1.6. Protoconch as for *G. tiberiana.* Teleoconch of little more than 3 convex whorls, with more-or-less marked subsutural ramp. Whorls sculptured by delicate to raised ribs, becoming obsolete to lacking on last whorl, crossed by finer spiral cords. Ribs weakly opisthocline or almost straight; 18–20 on penultimate whorl. Spiral cords quite narrow, numbering 3 on very early teleoconch, 4–6 and 9–11 on penultimate and last whorls, respectively. Each cord has pitted microsculpture, consisting of microscopic subcircular pores forming 4 spiral alignments. Pitted pattern formed by few flat threads connected by very short microscopic axial elements. Microsculpture between cords as for *G. tiberiana*. Last whorl inflated, well-expanded, comprising about 0.7 total shell height; two shells bear a single varix with angle of 180°. Aperture ovate, very rounded anteriorly, weakly angulated posteriorly, comprising 0.45–0.5 and 0.7 of total shell and last whorl heights, respectively. Outer lip very weakly

Fig. 15. Rissoid gastropod *Galeodinopsis* cf. *tiberiana* (Coppi, 1876), from the Late Zanclean–early Late Piacenzian, Pliocene of Altavilla Milicia, Palermo, NW Sicily. **A**. Specimen ex AR, MZPD Mal 2033c with varix, in apertural (A_1), dorsal (A_2), and profile (A_3) views, protoconch (A_6), detail of protoconch 1 with trace of the netted sculpture (A_4), the *Manzonia*-like teleoconch pitted microsculpture on spiral cord (A_5). **B**. Specimen ex AR, MZPD Mal 2033d without varix in apertural (B_1), dorsal (B_2), and profile (B_3) views, details of teleoconch sculpture (B_4, B_5) and microsculpture (B_6), protoconch in profile view (B_7). Note the variability of the outer lip: weakly sinuous and curved backward in the lower part (A_3) to almost straight and opisthocline (B_3). Black and white arrows indicate the protoconch 1/protoconch 2 and protoconch/teleoconch boundaries, respectively. Scale bars: A_1–A_3, B_1–B_3, 1 mm; A_6, B_4, B_5, B_7, 100 µm; A_4, A_5, B_6, 20 µm. →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sinuous, opisthocline to almost straight; internally smooth, with thin rim on its edge; externally with marked varicose swelling, covered with spiral sculpture, with very narrow ridge on its base, towards aperture, forming weak double rim. Inner lip weakly curved, with very narrow columellar thickening, forming obsolete umbilical chink.

Remarks.—It is difficult to establish whether the material described here as *Galeodinopsis* cf. *tiberiana* really represents an extreme case of intraspecific variability. No similar morphs have been observed within the abundant material (more than 200 shells) of *G. tiberiana* described above, and Coppi (1876) did not mention any intraspecific variation in the original description. Agatino Reitano (Tremestieri, Catania, Italy) provided this material as collected from unspecified layers from the Pliocene succession of Altavilla Milicia, in a lot containing also several shells indisputably belonging to *G. tiberiana* (Fig. 14A). Among these shells, three show a characteristic galeodiniform shape (Fig. 15A$_1$–A$_3$, B$_1$–B$_3$) strongly resembling species of *Alvania,* such as *A. carinata* (Da Costa, 1778) and *A. rosariae* Garilli, 2008 (see Garilli 2008: figs. 1, 2, 4–8, 62–69); one shell (Fig. 14D$_1$–D$_3$) with more prominent sculpture might be regarded as somewhat intermediate between the galeodiniform shells and those typical of *G. tiberiana*.

