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The Jurassic pleurotomarioidean gastropod *Laevitomaria* and its palaeobiogeographical history

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The genus *Laevitomaria* is reviewed and its palaeobiogeographical history is reconstructed based on the re-examination of its type species *L. problematica*, the study of material stored at the National Natural History Museum of Luxembourg, and an extensive review of the literature. The systematic study allows ascribing to *Laevitomaria* a number of Jurassic species from the western European region formerly included in other pleurotomariid genera. The following new combinations are proposed: *Laevitomaria allionta*, *L. amyntas*, *L. angulba*, *L. asurai*, *L. daityai*, *L. fasciata*, *L. gyroplata*, *L. isarensis*, *L. joannis*, *L. repeliniana*, *L. stoddarti*, *L. subplatyspira*, and *L. zonata*. The genus, which was once considered as endemic of the central part of the western Tethys, shows an evolutionary and palaeogeographical history considerably more complex than previously assumed. It first appeared in the Late Sinemurian in the northern belt of the central western Tethys involved in the Neotethyan rifting, where it experienced a first radiation followed by an abrupt decline of diversity in the Toarcian. Species diversity increased again during Toarcian–Aalenian times in the southernmost part of western European shelf and a major radiation occurred during the Middle Aalenian to Early Bajocian in the northern Paris Basin and southern England. After a latest Bajocian collapse of diversity, *Laevitomaria* disappeared from both the central part of western Tethys and the European shelf. In the Bathonian, the genus appeared in the south-eastern margin of the Tethys where it lasted until the Oxfordian.

Key words: Gastropoda, Pleurotomariidae, systematics, palaeobiogeography, Jurassic, western Tethys.

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Introduction

The biogeographical and evolutionary history of the Jurassic gastropod faunas of the western Tethys, including the European epicontinental shelf, was strongly influenced by the Late Sinemurian to Pliensbachian Neotethyan rifting (Conti and Monari 1991, 1995; Szabó 1992; Monari et al. 2008; Gatto and Monari 2010). In the central part of the western Tethys, this event led to the drowning of wide shallow water and carbonate platform areas, whereas the European epicontinental shelf remained essentially stable (e.g., Nairn et al. 1996; Dercourt et al. 2000 and references therein). In the drowned areas, a pelagic sedimentation took place and a benthic fauna originated showing marked taxonomic differences from the assemblages of the western European region. These differences are evident in most gastropod groups, including pleurotomarioideans. Several taxa of this superfamily from the pelagic sequences of the central western Tethys were described during the last decades, such as the genera *Anodomaria* Szabó, 1980, *Cyclostomaria* Szabó, 1980, *Trochotomaria* Conti and Fischer, 1981, *Urkutitoma* Szabó, 1984, and *Laevitomaria* Conti and Szabó, 1987.

In this paper, the genus *Laevitomaria* is reviewed and its palaeogeographical history is discussed. This genus has long been known only from its type species, *Laevitomaria problematica* (Szabó, 1980). More recently Szabó (2009) recorded four additional Early Jurassic species from the central western Tethys. The present systematic study reveals close similarities between the type species and a number of other Jurassic species from the western European region which are here ascribed to *Laevitomaria* for the first time.

Material and methods

The systematic analysis of the genus is primarily based on the revision of its type species, *Laevitomaria problematica* (Szabó, 1980). The type material housed in HNHM and HGM, is redescribed in depth. This material comes from the Bajocian sediments of the Bakony Mountains (Hungary) described by Szabó (1979). The specimens from the Early Bajocian of Umbria (Central Italy), stored in MPUR, which Conti and Monari (1986) tentatively ascribed to that species, are also re-examined. The reader is referred to the above mentioned papers for details on stratigraphy and localities.

The outstanding collections of Jurassic pleurotomarioideans from the Paris Basin stored in MNHNL are the basis for the study of the other *Laevitomaria* species described here. Most of the material was collected from the Lower Bajocian sediments of the Differdange area (south-western Luxembourg) (see details in Monari and Gatto 2013). A few specimens come from Piedmont (Longwy, Lorraine, north-eastern France), a village located 5 km west of Differdange, where the same Bajocian succession crops out. Most of the specimens have been measured and illustrated. Measurements are listed in Table 1. The abbreviations for the dimensions and their explanations are reported in Fig. 1. Morphological terminology follows Cox (1960a).

Institutional abbreviations.—HGM, Museum of the Hungarian Geological and Geophysical Institute, Budapest, Hungary; HNHM, Hungarian Natural History Museum, Budapest, Hungary; MNHNL, National Natural History Museum of Luxembourg, City of Luxembourg, Grand-Duchy of Luxembourg; MPUR, Palaeontological Museum, Department of Earth Sciences, University "La Sapienza", Rome, Italy.

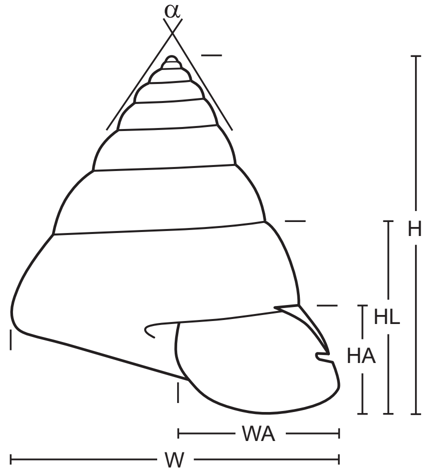


Fig. 1. Dimensions of the specimens reported in the systematic descriptions and in Table 1. Abbreviations: H, height of the shell; HA, height of the peristome; HL, height of the last whorl; W, width of the base; WA, width of the peristome; α, mean spire angle.

Table 1. Measurements of the specimens studied here. The linear measurements are in millimetres. Abbreviations: H, height of the shell; HA, height of the peristome; HL, height of the last whorl; W, width of the base; WA, width of the peristome; α, mean spire angle. The symbol P indicates measurements on incomplete specimens.

Specimen	H	HL	HA	W	WA	α
Laevitomaria problematica (Szabó, 1980)						
HGM J 10120	53.2P	26.5P	16.8P	46.2P	22.0P	50°
HNHM INV.2012.15.1	37.6P	19.1P	12.2P	32.0P	11.9P	56°
HNHM INV.2012.15.2	–	16.2P	9.8 P	31.5P	14.0P	48°
HNHM INV.2012.15.3	–	20.5P	14.P	35.3P	18.5P	60°
MPUR MAC127A	40.5	18.1	–	34.8	–	54°
MPUR MAC127B	28.6P	18.2P	–	36.0	–	57°
Laevitomaria amyntas (d'Orbigny, 1850)						
MNHNL ZS248	50.1	28.2	16.0	51.4	–	64°
MNHNL ZS314	25.1	16.0	10.2	25.6	12.4P	65°
MNHNL ZS494S1	30.8	20.0	–	31.1	–	66°
MNHNL MDB254	43.3	23.7	–	46.6	–	63°
MNHNL MDB275	50.5	28.4	18.3	49.0	–	62°
Laevitomaria fasciata (Sowerby, 1818)						
MNHNL ZS508	73.5	47.0	29.1	73.9	40.0P	67°
Laevitomaria cf. *subplatyspira* (d'Orbigny, 1850)						
MNHNL BU233	59.8P	41.9	24.4	72.4	35.3	64°

Systematic palaeontology

Class Gastropoda Cuvier, 1797

Subclass Archaeogastropoda Thiele, 1925

Order Vetigastropoda Salvini-Plawen, 1980

Family Pleurotomariidae Swainson, 1840

Genus *Laevitomaria* Conti and Szabó, 1987

Type species: *Pyrgotrochus*? *problematicus* Szabó, 1980 (Szabó 1980: 63, pl. 4: 1–3); Bajocian (*Stephanoceras humphriesianum* Zone to *Parkinsonia parkinsoni* Zone), Bakony Mountains (Hungary).

Emended diagnosis.—Shell conoidal, higher than wide, with cyrtoconoid apical spire. Early teleoconch whorls evenly and moderately convex. Adult whorls weakly to somewhat convex. Last whorls occasionally angulated at the selenizone. Periphery rounded-angular. Base low with a slightly convex surface, anomphalous to rather broadly phaneromphalous. Selenizone below mid-whorl, rarely just at mid-whorl, concave to flat on early shell, flat to markedly convex on fully adult shell. Selenizone of the adult shell moderately to quite wide. Early shell ornamented by a network of spiral threads and collabral riblets. Adult sculpture consisting only of spiral threads or striae which tend to vanish during the last growth. Base almost smooth or crossed by thin and sharp spiral lines.

Description.—The genus includes medium- to large-sized species (H about 30 to 110 mm). Commonly the shape of the shell is conoidal, with the apical spire feebly cyrtoconoid, and formed by more than eight whorls. The height of the spire is quite variable, the spire angle ranging from 40° to 75°. The earliest teleoconch whorls are regularly convex and edged by moderately impressed sutures. The shape of the adult whorls varies from almost flat, as in *Laevitomaria allionta* (d'Orbigny, 1850) to moderately convex, as in *Laevitomaria fasciata* (Sowerby, 1818), and the whole interspecific transition is represented. In the type species, *Laevitomaria problematica* (Szabó, 1980), and in *Laevitomaria gyroplata* (Eudes-Deslongchamps, 1849) this character is also quite variable intraspecifically. A shoulder on the last whorls, which commonly becomes sharper on the very last part of whorl, is present in *Laevitomaria problematica* (Szabó, 1980), *Laevitomaria amyntas* (d'Orbigny, 1850) and *Laevitomaria isarensis* (d'Orbigny, 1855). The periphery corresponds to a rounded angulation which is rarely marked by a shallow spiral swelling. The base is low and its surface is slightly to moderately convex. An umbilicus is present in most of the species. It is commonly narrow to moderately wide, but all transitional stages are represented, from anomphalous or cryptomphalous to rather widely umbilicated shells.

The selenizone commonly corresponds to the shoulder of the adult whorls, if present. Its position is submedian with its upper margin at the mid-line of the whorl surface. In some species, e.g., *L. problematica* and *Laevitomaria periferialis* (Szabó, 1980), the selenizone is well below the mid-line, i.e., in the lower third or quarter of the whorl surface. The selenizone is commonly rather wide, ranging in width from 12% to 20% of the whorl surface. The earliest teleoconch whorls show a slightly concave to flat selenizone ornamented by sharp, regularly spaced lunulae. Subsequently, a median thread appears. During growth, the selenizone may remain flat or very slightly convex. More frequently, it becomes prominent and somewhat convex to bulge-shaped, mainly by thickening of the middle thread. The lunulae attenuate and progressively change in dense growth lines. In some species, such as *Laevitomaria stoddarti* (Tawney, 1873), *L. fasciata*, and *L. problematica*, other spiral threads appear at the sides of the median thread. The spiral ornament tends to disappear on the last whorls leaving the selenizone smooth.