Galeodinopsis cf. *tiberiana* (as illustrated in Fig. 15B$_1$–B$_3$) resembles *Rissoa moniziana* Watson, 1873 (type of *Moniziella* Nordsieck, 1972), which has a somewhat atypical shell shape for *Manzonia*, but has the typical pitted surface of the genus (see Moolenbeek and Faber 1987c: figs. 58–60; Ponder 1985: figs. 102g and h). The two species share a strongly inflated shell and their sculptural pattern, with delicate, narrow spiral cords, a common character. However, *M. moniziana* has a paucispiral protoconch, indicating non-planktotrophic larval development, whereas *G.* cf. *tiberiana* has a multispiral protoconch indicating planktotrophic development. Furthermore, some specimens of *G.* cf. *tiberiana* bear varices on the last whorl, a typical *Galeodinopsis* character.

Discussion

Taxonomy and evolutionary notes.—The European Tertiary *Galeodinopsis* species are characterized by a conical-ovate/conical-turrited, *Alvania*/*Alvinia*-like shell shape, with a discretely to strongly inflated last whorl and a duplicated peristome outlining a wide aperture. The common occurrence of varices on the last whorl is another important character distinguishing *Galeodinopsis*. Whereas varices occur in galeodiniform species attributed to *Alvania* (as a possible case of non-phyletic convergence, see Garilli 2008), they never occur within *Alvinia* and they very rarely occur in *Manzonia*. To our knowledge, the only known case of a varicose *Manzonia* specimen, illustrated in the present paper (Fig. 3H), might be interpreted as a teratological case. The combination of a *Manzonia*-like netted protoconch 1 and pitted microsculpture possibly represents a further diagnostic character distinguishing *Galeodinopsis*. However, the characteristic microsculpture is manifested only from the Chattian (Late Oligocene), in *Galeodinopsis germanica* sp. nov., whereas the older *Galeodinopsis* species, *G. biangulata* and *G. semperi* (Late Eocene–Early Oligocene), have a sort of "protopitted" microsculpture that possibly represents an ancestral character. This microsculpture is due to the near absence (in *G. semperi*) or strong reduction (in *G. biangulata*) of the numerous microscopic axial ribs, forming very short bridges between the ridges of the primary spiral cords in the typical pitted pattern. This pattern is comparable to that shown by the living type species of *Alvinia* (*A. weinkauffi*), and it particularly resembles that shown by *Rissoa testae* (type species of *Actonia*) and *Turbo zetlandicus* (type of *Flemellia*). These last two species possibly are related to *Alvinia*, particularly the former species, which shows the typical turrited shell shape as in *A. weinkauffi*. It is noteworthy that both *Rissoa testae* and *Turbo zetlandicus* show characters (the netted pattern of protoconch 1, the profile of the outer lip and the duplicated peristome) comparable to those of *Manzonia* species, stressing a certain affinity to this genus. A sort of "protopitted" microsculpture can be seen also in *Alvinia planicincta* Le Renard, 1990 (see MNHN Fossil Database of Tertiary shells), which lived in the Paris Basin during the late Early Eocene (Early Lutetian), long before the first appearance of *Galeodinopsis*. Other *Alvinia* characters, such as the conical-turrited shells usually provided with a subsutural ramp, indicate that the relationship between this group and the oldest *Galeodinopsis* species is close. In particular, it is worth emphasizing that some of the oldest species attributed to *Alvinia* from the Eocene of the Paris Basin (see Le Renard 1990) resemble the typical inflated shape of *Galeodinopsis*. This taxonomical setting demonstrates that *Alvinia* is morphologically closer to *Galeodinopsis* than to *Manzonia*. However, the relationship between this last genus and *Alvinia* is still remarkable.

The oldest representatives of *Manzonia*, *M. foraminata* and *M. moulinsi*, date from the Oligocene of central western Europe, but its radiation occurred in the European Neogene, when different species lived in the Atlantic province, the Mediterranean area and the Paratethys. From the Oligocene onwards the European *Manzonia* species differentiated according to evolutionary trends generally involving the strengthening of axial sculpture (in most of the here considered species), a proportional decrease in peristome size and of the width/height ratio (particularly remarkable in the type species), and the remarkable strengthening of the basal cords (evident in the morphological lineage *M. foraminata*–*M. moulinsi*) (Fig. 16). Conversely, the greatest diversification within *Galeodinopsis* occurred in the Late Paleogene of France and Germany, with evolutionary trends involving strengthening of axial sculpture and proportional decrease in the peristome size (*G. semperi*–*G. germanica* sp. nov. lineage), on one side, and, on another side (*G. semperi*–*G. biangulata* lineage), reinflation of the last whorl (Fig. 16). As

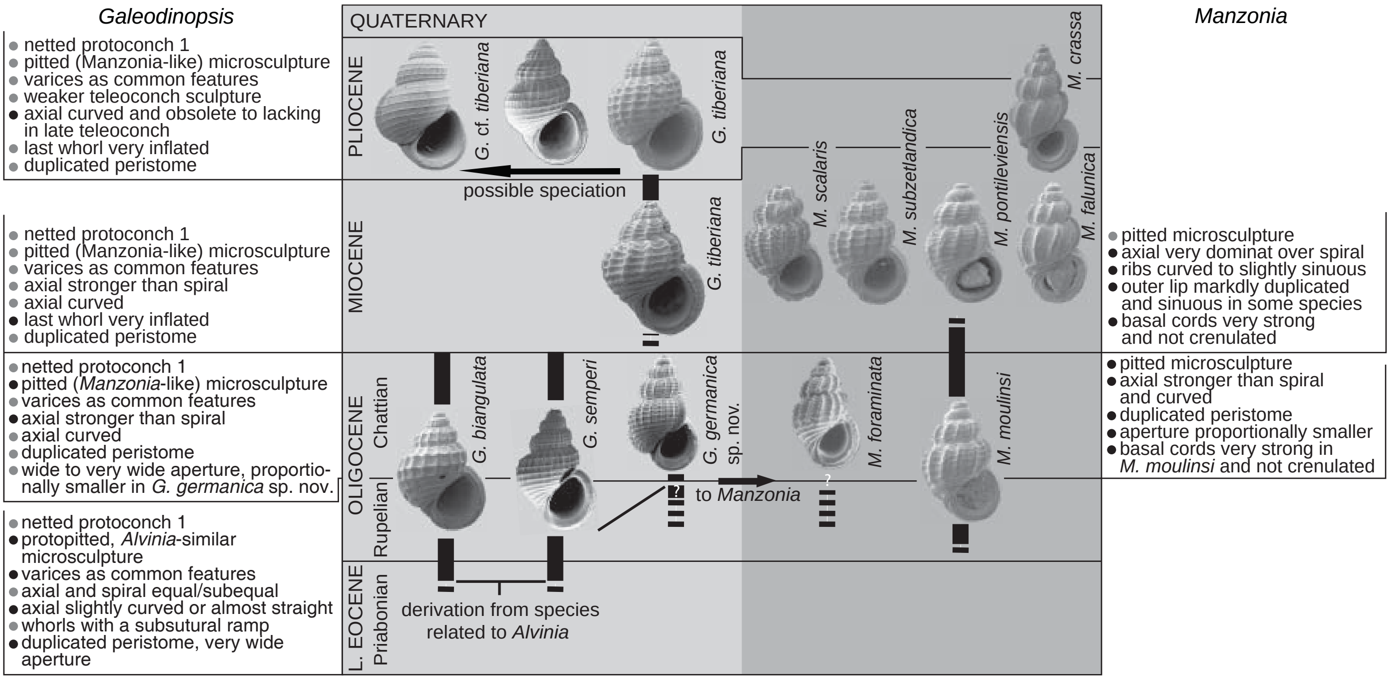

Fig. 16. Schematic trend of morphological variation/diversification and supposed lineages within Tertiary species of *Galeodinopsis* Sacco, 1895 and some Tertiary–Quaternary representatives of *Manzonia* Brusina, 1870, and synthetic view of the main features of species/group of species. Gray circles indicate stable taxonomic characters; black circles indicate novel characters. The image of *Manzonia foraminata* is modified from Lozouet (1998).