The ornament of the early shell consists of a variably regular network of spiral threads and collabral riblets often forming granules at their intersection. The collabral ornament disappears during the fully adult growth and its persistence is quite variable in the different species. On the fully adult shell, the spiral ornament is dominant. It consists of variably thin and dense spiral threads which are commonly more marked below the selenizone. The spiral ornament above the selenizone tends to vanish along the final part of the last whorl, but this tendency is quite variable, also at species rank. The base is smooth or ornamented by thin and sharp spiral threads.

Remarks.—Most of the species included by Hudleston (1895: 394–395) in his section "Fasciatae" of *Pleurotomaria* (*P. subplatyspira*, *P. fasciata*, *P. stoddarti*, *P. transilis*, *P. alimena*, *P. allica*) and the high-spired species assigned by Fischer and Weber (1997) to the Oligocene to Recent genus *Perotrochus* Fischer, 1885 (*P. isarensis*, *P. repelinianus*, *P. allionta*, *P. subplatyspira*, *P. gyroplata*) are here ascribed to the genus *Laevitomaria* Conti and Szabó, 1987. They all share with the type species the conoidal shape, the low base, the wide selenizone at or below mid-whorl, a reticulate ornamentation on the early whorls, and a predominantly spiral sculpture on the adult whorls.

Conti and Szabó (1987) regarded *Laevitomaria* as closely related to *Trochotomaria* Conti and Fischer, 1981 in sharing a conoidal shell shape, the selenizone below mid-whorl, and the early teleoconch ornamented by a network of spiral threads and collabral riblets. However, in *Trochotomaria*, the reticulate ornament persists on the fully adult shell and the adult selenizone is concave. The occasional appearance of an angulation on the last whorls makes *Laevitomaria* similar to some high-spired species of *Bathrotomaria* Cox, 1956. In *Laevitomaria* the shoulder appears only in the latest growth stages whereas in *Bathrotomaria* it develops on the early whorls. For this reason, the general shell shape of *Bathrotomaria* is clearly gradate and trochiform, rather than conoidal. Some *Laevitomaria* species with flat whorls, e.g., *Laevitomaria allionta* (d'Orbigny, 1850), are reminiscent of *Pyrgotrochus* Fischer, 1885 and *Conotomaria* Cox, 1959. *Pyrgotrochus* can be easily distinguished from *Laevitomaria* by its coeloconoid and more strongly ornamented shell. Furthermore, the whorl surface is concave and the periphery is markedly swollen and variably nodose. In *Conotomaria*, the selenizone is mainly above mid-whorl and the periphery is sharply angular and frequently marked by a spiral bulge. Moreover, a clearly reticulate ornament on the early spire seems to be absent in *Conotomaria*. The type species, *Pleurotomaria mailleana* d'Orbigny, 1843 has a very narrow selenizone distinctly above mid-whorl. *Laevitomaria* shares with *Perotrochus* the smoothly convex whorls, the position and the size of the selenizone, and the dominant spiral ornament on the adult whorls. In *Laevitomaria*, the shape of the shell is higher and conoidal, whereas it is more trochiform in *Perotrochus*. The apical shell of *Perotrochus* differs from that of *Laevitomaria* in being more acute and coeloconoid, sometimes submamillated, and in being composed of slightly convex to flat whorls.

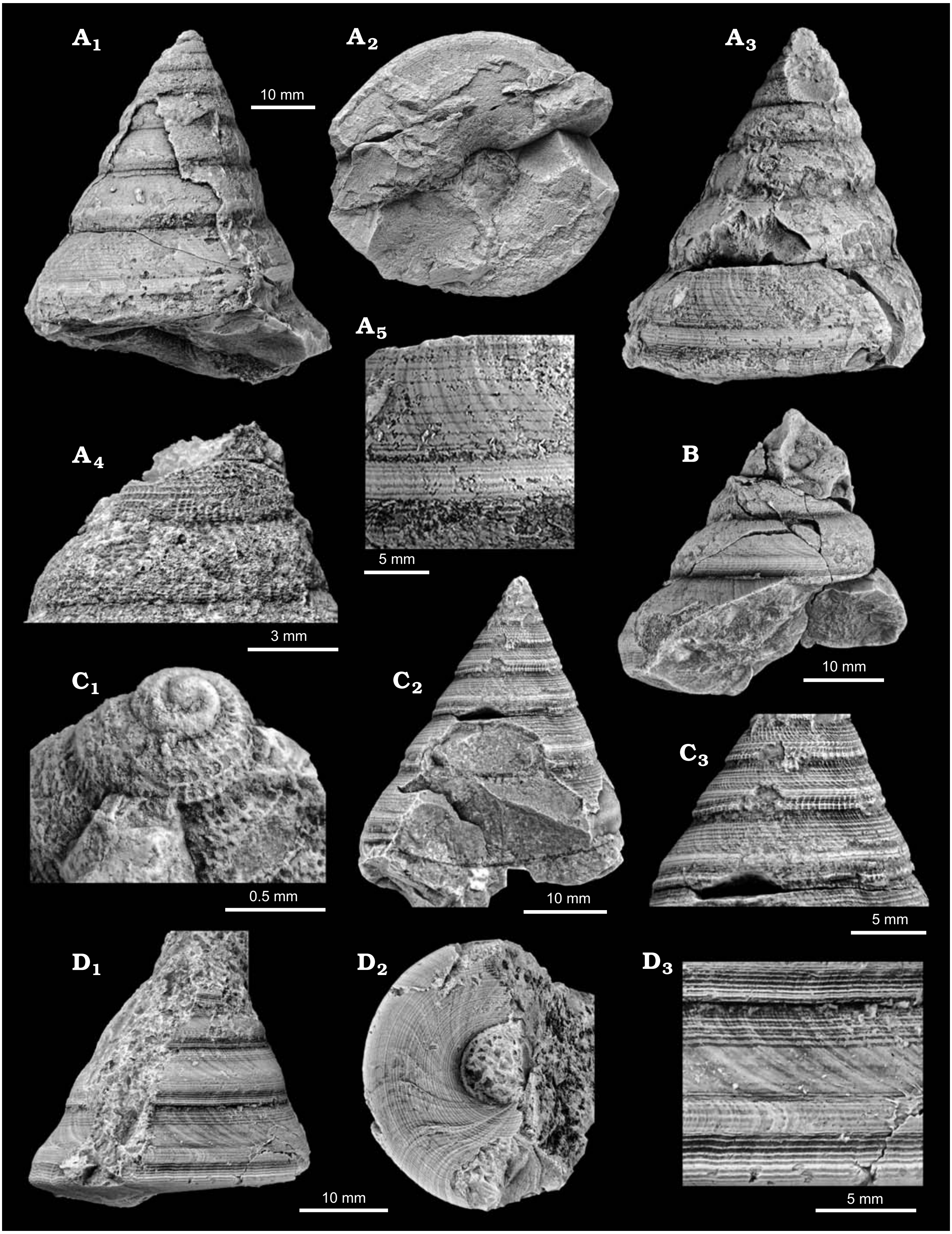
Stratigraphic and geographic range.—Late Sinemurian to Bajocian of the central region of the western Tethys (Northern Calcareous Alps, Bakony Mountains, central Italy, western Sicily); Pliensbachian to Aalenian of the north-eastern margin of western Tethys (western Pontides, Caucasus); Toarcian–Bajocian of the western European epicontinental seas (Rhone Basin, Paris Basin, south-western England, southern Germany); Late Bathonian to Oxfordian of the south-eastern Tethys (western India).

Laevitomaria problematica (Szabó, 1980)

Figs. 2, 3.

1980 *Pyrgotrochus*? *problematicus* sp. n.; Szabó 1980: 63, pl. 4: 1–3.
1986 *Trochotomaria*? cf. *problematica* (Szabó); Conti and Monari 1986: 182, pl. 2: 1, 2, 5.

Material.—Holotype (HGM J 10120), 15 paratypes (HNHM INV.2012.15.1–2012.15.7, HNHM INV.2012.16.1–2012.16.6, HNHM INV.2012.18.1, HNHM INV.2012.19.1), and 6 specimens (HNHM INV.2012.17.1–2012.17.6). Additional 5 unnumbered specimens are stored in the HGM. Bajocian


A1
10 mm
A2
A3
A5
A4
5 mm
B
3 mm
10 mm
C1
C2
C3
0.5 mm
10 mm
5 mm
D1
D2
D3
10 mm
5 mm