for *G. tiberiana*, this species shows shell characters shared by *G. biangulata* and *G. semperi* (mainly the very inflated last whorl) and by *G. germanica* sp. nov. (mainly the curved axials prevailing over spirals). It is therefore difficult to indicate the origin of *G. tiberiana,* even hypothetically. However, its pitted teleoconch microsculpture might suggest a possible lineage with *G. germanica* sp. nov. Particularly, *G. germanica* sp. nov. has (more than any other congeners) characters so close to those of the Chattian species *Manzonia foraminata* that the lineage *G. germanica* sp. nov.–*M. foraminata* might be interpreted as a transitional step from *Galeodinopsis* to *Manzonia*. However, the hypothesis that *Manzonia* derives from *Galeodinopsis* through this lineage should be based on a more exhaustive data set. Actually, on the basis of the material studied here, the origin of *Manzonia* is to be backdated to the Early Oligocene, as *Manzonia moulinsi* has been recorded from the Rupelian of Germany and therefore preceded the first appearances of *G. germanica* sp. nov. and *M. foraminata* (very recently described from the Chattian of the North Sea and Aquitaine Basins, respectively). However, due to the problems of classifying these fossil rissoids and the obsolete approach dedicated to this group, often badly illustrated, especially by old authors (see also Lozouet 1998, for a discussion), it seems to be implausible that these last two species may have been recorded from the Early Oligocene sites under different names.

The shells of *Galeodinopsis tiberiana* (AR coll.) from the Pliocene of Altavilla (Sicily) are from a mixture of samplings collected at different layers of the Altavilla Milicia succession. These shells showed such wide variation that a somewhat doubtful determination as *G.* cf. *tiberiana* was preferred for the smaller ones bearing more numerous axial ribs, which are obsolete to lacking on the last whorl. This characteristic morph, never observed from other localities, appears so distant from the typical ones that it might be interpreted as the result of incipient speciation (chronospeciation?). Detailed, microlayer-by-microlayer sampling of the Altavilla succession, allowing understanding of chronological variations through transitional morphs, possibly would help to verify this assumption.

A few living species from the Macaronesian area, *Rissoa moniziana* Watson, 1873 and *R. spreta* Watson, 1873, show some similarities to *Galeodinopsis*, in particular in their quite inflated last whorl, the weak basal cords and the *Manzonia*-like microsculpture (Moolenbeek and Faber 1987c: figs. 58–60). The former species has been regarded as belonging to *Manzonia* (*Moniziella*) (Moolenbeek and Faber 1987c); the latter has been considered a species of *Manzonia* (*Flemellia*) (Moolenbeek and Faber 1987c). The identity of *Moniziella* is uncertain (see Moolenbeek and Faber 1987c). However, Ponder (1985) put it in synonymy with *Alvinia.* We have shown that *Alvinia* and *Flemellia* lack the pitted surface; therefore the placement of *R. moniziana* in this group should be questioned.

Palaeobiogeography and palaeoecology.—The oldest occurrences of *Galeodinopsis* are from the Late Eocene/very Early Oligocene in the North Sea Basin, as testified by the records of *G. biangulata* and *G. semperi* in the Latdorfian beds of Germany and of *G. semperi* in the Late Tongrian of Belgium. The German part of this area, including the satellite

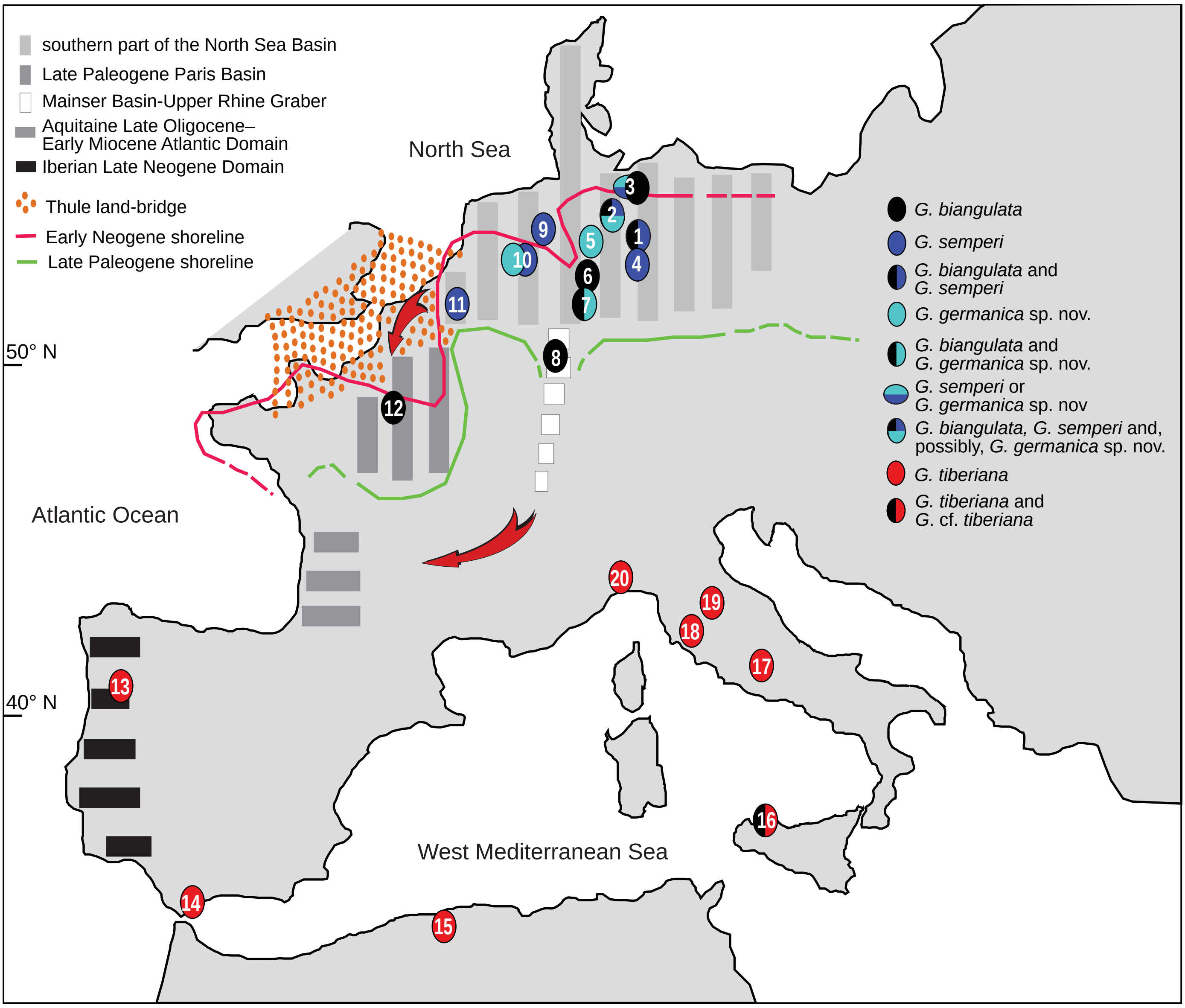

Fig. 17. Distribution of European species of *Galeodinopsis* Sacco, 1895, based on material studied and that from the literature. Dark and light grey vertical segments roughly indicate the Late Paleogene Paris Basin and the southern part of the North Sea Basins, respectively; white segments represent the Mainzer Basin–Upper Rhine Graben (from Rögl 1999 and Rasser et al. 2008, modified). The horizontal black and dark grey segments approximate the Iberian Late Neogene and Aquitaine Late Oligocene–Early Miocene Atlantic domains, respectively; orange dots indicate the southernmost part of the Thule land-bridge joining England with continental Europe (from Vincent 1990, adapted and modified); green line indicates a hypothetical reconstruction of the Late Paleogene shoreline in the North Sea and Paris Basins, allowing communication (smaller red arrow) between the two areas from the Early Oligocene. The red line indicates part of the Central European shoreline (according to Rögl 1999) during very Early Neogene time, showing northwards shifting of the southern coasts of the North Sea Basin. The larger red arrow indicates the hypothesized connection to the Aquitaine Basin. 1, Upper Eocene/very early Oligocene, Latdorf (Koenen 1867; Tembrock, 1964) and Magderburg (Müller 2011); 2, Oligocene, Rupelian, Söllingen (Speyer 1864; Koenen 1867); 3, Oligocene, Chattian, Sternberg (Wiechmann 1871; Anderson 1960); 4, Oligocene, Rupelian, Amsdorf (Gründel 1997); 5, Oligocene, Chattian, Freden (Anderson 1960); 6, Oligocene, Chattian, Ahnetal (Anderson 1960); 7, Oligocene, Chattian, Glimmerode; 8, Middle Oligocene, Magonza basin at Waldböckelheim (Sandberger 1863; Anderson 1960); 9, Oligocene, Chattian, Doberg (Wiechmann 1871); 10, Oligocene, Chattian, Krefeld (Wiechmann 1871), Rumeln (Anderson 1960), and Moers (Janssen 1978a); 11, Oligocene, early Rupelian, Klein-Spauwen (Nyst 1845); 12, Oligocene, Rupelian, Paris Basin (Deshayes 1864); 13, Middle Pliocene, Mondego (Landau et al. 2004); 14, Pliocene, Estepona (Landau et al. 2004); 15, Pliocene, Sidi Moussa (Cossmann 1921); 16, Pliocene, Altavilla and Trappeto (Garilli 2008); 17, Lower Pliocene, Magliano Sabina (Garilli 2008); 18, Lower Pliocene, Siena (Chirli 2006); 19, Mio-Pliocene, Modena, Parma, and Piacenza (Coppi 1876; Garilli 2008); 20, Lower to Upper Pliocene, Savona and Asti (Garilli, 2008).