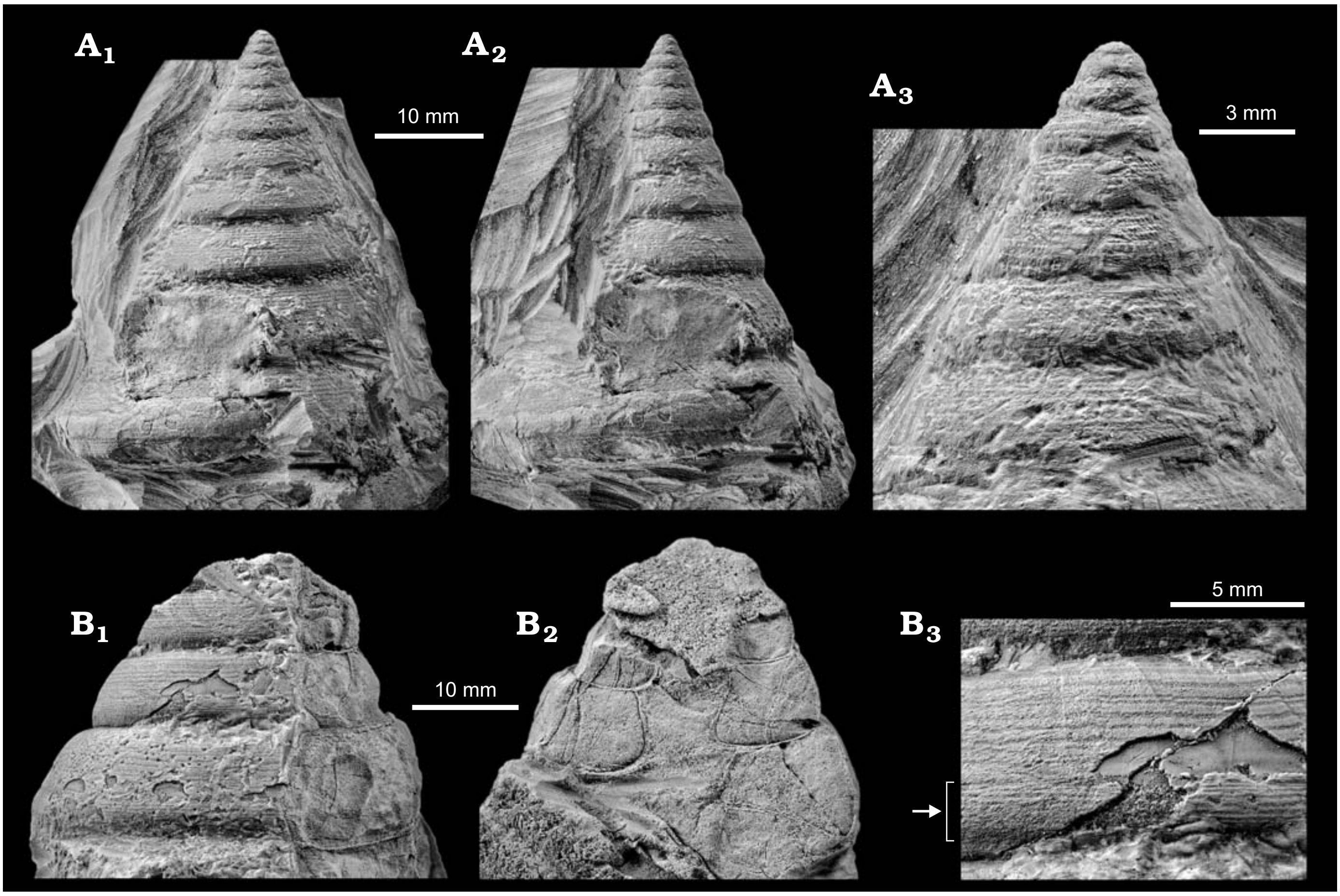


Fig. 3. Pleurotomarioidean gastropod *Laevitomaria problematica* (Szabó, 1980) from the Early Bajocian (*Stephanoceras humphriesianum* Zone) of Martani Mountains (central Apennine, Italy). **A**. MPUR MAC127A, dorsal (A_1) and lateral (A_2) views, and detail of the apical shell (A_3). **B**. MPUR MAC127B, dorsal view (B_1), natural section showing the umbilicus (B_2), and detail of the surface of the last whorl (B_3). The arrow indicates the position of the selenizone.

(*Stephanoceras humphriesianum* Zone to *Parkinsonia parkinsoni* Zone), Somhegy, Bakony Mountains (Hungary). Four specimens (MPUR MAC127A–D) from Bivio Macerino (Martani Mountains, central Apennine, Italy), Early Bajocian (*Stephanoceras humphriesianum* Zone).

Description.—The shell is conoidal and composed of about ten whorls. The apical spire is slightly cyrtoconoid. The protoconch is dome-like, with globose nucleus followed by a well-rounded volution. The early teleoconch whorls are slightly and evenly convex gradually changing in moderately convex during the growth. The last three whorls are obtusely angular at the selenizone. Their outer face is narrow and flat, becoming a slightly concave band during the latest growth stage. The suture is moderately impressed. The selenizone is concave at the beginning. On the earliest teleoconch whorls it is wide, flat and edged by sharp marginal spiral threads. On the subsequent whorls, the selenizone becomes rather convex. Its width is about 20% of the whorl surface. It runs clearly below the mid-whorl and becomes markedly convex concomitantly to the development of the angulation of last whorls. The periphery is markedly angulated on the early shell and becomes rounded-angular and slightly swollen on the fully adult shell. The base is phaneromphalous, somewhat flat and with a slightly convex surface. The umbilicus is rather wide with a rounded but somewhat sharp periumbilical edge.

The early shell is ornamented by sharp, equally sized and regularly spaced spiral threads and collabral riblets which give rise to an even network with small granules at crossing points. On the first preserved whorls, there are three to four spiral threads above the selenizone and two spiral threads below it. They increase in number during the growth. The reticulate ornament persists, though gradually attenuating, on the first five teleoconch whorls. On the last whorls the col-

← Fig. 2. Pleurotomarioidean gastropod *Laevitomaria problematica* (Szabó, 1980) from the Bajocian (*Stephanoceras humphriesianum* Zone–*Parkinsonia parkinsoni* Zone) of Somhegy (Bakony Mountains, Hungary). **A**. Holotype HGM J 10120, apertural (A_1), basal (A_2), and dorsal (A_3) views, detail of the apical shell (A_4), and detail of the surface of the last whorl (A_5). **B**. Paratype HNHM INV.2012.15.3, dorsal view. **C**. Paratype HNHM INV.2012.15.1, detail of the apical shell (C_1), dorsal view (C_2), and detail of the ornament (C_3). **D**. Paratype HNHM INV. 2012.15. 2, dorsal (D_1) and basal (D_2) views, and detail of the surface of the last whorl (D_3).

labral riblets become sharp growth lines. These cross weak and quite closely spaced spiral threads, making them slightly granulated. About ten spiral threads are present above the selenizone and about five below it. The spiral threads attenuate on the last whorl. They also flatten and widen so that their interspaces become striae. The base is covered by thin, sharp and dense spiral threads. The selenizone of the earliest whorl is ornamented only by sharp and regularly spaced lunulae. From the second to third whorl onward, a median spiral thread appears. Other spiral threads appear during adult growth while the lunulae gradually change in growth lines. The selenizone of the last whorls bears about five shallow and slightly variably sized spiral threads which tend to vanish during the last growth stage. The growth lines are prosocline and widely prosocyrt above the selenizone, almost orthocline and prosocyrt below the selenizone, opisthocline-falciform on the base i.e., markedly opisthocyrt on its abaxial region and slightly and widely prosocyrt on its adaxial region.

Remarks.—*Laevitomaria problematica* (Szabó, 1980) is a rather variable species. The spiral angle ranges from about 50° to 60°. The fully adult whorls are moderately to decidedly convex. The ramp of the last whorls is slightly convex to flat or also weakly concave on the final part of the last whorl. In some specimens (e.g., in the holotype), the surface of the last whorls above the selenizone shows weak and regularly spaced spiral lines. In other specimens, the spiral ornament is sharper and denser, in some cases more marked along the subsutural band. The prominence of the selenizone is also variable. The base is always very low, but the convexity of its surface may vary.

Conti and Monari (1986) tentatively ascribed some specimens from the Early Bajocian of central Italy to *L. problematica*. Subsequently, Conti and Szabó (1987) suggested that they probably belong to a different species, although the poor preservation prevents a safe assignment. However, the re-examination of that material and a better documentation of the variability of *L. problematica* as presented here enable to identify these specimens as *L. problematica*. They differ from the type material of *L. problematica* only in having a less prominent selenizone and slightly lower whorls.

Stratigraphic and geographic range.—Bajocian (*Stephanoceras humphriesianum* Zone to *Parkinsonia parkinsoni* Zone), Somhegy, Bakony Mountains (Hungary). Early Bajocian (*Stephanoceras humphriesianum* Zone), Martani Mountains (central Apennine, Italy).

Laevitomaria amyntas (d'Orbigny, 1850) comb. nov.

Fig. 4.

1850 *Pleurotomaria amyntas*; d'Orbigny 1850: 268.

1856 *Pleurotomaria amyntas* d'Orb.; d'Orbigny 1856: 495, pl. 392: 6–10.

1873 *Pleurotomaria amyntas* d'Orbigny; Tawney 1873: 41.

1895 *Pleurotomaria* (?*Leptomaria*) *amyntas* d'Orbigny; Hudleston 1895: 415, pl. 35: 12.

non 1919 *Pleurotomaria* (*Leptomaria*) *amyntas* d'Orbigny; Cossmann 1919 : 431, pl. 16 : 6, 7.

non 1937 *Pleurotomaria amyntas*; Pchelincev 1937: 23, pl. 1: 20.

1997 *Bathrotomaria amyntas* (d'Orbigny); Fischer and Weber 1997: 187, pl. 33: 2a, b.

2011 *Bathrotomaria amyntas* (d'Orbigny)? [sic!]; Gründel et al. 2011: 100, pl. 1: 11–15.

Material.—Five specimens: MNHNL ZS248, MNHNL MDB254 (Giele Botter, Differdange, south-western Luxembourg), MNHNL ZS314 (Rollesbierg, Differdange, south-western Luxembourg), MNHNL ZS494S1, MNHNL MDB275 (Rollesbierg or Giele Botter, Differdange area, south-western Luxembourg). Early Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Description.—The shell is conoidal to slightly cyrtoconoid, roundedly gradate, consisting of about ten whorls. The apical spire is feebly cyrtoconoid. The early whorls are convex and with a poorly defined, narrow ramp. The sutures are impressed. The convexity of whorls diminishes during growth. On the last whorl an obtuse shoulder develops on the lower third of the whorl surface. This shoulder separates a wide, feebly concave to convex ramp from a narrower, flat or slightly convex outer face. The periphery is distinctly angulated on the immature shell and becomes obtusely angulated on the adult shell. The selenizone of the early shell is concave and edged by sharp marginal spiral threads. It runs clearly below the maximum convexity of the whorl and rapidly becomes flat and then convex during growth. On the adult whorls the selenizone is slightly cord-like and moderately wide, its width being 12% of the whorl surface. It runs clearly below the mid-whorl and on the angulation of the last whorl. Its lower and upper edges correspond to sharp spiral striae. The base is rather flat and slightly convex. The umbilicus is deep and moderately wide, almost funnel-shaped in the fully adult shell. The aperture is subpentagonal. The slit extends less than one fourth of the last whorl length.