basins (e.g., those in the Rhine Graben), was the main hosting area for *Galeodinopsis* species, as three of its four species lived there; *G. biangulata* also lived in the Early Oligocene Paris Basin (Fig. 17). The Late Eocene–Oligocene palaeogeographic reconstructions of those areas (Vincent 1990; Rögl 1999: figs. 2, 3; Rasser et al. 2008, with references) outline the North Sea and Paris Basins (N Atlantic realm) as distinct marine provinces separated by the Thule bridge, a wide land-passageway putting Great Britain in communication with central-western continental Europe until the Late Oligocene. At this time sporadic communications between the Atlantic and North Sea Basin occurred in the Channel area, as indicated by Janssen (1978b) on the basis of some Late Oligocene marine faunal affinities between the North Sea Basin and the Aquitaine Basin. However, it is possible that a southernmost connection favoured these interchanges as supposed by Rasser et al. (2008). The distribution of *G. biangulata* (Fig. 17) indicates that a faunal interchange (possibly unidirectional) between the North Sea and Paris Basins started in the Early Oligocene, when the Thule land-bridge was already in-filled (at least intermittently) in the Channel area, much earlier than had been supposed. The linkage between *G. germanica* sp. nov. and *Manzonia foraminata* (from the North Sea and Aquitaine Basins, respectively) suggested here, as well as the Oligocene distribution of *M. moulinsi* (Aquitaine and North Sea Basins), support the existence of an alternative, southern route towards the Atlantic domain of the Aquitaine Basin, likely through the Upper Rhine Graben (Fig. 17). More palaeobiogeographical data could be useful for understanding whether this interchange was unidirectional, from the North Sea Basin southwards, as suggested by the oldest occurrence of *M. moulinsi* in the Early Oligocene of Germany.

From a palaeocological point of view, it is remarkable that all *Galeodinopsis* species studied have a multispiral protoconch, indicative of planktonic larval development and, in general, of a high dispersal capability, higher than in species with direct larval development. Notwithstanding this, *Galeodinopsis* seems never to have lived in the eastern part of the southern margin of the North Sea Basin, nor in the Paratethyan area, even though communication between the North Sea and Mediterranean/Paratethyan areas was established during that time, especially in the Early Oligocene, when ocean circulation supplied water from the North Sea to the Paratethys (Rögl 1999: figs. 1, 2). The distributional gap in the North Sea Basin may be at least partially explained by the paralic condition that affected the southeastern part of the North Sea Basin during Late Oligocene time (Rasser et al. 2008).

Galeodinopsis tiberiana is the only Neogene *Galeodinopsis*, from the Mio-Pliocene (palaeo)Mediterranean and the Pliocene of Atlantic Portugal, namely areas with a tropical-subtropical climate (Monegatti and Raffi 2001). Today this species is the sole well-established living species of *Galeodinopsis*, having been recorded from an area (West African coasts, from Mauritania to Angola) that is constrained by an analogous climatic setting. This suggests that the extinct *Galeodinopsis* species also required warm climatic conditions. Tropical to warm-temperate conditions have been inferred for the Palaeogene of Europe (Vincent 1990) and, more specifically, subtropical conditions were indicated for the Late Oligocene of the North Sea Basin (Rasser et al. 2008). Actually, a warm (possibly tropical-subtropical) climatic regime in the Paleogene of the North Sea Basin is suggested by the analogies (at least at genus level) between the highly diverse molluscan assemblages from the Mediterranean Neogene and the Late Eocene–Oligocene of Germany, southwards to the Mainz basin: several molluscan taxa characteristic for warm climate, such as *Bathytoma* Harris and Burrows, 1891, *Isognomon* Lightfoot, 1786, *Ficus* Röding, 1798, *Gemmula* Weinkauff, 1875 and others, have been recorded in those areas (Janssen 1978b, 1979; Gründel 1997; Monegatti and Raffi 2001; Müller 2011). Furthermore, warm, tropical to subtropical, marine climatic conditions were inferred for this part of central Europe with particular regard to the Latdorfian faunal complex and similar assemblages of younger (Oligocene) age (Müller 2011). It is remarkable that from the middle Eocene onwards, the Cenozoic continental history of central Europe, in accordance with global marine oxygen isotope records, was characterized by the increasing degree of seasonality, and a short-term cooling at the base of the Aquitanian, approximating the Oligocene/Miocene boundary, was recorded in the Weisselster Basin, in central Germany (Mosbrugger et al. 2005). Also from a palaeogeographical point of view, the area of central-western Europe underwent remarkable changes. During the Early Miocene, marine regressive conditions rewrote the palaeogeography of the North Sea Basin, triggering the progressive reduction of its southernmost part, which was constrained to higher (presumably relatively colder) latitudes. Regressive conditions also caused the disappearance of satellite basins such as those in the Rhine Graben (e.g., the Mainz Basin; Rögl 1999). This palaeogeographic-climatic evolution was possibly responsible for the disappearance of *Galeodinopsis* from the mid-high latitudes of Central Europe and for its migration to the Iberian Atlantic coasts and into the (paleo)Mediterranean during Mio-Pliocene time. At the end of the Pliocene, at around 2.6 My B.P. (approximating the Piacenzian/Gelasian boundary), the marked onset of the continental ice sheet in the Northern Hemisphere (Shackleton et al. 1984) triggered stepwise climatic deteriorations at lower latitudes, causing the Mediterranean extinction of several molluscan taxa (Monegatti and Raffi 2001). The new climatic regime probably was the main cause of the disappearance of *Galeodinopsis* from the Mediterranean and its further migration towards the subtropical-tropical West Africa coasts, where this genus still lives.

As for the ecological/bathymetrical requirements of *Galeodinopsis*, it is remarkable that for the Late Paleogene around Magderburg and Glimmerode (southern part of the North Sea Basin), where *G. biangulata* and *G. semperi* lived, the palaeofauna indicates normal marine conditions in rocky-sandy shore environments (Janssen 1978b; Mueller 2008, 2011). Also, the requirements of *G. tiberiana* are comparable, as indicated by its occurrence in the Pliocene sands of the Mediterranean Altavilla site, the depositional setting of which was mainly referred to infra-circalittoral shelf conditions (Dell'Angelo et al. 2012).