The ornament of the immature spire consists of a dense and quite regular network of fine spiral threads and collabral riblets. Collabral riblets are more distinct above the selenizone and disappear during the growth of the fourth teleoconch whorl. The spiral threads are evenly sized and densely spaced. They increase in number during growth. The third to fourth whorl bears 8–10 spiral threads above the selenizone and 4–5 spiral threads below it. On the seventh whorl there are about 15 spiral threads above the selenizone and 7–8 below it. The spiral ornament persists longer than the collabral sculpture. On the last whorls the spiral threads tend to disappear too, leaving only obscure lines that are more pronounced below the selenizone. On the earliest teleoconch whorls the selenizone is sculptured only by sharp and regularly spaced lunulae. Subsequently, a middle spiral thread appears. This thread rapidly strengthens so that the selenizone finally appears as a slightly raised cord crossed only by dense and very faint growth lines. The base bears numerous fine, almost obscure spiral threads. The growth lines are strongly prosocline and slightly prosocyrt above the selenizone and

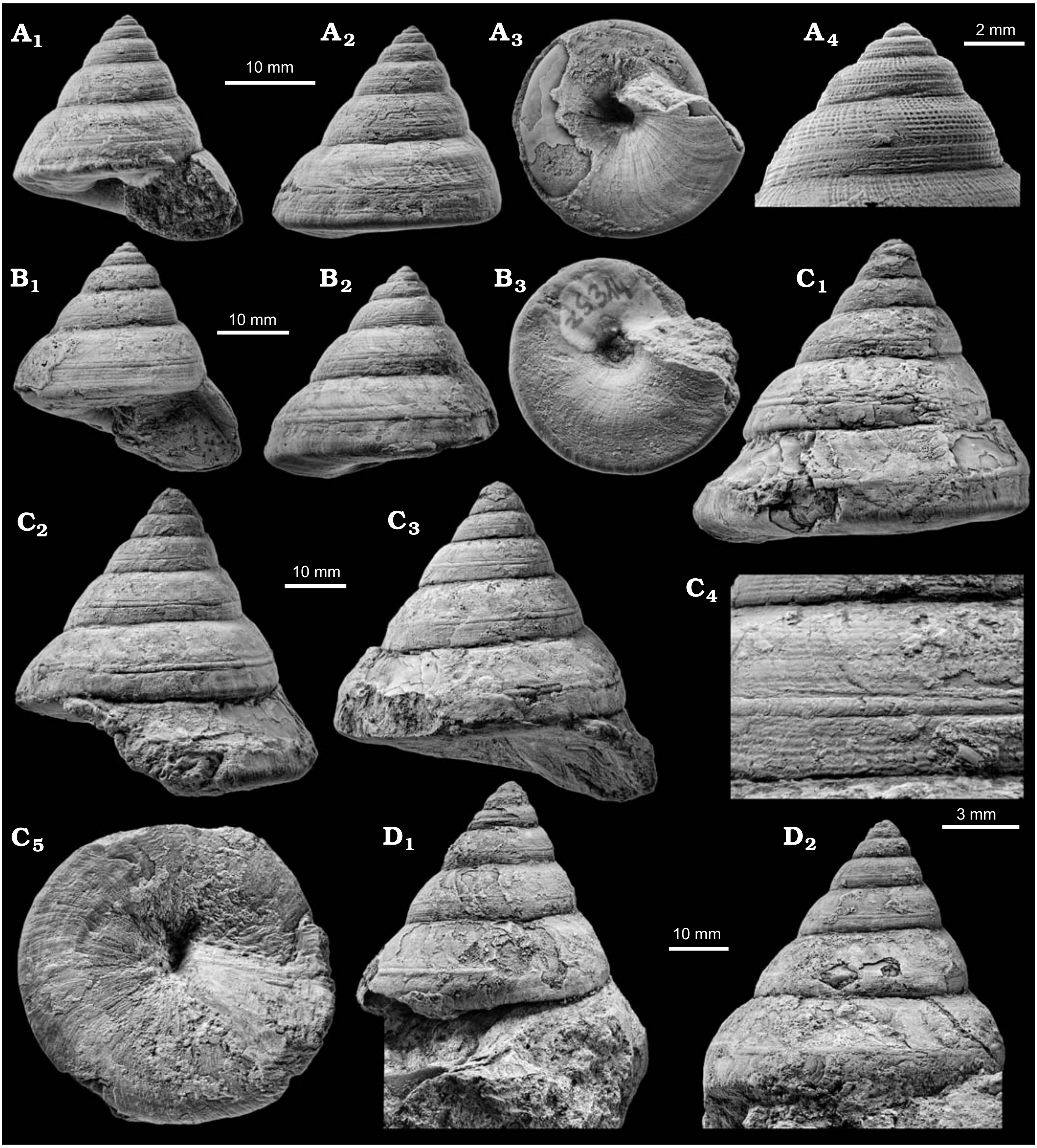


Fig. 4. Pleurotomarioidean gastropod *Laevitomaria amyntas* (d'Orbigny, 1850) from the Early Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone) of south-western Luxembourg. **A**. MNHNL ZS314, apertural (A_1), dorsal (A_2), and basal (A_3) views, detail of the apical shell (A_4); Differdange area (Rollesbierg). **B**. MNHNL ZS494S1, apertural (B_1), dorsal (B_2), and basal (B_3) views; Differdange area (Rollesbierg or Giele Botter). **C**. MNHNL ZS248, dorsal (C_1), lateral (C_2), and apertural (C_3) views, detail of the whorl surface (C_4), and basal view (C_5); Differdange area (Giele Botter). **D**. MNHNL MDB275, apertural (D_1) and dorsal (D_2) views; Differdange area (Rollesbierg or Giele Botter).

slightly opisthocline and prosocyrt below it. The base bears widely opisthocyrt growth lines becoming prosocyrt on the periumbilical area.

Remarks.—The specimens from Luxembourg differ from the holotype of *Laevitomaria amyntas* (d'Orbigny, 1850) in having a more obtuse adult spire angle and a less marked spiral ornament of the adult shell. The specimen identified by Hudleston (1895) as *Pleurotomaria* (?*Leptomaria*) *amyntas* has a narrower spire angle, but the other characters correspond exactly to those of the specimen from Luxembourg. In particular, Hudleston (1895) described a fine reticulate ornament of the apical shell and the disappearance of the spiral ornament on the spire whorls and on the base during the adult growth. Tawney (1873) mentioned a specimen with a spire angle of 58°, i.e., intermediate between the holotype (54°) and the specimens from Luxembourg (62–66°).

Gründel et al. (2011) tentatively identified two specimens from Late Aalenian of southern Germany as *L. amyntas*. According to these authors, their material differs from the holotype in showing a weaker shoulder at the selenizone. In the fully adult specimens described here the shoulder appears during the growth of the last whorls. In one specimen (ZS248) it becomes quite sharp on the last whorl and edges a slightly concave ramp. Tawney (1873) pointed out that one of his largest specimens exhibits a slightly concave ramp on the last whorl. However, in another specimen from Luxembourg (MDB275), the shoulder is much less evident and the ramp is convex. These observations indicate that the sharpness of the shoulder and the shape of the ramp of the adult shell are rather variable in *L. amyntas*. The specimens from southern Germany fall within this range of variability.

Laevitomaria gyroplata (Eudes-Deslongchamps, 1849) differs from *L. amyntas* in having a narrower spire angle (40–50°; Fischer and Weber 1997) and less convex whorls. Moreover, the umbilicus is absent to fissure-like. As underlined by Fischer and Weber (1997), the specimens from the Bajocian of Nievre (France) assigned by Cossmann (1919) to *Pleurotomaria* (*Leptomaria*) *amyntas* d'Orbigny, 1850 do not belong to that species. They show characters more comparable with those of *Bathrotomaria subreticulata* (d'Orbigny, 1850). The specimen described by Pchelincev (1937) as *Pleurotomaria amyntas* d'Orbigny, from the Aalenian of the Caucasus, is represented by an inner mould. The general morphology of the shell indicates that it belongs to *Laevitomaria*. This specimen differs from *L. amyntas* in having a more acute shell, less convex whorls and last whorl without angulation. Its poor state of preservation prevents further comparisons.

Stratigraphic and geographic range.—Undifferentiated Middle to Late Aalenian, Vendée (western France). Middle to Late Aalenian, south-western England. Late Aalenian, Baden-Württemberg (southern Germany). Early Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone), south-western Luxembourg.

Laevitomaria fasciata (Sowerby, 1818) comb. nov.

Fig. 5.

1818 *Trochus fasciatus*; Sowerby 1818: 37, pl. 220: 1.
non 1844 *Pleurotomaria fasciata* Sandberger; Goldfuss 1844; 64, pl. 183: 1.
1873 *Pleurotomaria fasciata* Sowerby; Tawney 1873: 51.
1895 *Pleurotomaria fasciata* Sowerby; Hudleston 1895: 416, pl. 36: 3.
1884 *Pleurotomaria fasciata* Sw.; Quenstedt 1884: 347, pl. 198: 37.
non 1886 *Pleurotomaria fasciata* Sowerby; Vacek 1886: 106, pl. 18: 2.
1907 *Pleurotomaria fasciata* Sowerby; Sieberer 1907: 32, pl. 4: 5.

Material.—One specimen: MNHNL ZS508, Piedmont (Longwy, Lorraine, eastern France), Early Bajocian.

Description.—The shell is conoidal-trochiform, subgradate, and it is composed of about 8–9 whorls. The last whorl makes up about two third of the height of the shell. The juvenile spire is slightly cyrtoconoid with moderately convex surface of the whorls. The adult whorls are distinctly convex and edged by a clearly impressed suture. They have a convex ramp which smoothly passes into the almost flat outer face. The suture runs on a roundedly angulated and slightly swollen periphery of the preceding whorl. The periphery becomes partially exposed on the last whorls. The selenizone is rather wide, its width being almost 15% of the whorl surface. It is situated slightly below mid-whorl and along the line of maximum convexity of the whorl surface. It is feebly concave on the early whorls, where it is edged by sharp marginal spiral threads, and becomes flat or very feebly convex during the growth. The base is almost flat, with a slightly convex surface and a narrow umbilicus. The aperture is subpentagonal-elliptical and wider than high.

The ornament of the juvenile shell is quite roughly reticulated, being composed of collabral riblets crossing spiral threads with small, flattish granules at the intersections. The surface of the early whorls above the selenizone bears about 6–8 spiral threads, among which the most adapical three are stronger and more distant to each other. The collabral riblets are coarse and slightly irregular in size. Below the selenizone, the early whorls are ornamented by 4–6 thin, subequally sized and evenly spaced spiral threads intersected by collabral riblets. These collabral riblets are finer and sharper than those present above the selenizone. The ornament of the early shell attenuates during growth. The spiral threads sculpturing the adult whorl surface above the selenizone become shallower and almost obscure and the collabral riblets gradually change in dense growth lines. In contrast, the spiral ornament below the selenizone is more persistent and slightly roughed by intersection with very thin, closely spaced, collabral riblets. The selenizone of the early whorls bears a median spiral thread and it is sculptured by well-marked and evenly spaced lunulae. On the adult shell, the lunulae become gradually finer and less pronounced. A further spiral thread on both sides of the median thread appears. These threads are shallower than the median one and slightly granulated by intersection with the low lunulae. The spiral ornament of the selenizone fades out and becomes obscure on the last whorls. The base is seemingly smooth. The growth lines are strongly prosocline and slightly prosocyrt above the selenizone, almost orthocline and feebly prosocyrt below it. On the base, the growth lines are widely opisthocyrt and become prosocyrt on the periumbilical area.

Remarks.—Among the material assigned by previous authors to *Laevitomaria fasciata* (Sowerby, 1818), the shell illustrated by Sieberer (1907) is the most similar to the specimen here

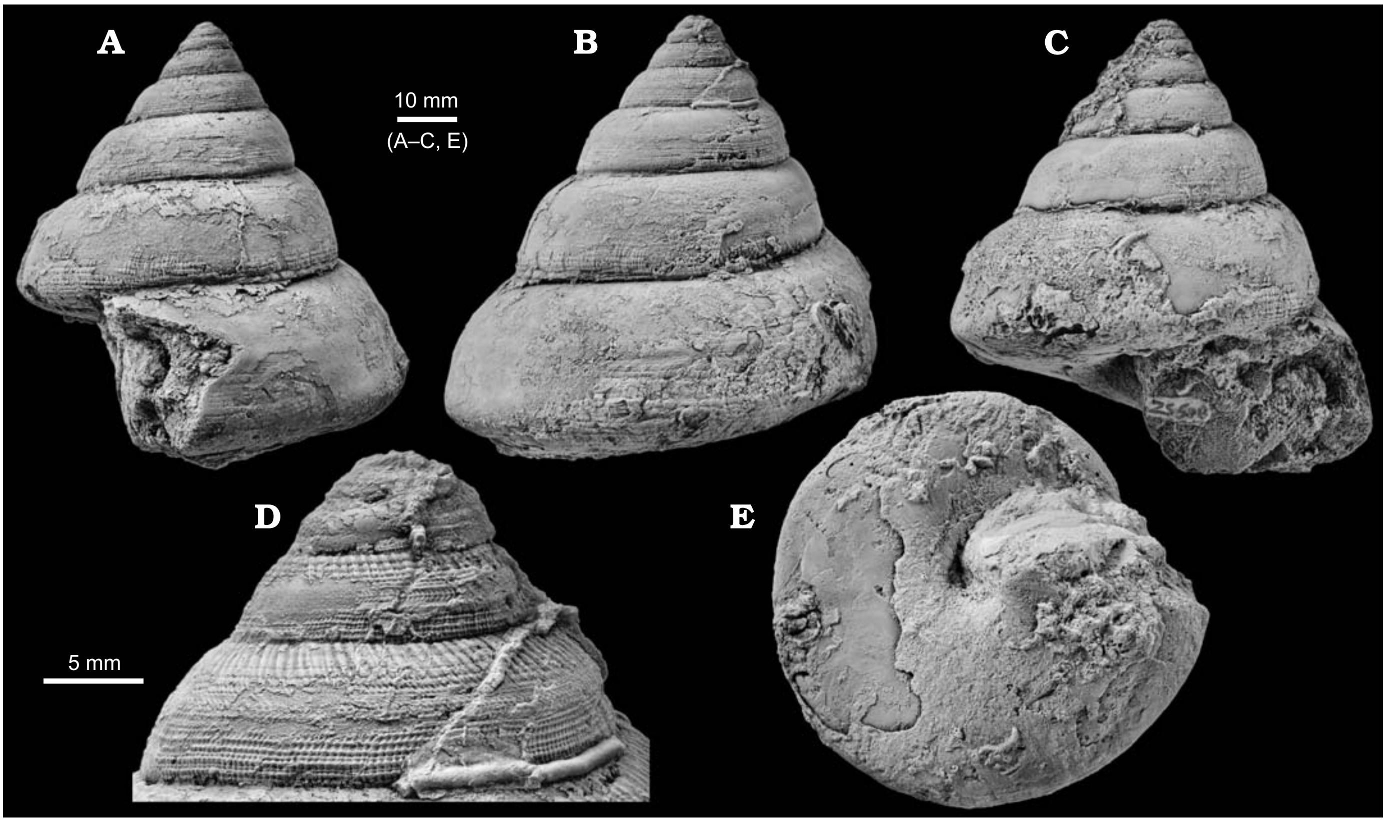


Fig. 5. Pleurotomarioidean gastropod *Laevitomaria fasciata* (Sowerby, 1818) from the Early Bajocian of Piedmont (Longwy, Lorraine, eastern France). MNHNL ZS508, lateral (**A**), dorsal (**B**), and apertural (**C**) views, detail of the apical shell (**D**), and basal view (**E**).

described. The specimen figured by Hudleston (1895) differs in having a fine spiral ornament on the base. Its periphery is roundedly angulated whereas in the specimen here described it is slightly swollen. These differences are here considered as representing the intraspecific variation of *L. fasciata*.

The feebly swollen periphery and the attenuation of the ornament on the surface of the shell above the selenizone make the specimen here described closely reminiscent of *Laevitomaria stoddarti* (Tawney 1873: 50, pl. 3: 5; Hudleston 1895: 418, pl. 36: 2). The latter taxon has a wider spire angle, a more distinctly swollen periphery, a deeper suture running below the periphery of the preceding whorl, and a consistently wider umbilicus.

Laevitomaria amyntas (d'Orbigny, 1850) differs from *L. fasciata* in having lower whorls with sharper periphery, and the last whorls subangulated at the selenizone. In *L. amyntas* the selenizone is more prominent and situated distinctly below the mid-whorl. Furthermore, the immature spire whorls are ornamented by a fine and regular network of spiral threads and collabral riblets whereas in *L. fasciata*, the reticulate sculpture of the early shell is coarser.

The specimen attributed by Vacek (1886) to *Pleurotomaria* fasciata (Sowerby, 1818) and classified by Conti and Szabó (1989: 32, pl. 1: 7) as *Leptomaria* aff. *fasciata* differs from Sowerby's (1818) species in having a definitely wider umbilicus and an early shell ornamented by a sharper and much more regular network of spiral threads and collabral riblets.

Stratigraphic and geographic range.—Early Bajocian, southwestern England, Swabia (southern Germany), Lorraine (eastern France).

Laevitomaria cf. *subplatyspira* (d'Orbigny, 1850)

Fig. 6.

Material.—One specimen: MNHNL BU233, Piedmont (Longwy, Lorraine, eastern France), Early Bajocian.

Description.—The adult shell is conoidal-trochiform. It is composed of moderately convex whorls separated by impressed sutures. The selenizone is flat and moderately wide, its width being almost 15% of the whorl surface. It is almost at mid-whorl on the spire and shifts slightly below it on the last whorls. The periphery is evidently angulated. The base is rather flat and phaneromphalous. Its surface is slightly convex. The umbilicus is moderately wide. The aperture has a subpentagonal section. Small shell remains indicate that the ornament of the adult shell is most probably very weak or absent. Some obscure spiral lines are visible below the selenizone. The base is seemingly smooth.

Remarks.—The material is represented only by a specimen lacking the apical spire and mostly preserved as inner mould. The few observable characters agree rather well with those described in *Laevitomaria subplatyspira* (d'Orbigny, 1850). These characters concern the size of the whorls and its increment during the growth, a quite sharp periphery, a flat base,

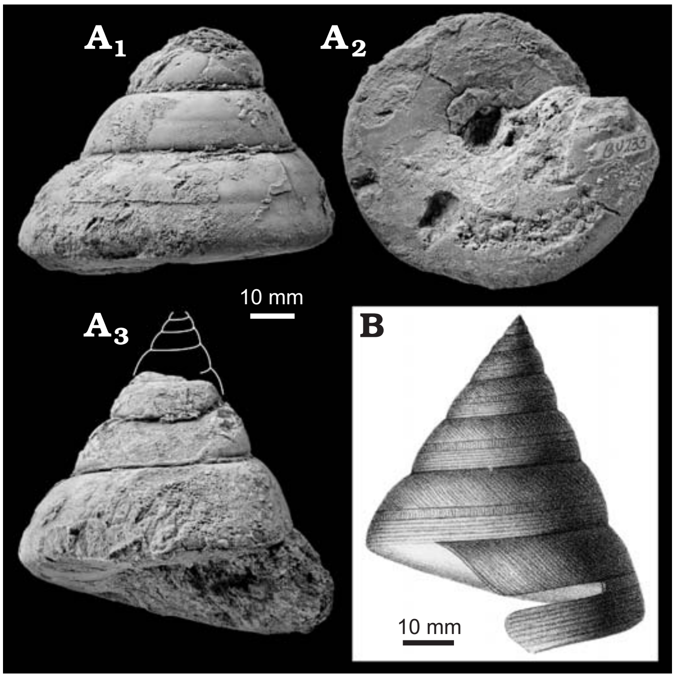


Fig. 6. Pleurotomarioidean gastropods. **A**. *Laevitomaria* cf. *subplatyspira* (d'Orbigny, 1850) from the Early Bajocian of Piedmont (Longwy, Lorraine, eastern France), MNHNL BU233, in dorsal (A_1), basal (A_2), and apertural (A_3) views. **B**. *Laevitomaria subplatyspira* (d'Orbigny, 1850) from the Early Bajocian, Bayeux (Calvados, northern France); figured by d'Orbigny (1856: 469, pl. 393: 1).

and a moderately wide and flat selenizone running almost at mid-whorl on the spire and shifting slightly below mid-whorl during the last growth. Remains of the shell seem to indicate that the ornament is very weak or absent on the last whorls and on the base, as it is the case in *L. subplatyspira*. However, due to its poor state of preservation the specimen is left in open nomenclature. Caution is also needed because of the uncertainty about the status of *L. subplatyspira*. As underlined by Fischer and Weber (1997: 187), the species was erected by d'Orbigny (1850: 269) based on the material on which Eudes-Deslongchamps (1849: 54, pl. 6: 2a–c) described *Pleurotomaria fasciata* var. *platyspira*. D'Orbigny (1850) changed the name in *subplatyspira* because the original name (*platyspira*) was already employed by him to raise *Pleurotomaria debuchii* var. *platyspira* Eudes-Deslongchamps, 1849 to species rank. The type material of *L. subplatyspira* is missing and no other specimen was found in the type locality (Fischer and Weber 1997).

As remarked by Fischer and Weber (1997), *L. subplatyspira* differs from *Laevitomaria fasciata* (Sowerby, 1818) in having less convex whorls, a sharper periphery and a less convex base. In *L. fasciata* the whorls are higher and the umbilicus is narrower. *Laevitomaria amyntas* (d'Orbigny, 1850) has a narrower and convex selenizone and its last whorls are angulated, whereas in *L. subplatyspira* they are evenly convex. *Laevitomaria stoddarti* (Tawney, 1873) differs from *L. subplatyspira* in having a wider spire angle and more convex whorls and base. In *L. stoddarti*, the ornament is coarser and the periphery is swollen.

Palaeobiogeographical history

During the Jurassic, the wide western European epicontinental shelf was an essentially stable region forming the northern marginal area of the western Tethys. In contrast, the central part of western Tethys was subject to a highly dynamic tectonic evolution. In this region, wide parts of shallow water and carbonate platform areas were drowned as an effect of the Neotethyan rifting mainly during the Late Sinemurian to Pliensbachian time span. In these areas, pelagic sedimentation took place and a gastropod stock originated (the Alpine faunal type sensu Szabó 1988), which was different from the gastropod faunas of the carbonate platforms and of the European epicontinental shelf. This stock maintained its individuality at least up to the Bajocian (Conti and Fischer 1984a, b; Conti and Monari 1986, 1991, 1995, 2001; Conti and Szabó 1987, 1988; Szabó 1988, 1992, 1994; Conti 1989; Monari et al. 2008; Gatto and Monari 2010).