Conclusions

At least four European rissoid species are identified as belonging to *Galeodinopsis*: *G. biangulata*, *G. germanica* sp. nov., *G. semperi*, and *G. tiberiana*. A possible incipient speciation from *G. tiberiana* to the morph here tentatively determined as *G.* cf. *tiberiana* should be verified by in-depth studies based on more material well dated stratigraphically.

Species of *Galeodinopsis* are warm, marine, shallow-water taxa, from rocky or sandy bottoms. The genus originated during the Late Eocene–Early Oligocene in the southern part of the North Sea Basin. A combination of palaeogeographical and climatic events probably played an important role in determining the disappearance of *Galeodinopsis* from central Europe at the end of the Oligocene, and its Neogene shifting to lower Euro-Mediterranean latitudes. Climatic deterioration events are possibly the main cause of the disappearance of this genus from the Mediterranean and the eastern Atlantic mid-high latitudes during the Pliocene and its later migration to the Recent tropical coasts of West Africa. The palaeobiogeography deduced for *Galeodinopsis* indicates that connections between the North Sea and Paris Basins through the Channel area commenced during the Early Oligocene. Also, a connection between the Aquitaine Basin and the southernmost part of the North Sea Basin likely formed during the Late Oligocene, possibly through the Upper Rhine Graben, as testified by the occurrence in those areas of *Manzonia moulinsi*.

In the light of the in-depth taxonomic data set provided here, the combination of characters such as the teleoconch microsculpture and the netted pattern of protoconch 1 represents a very diagnostic key within *Galeodinopsis* and *Manzonia,* which should be regarded as a monophyletic group much closer to *Alvinia* than to *Alvania*. As for *Alvinia*, species such as *Turbo zetlandicus* (type of *Flemellia*) could be regarded as belonging therein; even *Rissoa testae*, type of *Actonia*, might be included therein, although more exhaustive argumentations are needed. In particular, the chronological/transitional lineage *Alvinia–Galeodinopsis–Manzonia* is supported by shell and protoconch 1 characters and, above all, by the analyzed microsculpture: raised and variably closely spaced ridges in *Alvinia*; wider and closely spaced ridges in the ancestral species of *Galeodinopsis*, flat and almost fused ridges in other *Galeodinopsis* and *Manzonia* species. Effectively, on one side, the oldest *Galeodinopsis* species appear to have evolved from some early Late Eocene species that could be regarded as *Alvinia;* the strong relationship between *Alvinia* and *Galeodinopsis* is supported by several characters shared by *G. biangulata* and, especially, *G. semperi*, and the type species of *Alvinia* and *Flemellia*. On the other side, the similarities between *Galeodinopsis* and *Manzonia* are so obvious, particularly for the hypothesized lineage *G. germanica* sp. nov.–*Manzonia foraminata,* that the latter genus appears to have evolved during the Oligocene from the former rather than from *Alvania*/*Alvinia*. Therefore, *Galeodinopsis* can be seen as a taxon intermediate between *Alvinia* and *Manzonia*.

The only well-established living species of *Galeodinopsis*, *G. tiberiana,* could be seen as a very interesting tool for investigating the supposed lineage *Alvinia–Galeodinopsis–Manzonia*. In particular, more independent characters, such as those based on genetic and anatomical comparisons between *Manzonia* species (such as the Euro-Mediterranean type species *M. crassa*), *Alvinia* species (such as the NE Atlantic-Mediterranean species *A. weinkauffi* and *A. zetlandica*) and the West African species *G. tiberiana* could be extremely interesting for this purpose. Similar studies on the Macaronesian *Rissoa moniziana* and *R. spreta*, which show intermediate character between *Manzonia* and *Galeodinopsis*, would be useful as well to shed light on a number of living species of *Galeodinopsis*.

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