In the western European epicontinental seas, the pleurotomarioideans were mainly represented by long-ranging genera with high species diversity, such as *Pleurotomaria* Defrance, 1826, *Bathrotomaria* Cox, 1956, *Pyrgotrochus* Fischer, 1885, and *Trochotoma* Eudes-Deslongchamps, 1843 (e.g., Sieberer 1907; Cox 1960b; Fischer and Weber 1997; Gründel 2003; Kollmann 2005; Monari et al. 2011; Monari and Gatto 2013). In contrast, these genera were either absent or rare and short-lived in the central region of western Tethys. For example, in the Early Jurassic, *Trochotoma* radiated in the western European shelf and in the carbonate platforms areas (Monari et al. 2011), whereas it was absent in the areas of the central western Tethys characterized by pelagic sedimentation. Again, *Pleurotomaria* occurred from the Early Jurassic to the Early Cretaceous in the European shelf, where it was represented by at least fifty species. In contrast, only few Sinemurian–Pliensbachian species are known from the pelagic sequences of central western Tethys (Monari and Gatto 2013).

The pleurotomarioideans of the Alpine faunal stock were significantly different from those of the western European region. Besides relict genera inherited from Triassic faunas, namely *Worthenia* De Koninck, 1883, *Wortheniopsis* Böhm, 1895, and *Sisenna* Koken, 1896 (see Szabó 2009), the bulk was represented by *Anodomaria* Szabó, 1980, *Cyclostomaria* Szabó, 1980, *Trochotomaria* Conti and Fischer, 1981, *Laevitomaria* Conti and Szabó, 1987, and *Urkutitoma* Szabó, 1984. These taxa were considered as endemic of the central western Tethys (Conti and Fischer 1984b; Szabó 1988, 1992; Vörös et al. 2003), but some of them were recently recorded also in western Europe, i.e., *Anodomaria* in the Hettangian of southern Luxembourg (Monari et al. 2011) and *Cyclostomaria* in the Late Bathonian–Early Callovian of Poland (Gründel 2012). *Anodomaria* is quoted in the Late Bathonian–Callovian of western India as well (Jaitly et al. 2000).

Laevitomaria is another genus showing both a wider palaeogeographical distribution and a higher diversity than

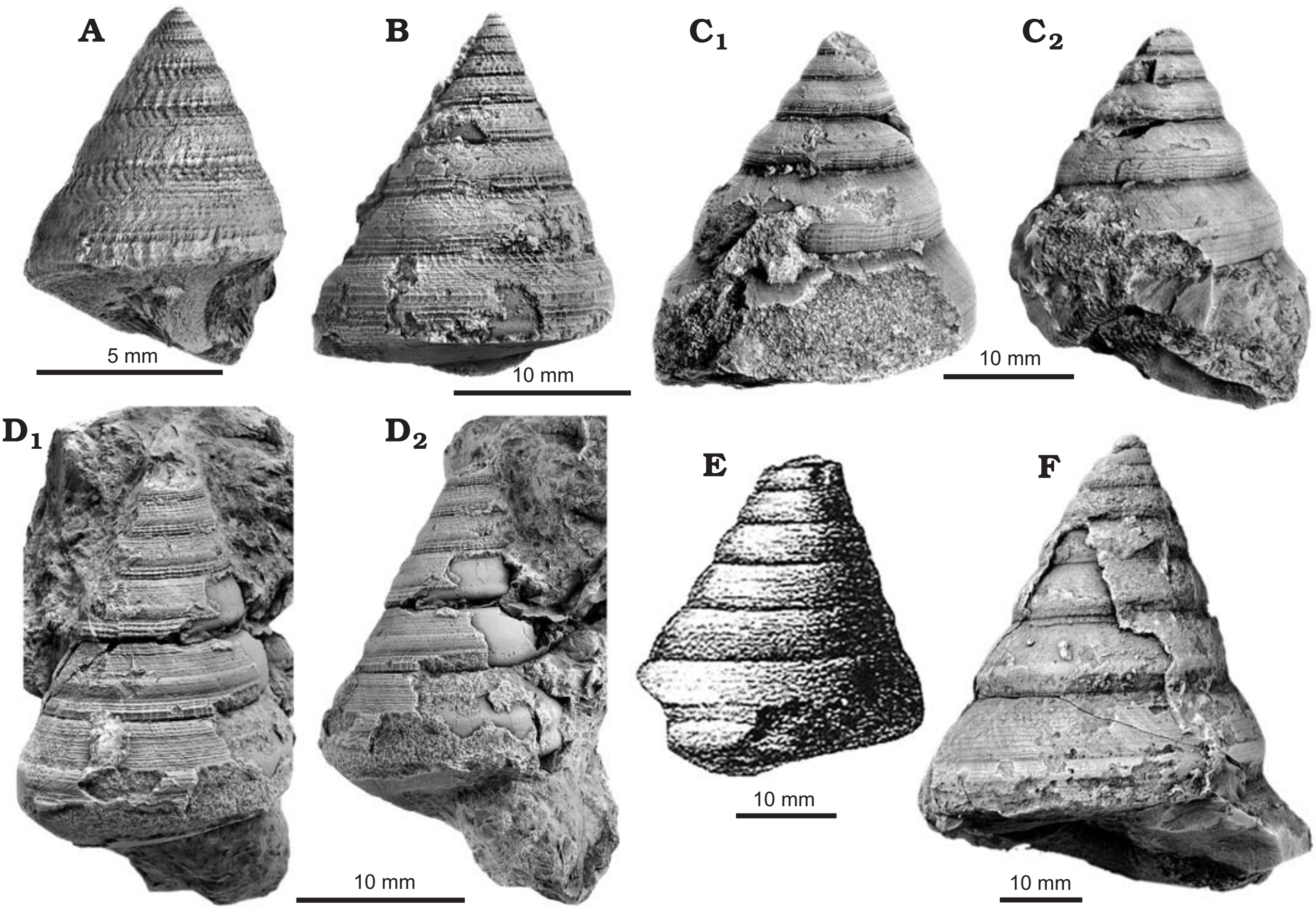


Fig. 7. Jurassic species of pleurotomarioidean gastropods *Laevitomaria* from the pelagic sediments of the central region of western Tethys. **A**. *Laevitomaria hierlatzensis* (Hörnes in Hauer, 1853), lectotype figured by Szabó (2009: 49, fig. 42D), apertural view, Late Sinemurian (*Oxynotoceras oxynotum* Zone), Halstatt (Hierlatz Alpe, Northern Calcareous Alps, Austria). **B**. *Laevitomaria danii* Szabó, 2009, holotype figured by Szabó (2009: 49, fig. 43C), dorsal view, Late Pliensbachian, Lókút (Bakony Mountains, Hungary). **C**. *Laevitomaria coarctata* (Stoliczka, 1861), specimen figured by Szabó (2009: 47, figs. 40D, E), dorsal (C_1) and apertural (C_2) views, Late Pliensbachian, Schafberg (Northern Calcareous Alps, Austria). **D**. *Laevitomaria periferialis* (Szabó, 1980), holotype HGM J 9599, figured by Szabó (2009: 48, fig. 41B), subapertural (D_1) and apertural (D_2) views, Late Sinemurian–Early Pliensbachian (mixed *Asteroceras obtusum* Zone–*Prodactylioceras davoei* Zone), Kericser (Bakony Mountains). **E**. *Laevitomaria angulba* (De Gregorio, 1886), specimen figured by Greco (1899: 117, pl. 9: 5), dorsal view, Early Aalenian, Rossano Calabro (northern Calabrian Arc, southern Italy). **F**. *Laevitomaria problematica* (Szabó, 1980), holotype, HGM J 10120, apertural view, Bajocian (*Stephanoceras humphriesianum* Zone–*Parkinsonia parkinsoni* Zone), Somhegy (Bakony Mountains, Hungary).

previously assumed. In addition to the species described in the systematic part, an extensive analysis of the literature sources allows to ascribe to *Laevitomaria* several other species (Tables 2 and 3). Most of them are illustrated in Figs. 7 and 8. On the basis of these data, *Laevitomaria* first appeared in areas belonging to the northern belt of central western Tethys, just at the time when these areas were involved in the Neotethyan rifting. In fact, the oldest species known, namely *Laevitomaria hierlatzensis* (Hörnes in Hauer, 1853) (Fig. 7A), comes from the Late Sinemurian deposits of Hierlatz (Northern Calcareous Alps). Other species, such as *Laevitomaria danii* Szabó, 2009 (Fig. 7B), *Laevitomaria coarctata* (Stoliczka, 1861) (Fig. 7C), and *Laevitomaria periferialis* (Szabó, 1980) (Fig. 7D) are known from the Pliensbachian of Hierlatz and Bakony Mountains (Hungary). The occurrence of the genus also in the Late Sinemurian–Early Pliensbachian of Western Pontides (Table 2) suggests a great extension of the distribution of *Laevitomaria* along the northern margin of western Tethys (Fig. 9A) and a fast dispersal after its appearance. Pchelincev (1937) recorded two species in the Aalenian of the Caucasus (Table 2). Although mainly represented by inner moulds which do not enable a safe species assignment, they most probably belong to *Laevitomaria*. This would demonstrate that in the earliest Middle Jurassic the distribution of the genus continued to include the north-eastern margin of western Tethys (Fig. 9B). In the central region of western Tethys, the younger species known is *Laevitomaria problematica* (Szabó, 1980) (Figs. 2, 3, 7F), which dates to the Bajocian (Fig. 9C).

Although the first radiation of *Laevitomaria* took place in the above mentioned areas, the highest diversification of

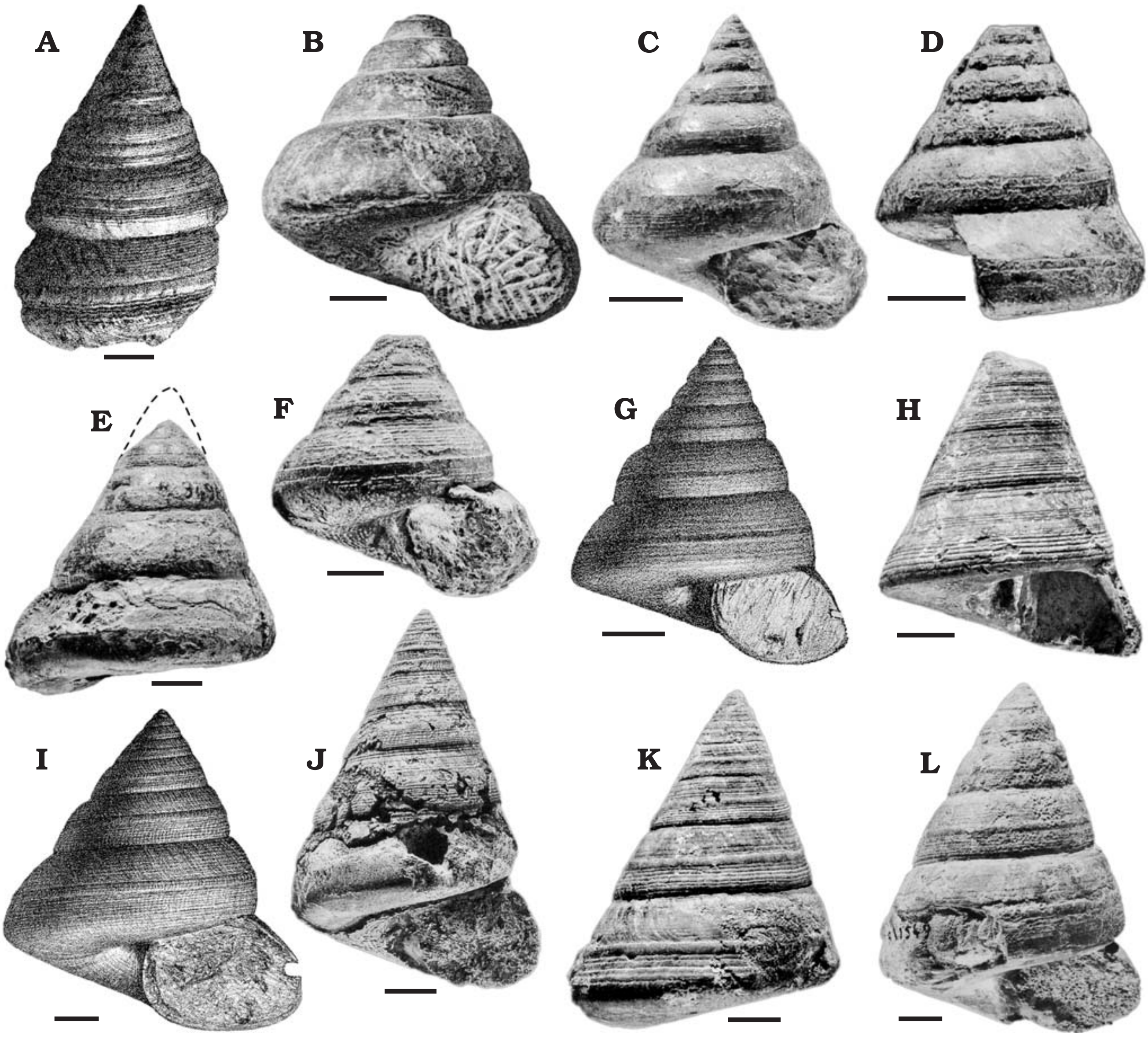


Fig. 8. Jurassic species of pleurotomarioidean gastropods *Laevitomaria* from the western European epicontinental region. **A**. *Laevitomaria joannis* (Dumortier, 1874), specimen figured by Dumortier (1874: 152, pl. 36: 10), dorsal view, Toarcian, Isère (southern France). **B**. *Laevitomaria zonata* (Goldfuss, 1844), specimen figured by Sieberer (1907: 23, pl. 2: 3), apertural view, Late Toarcian, Heiningen (Swabia, southern Germany). **C**. *Laevitomaria repeliniana* (d'Orbigny, 1855), lectotype figured by Fischer and Weber (1997: 166, pl. 31: 5a), apertural view, undifferentiated Toarcian–Aalenian, La Verpillière (Isère, southern France). **D**. *Laevitomaria repeliniana* (d'Orbigny, 1855), holotype of *Pleurotomaria serena* d'Orbigny, 1855, lateral view, figured by Fischer and Weber (1997: 167, pl. 31: 7), undifferentiated Toarcian–Aalenian, La Verpillière (Isère, southern France). **E**. *Laevitomaria repeliniana* (d'Orbigny, 1855), holotype of *Pleurotomaria bertheloti* d'Orbigny, 1855 figured by Fischer and Weber (1997: 167, pl. 31: 8b), dorsal view, undifferentiated Toarcian–Aalenian, La Verpillière (Isère, southern France). **F**. *Laevitomaria isarensis* (d'Orbigny, 1855), holotype figured by Fischer and Weber (1997: 167, pl. 31: 2b), apertural view, undifferentiated Toarcian–Aalenian, La Verpillière (Isère, south-eastern France). **G**. *Laevitomaria amyntas* (d'Orbigny, 1850), specimen figured by Hudleston (1895: 415, pl. 35: 12), apertural view, Middle Aalenian, Burton Bradstock (south-western England). **H**. *Laevitomaria allionta* (d'Orbigny, 1850), holotype figured by Fischer and Weber (1997: 185, pl. 31: 10a), apertural view, Middle Aalenian (*Ludwigia murchisonae* Zone), Moutiers-en-Cinglais (Calvados, northern France). **I**. *Laevitomaria fasciata* (Sowerby, 1818), specimen figured by Hudleston (1895: 416, pl. 36: 3), apertural view, Early Bajocian, Dundry (south-western England). **J**. *Laevitomaria gyroplata* (Eudes-Deslongchamps, 1849), holotype of *Pleurotomaria allica* d'Orbigny, 1850 figured by Fischer and Weber (1997: 185, pl. 32: 4), apertural view, Early Bajocian (*Stephanoceras humphriesianum* Zone), Moutiers-en-Cinglais (Calvados, northern France). **K**. *Laevitomaria gyroplata* (Eudes-Deslongchamps, 1849), specimen figured by Fischer and Weber (1997: 181, pl. 32: 3), dorsal view, Early Bajocian (*Stephanoceras humphriesianum* Zone), Moutiers-en-Cinglais (Calvados, northern France). **L**. *Laevitomaria gyroplata* (Eudes-Deslongchamps, 1849), lectotype of *Pleurotomaria saccata* d'Orbigny, 1850 figured by Fischer and Weber (1997: 176, pl. 32: 5), apertural view, Late Bajocian (*Strenoceras niortense* Zone–*Garantiana garantiana* Zone), Saint Vigor-le-Grand (Calvados, northern France). Scale bars 10 mm.

the genus occurred during post-Pliensbachian times in the western European epicontinental seas. In that region, the oldest species known is *Laevitomaria joannis* (Dumortier, 1874) (Fig. 8A), from the Toarcian of Isère (Rhone Basin, southern France) and *Laevitomaria zonata* (Goldfuss, 1844) (Fig. 8B), from the Late Toarcian of Swabia (southern Ger-

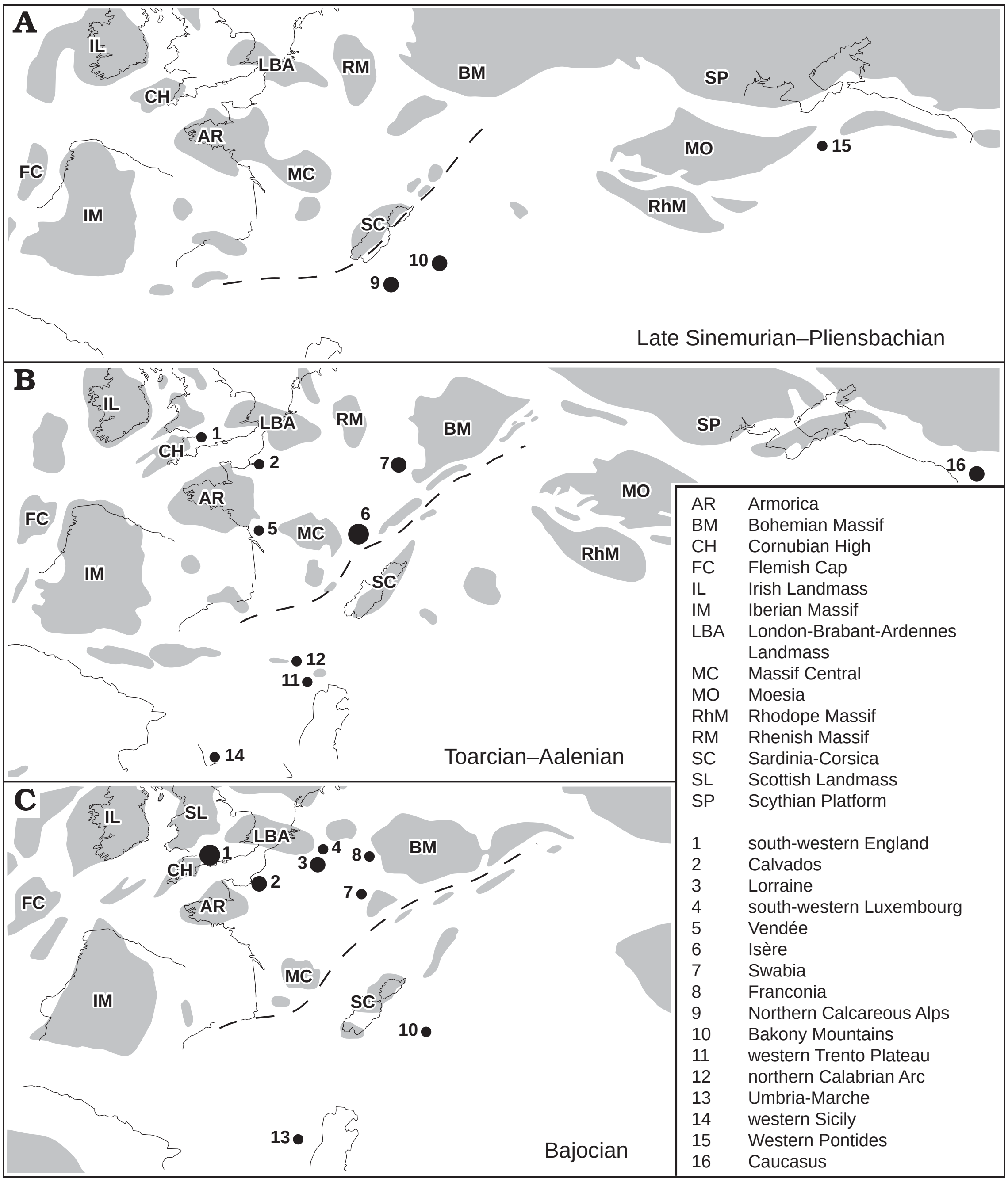


Fig. 9. Palaeogeographical distribution of *Laevitomaria* in western European epicontinental seas and central region of western Tethys during the Jurassic. **A**. Late Sinemurian–Pliensbachian. **B**. Toarcian–Aalenian. **C**. Bajocian. Exposed lands are in grey and main units are indicated by acronyms. Dashed line denotes approximate southern margin of European epicontinental shelf. The localities of occurrence are indicated by numbers. Circle size is proportional to number of species (small: one species, medium: two species, large: three or more species). See Tables 2 and 3 for references. Maps redrawn and simplified from Ziegler (1988), Bradshaw et al. (1992), and Dercourt et al. (2000).

many). Other species are recorded from Toarcian–Aalenian deposits of the Rhone Basin, i.e., *Laevitomaria repeliniana* (d'Orbigny, 1855) (Fig. 8C–E) and *Laevitomaria isarensis* (d'Orbigny, 1855) (Fig. 8F). All these occurrences concern the southernmost belt of the western European epicontinental shelf (Fig. 9B).

The genus experienced its major radiation in the Middle Aalenian to the Early Bajocian of the western European shelf with at least six species. These are *Laevitomaria amyntas* (d'Orbigny, 1850) (Figs. 4, 8G), *Laevitomaria allionta* (d'Orbigny, 1850) (Fig. 8H), *Laevitomaria fasciata* (Sowerby, 1818) (Figs. 5, 8I), *Laevitomaria subplatyspira* (d'Orbigny, 1850) (Fig. 6B), *Laevitomaria stoddarti* (Tawney, 1873), and *Laevitomaria gyroplata* (Eudes-Deslongchamps, 1849) (Fig. 8J–L) (Table 3). Their occurrence in the early Middle Jurassic deposits of Swabia and Franconia (southern Germany), Lorraine (eastern France), south-western Luxembourg, Vendée (western France), Calvados (northern

Table 2. List of Jurassic *Laevitomaria* species from localities representing the central region of western Tethys, its north-eastern margin, and south-eastern Tethyan area.

Species	References	Age and localities
Central region of western Tethys		
Laevitomaria hierlatzensis (Hörnes in Hauer, 1853)	Hörnes in Hauer 1853: 762; Stoliczka 1861: 187, pl. 4: 2a, b; Szabó 2009: 49, figs. 42A–F	Late Sinemurian (*Oxynotoceras oxynotum* Zone), Hierlatz Alpe (Northern Calcareous Alps, Austria)
Laevitomaria danii Szabó, 2009	Szabó 1980: 60, pl. 3: 5, as "*Leptomaria* sp."; Szabó 2009: 49, figs. 43A–H	Late(?) Sinemurian and Late Pliensbachian, Bakony Mountains (Hungary)
Laevitomaria periferialis (Szabó, 1980)	Szabó 1980: 62, pl. 3: 6; Conti and Szabó 1987: 46; Szabó 2009: 48, figs. 41A, B	Late Sinemurian–Early Pliensbachian (mixed *Asteroceras obtusum* Zone–*Prodactylioceras davoei* Zone) and Early Pliensbachian (*Prodactylioceras davoei* Zone), Bakony Mountains (Hungary)
Laevitomaria coarctata (Stoliczka, 1861)	Stoliczka 1861: 188, pl. 4: 3a, b; Szabó in Vörös et al. 2003: 61, figs. 5,4–7 Szabó 2009: 47, figs. 40A–E	Late Pliensbachian, Schafberg (Northern Calcareous Alps, Austria)
Laevitomaria angulba (De Gregorio, 1896) comb. nov.	De Gregorio 1886: 7, pl. 1: 5; Greco 1899: 117, pl. 9: 4, 5	Aalenian, Monte Erice (north-western Sicily, Italy); Early Aalenian, Rossano Calabro (northern Calabrian Arch, southern Italy)
Laevitomaria aff. *fasciata* (Sowerby, 1818)	Vacek 1886: 106, pl. 18: 2, as "*Pleurotomaria fasciata* (Sowerby)"; Conti and Szabó 1989: 32, pl. 1: 7	Aalenian, Capo San Vigilio (Trento Plateau, southern Alps)
Laevitomaria problematica (Szabó, 1980)	this paper	Bajocian (*Stephanoceras humphriesianum–Parkinsonia parkinsoni* zones), Bakony Mountains (Hungary); Early Bajocian (*Stephanoceras humphriesianum* Zone), Martani Mountains (Umbria, central Italy)
North-eastern margin of western Tethys		
Laevitomaria cf. *periferialis* (Szabó, 1980)	Conti and Monari 1991: 266, pl. 5: 12, as "Pleurotomarioidea indet. 1"	Late Sinemurian–Early Pliensbachian (*Echioceras raricostatum–Tragophylloceras ibex* zones), Western Pontides (Turkey)
Laevitomaria sp.	Pchelincev 1937: 23, pl. 1: 18, as "*Pleurotomaria fasciata* var. *siebereri* Pchelincev"	Aalenian, Caucasus
Laevitomaria sp.	Pchelincev 1937: 23, pl. 1: 20, as "*Pleurotomaria amyntas* d'Orbigny"	Aalenian, Caucasus
South-eastern Tethyan margin		
Laevitomaria asurai (Das, Bardhan, and Case, 2005) comb. nov.	Das et al. 2005: 341, figs. 9A–G	Late Bathonian, Kutch (western India)
Laevitomaria daityai (Das, Bardhan, and Case, 2005) comb. nov.	Das et al. 2005: 341, figs. 8A–D	Early Callovian–Oxfordian, Kutch (western India)

France), and south-western England indicates that during these times *Laevitomaria* expanded greatly its geographic range over the western European region (Fig. 9C). In particular, during the Bajocian, the species occurrences were mainly located in northern France and south-western England. This perhaps indicates a northward shift of the area of maximum species diversity of the genus during the Jurassic, from the northern part of central western Tethys in the Late Sinemurian–Pliensbachian, to the southernmost part of western European shelf in the Toarcian–Aalenian, and finally to the northern Paris Basin and southern England in the Late Aalenian–Bajocian. Interestingly, Liu (1995) and Liu et al. (1998) described a progressive Toarcian to Bathonian northward shift of the distribution of several bivalve taxa (named "Tethyan Spread") reflecting a northward displacement of the tropical-subtropical climatic belts. This climatic change might also have driven the distribution pattern of *Laevitomaria*.

In the latest Bajocian, *Laevitomaria* disappeared abruptly both in the central part of western Tethys and in the European shelf. *Laevitomaria asurai* (Das, Bardhan, and Case, 2005) from Late Bathonian of Kutch (western India) and *Laevitomaria daityai* (Das, Bardhan, and Case, 2005) from Early Callovan to Oxfordian of the same region (Table 2) would demonstrate that the distribution of *Laevitomaria* in post-Bajocian times moved to the south-eastern margin of the Tethys. Recent studies on the systematics of the Indian gastropod faunas (Das et al. 1999, 2005; Jaitly et al. 2000; Das 2002, 2007; Szabó and Jaitly 2004; Jaitly and Szabó 2007) revealed that several gastropod taxa characteristic of western Europe appeared in this region starting from the Bathonian. Thus, the change of distribution of *Laevitomaria* might be part of a more generalized event of dispersal. The lack of information concerning the Early Jurassic and earliest Middle Jurassic of intermediate areas, such as the African and Arabian margins, currently prevents to verify this hypothesis.

Table 3. List of Jurassic *Laevitomaria* species from localities representing the western European epicontinental shelf.

Species	References	Age and localities
Laevitomaria joannis (Dumortier, 1874) comb. nov.	Dumortier 1874: 152, pl. 36: 10, 11	Toarcian, Isère (south-eastern France)
Laevitomaria zonata (Goldfuss, 1844) comb. nov.	Goldfuss 1844: 73, pl. 186: 2; Quenstedt 1858: 289, pl. 41: 9; Quenstedt 1884: 355, pl. 189: 1; Sieberer 1907: 23, text-fig. 4, pl. 2: 3	Late Toarcian, Swabia (southern Germany)
Laevitomaria repeliniana (d'Orbigny, 1855) comb. nov.	d'Orbigny 1855: 435, pl. 359: 1–5; d'Orbigny 1855: 438, pl. 361: 1–5, as "*Pleurotomaria serena* d'Orbigny"; d'Orbigny 1855: 439, pl. 361: 6–10, as "*Pleurotomaria bertheloti* d'Orbigny"; Fischer and Weber 1997: 166–167, pl. 31: 5–8	Undifferentiated Toarcian–Aalenian, Isère (south-eastern France)
Laevitomaria isarensis (d'Orbigny, 1855) comb. nov.	d'Orbigny 1855: 440, pl. 362: 1–5; d'Orbigny 1855: 441, pl. 362: 6–10, as "*Pleurotomaria rosalia* d'Orbigny"; d'Orbigny 1855: 445, pl. 364, figs. 1–6, as "*Pleurotomaria subdecorata* Münster"; Fischer and Weber 1997: 167–169, pl. 31: 2–4	Undifferentiated Toarcian–Aalenian, Isère (south-eastern France)
Laevitomaria allionta (d'Orbigny, 1850) comb. *nov.*	d'Orbigny 1850: 268; d'Orbigny 1856: 491, pl. 391: 1–5; Fischer and Weber 1997: 185, pl. 31: 10a, b	Middle Aalenian (*Ludwigia murchisonae* Zone), Calvados (northern France)
Laevitomaria amyntas (d'Orbigny, 1850) comb. nov.	this paper	Undifferentiated Middle–Late Aalenian, Vendée (western France); Middle–Late Aalenian, south-western England; Late Aalenian, Swabia (southern Germany); Early Bajocian, south-western Luxembourg
Laevitomaria fasciata (Sowerby, 1818) comb. nov.	this paper	Early Bajocian, south-western England, Swabia (southern Germany), Lorraine (eastern France)
Laevitomaria subplatyspira (d'Orbigny, 1850) comb. nov.	this paper	Early Bajocian, south-western England, Calvados (northern France), ?Lorraine (eastern France)
Laevitomaria stoddarti (Tawney, 1873) comb. nov.	Tawney 1873: 50, pl. 3: 5a, b; Hudleston 1895: 418, pl. 36: 2	Early Bajocian, south-western England
Laevitomaria gyroplata (Eudes-Deslongchamps, 1849) comb. nov.	Eudes-Deslongchamps 1849: 54, pl. 6: 3, 4; Eudes-Deslongchamps 1849: 57, pl. 7: 1–3, as "*Pleurotomaria gyrocycla* Eudes-Deslongchamps"; Chapuis and Dewalque 1853: 101, pl. 14: 2a–b; d'Orbigny 1855: 478, pl. 384: 1–5; d'Orbigny 1855: 462, pl. 377: 1–3, pl. 378: 1, as "*Pleurotomaria alimena* d'Orbigny"; d'Orbigny 1855: 464, pl. 379: 1–5, as "*Pleurotomaria saccata* Eudes-Deslongchamps"; d'Orbigny 1855: 480, pl. 385: 1–4, as "*Pleurotomaria gyrocycla* Eudes-Deslongchamps"; d'Orbigny 1856: 482, pl. 386: 1–4, as "*Pleurotomaria transilis* Eudes-Deslongchamps"; d'Orbigny 1856: 490, pl. 390: 1–5, as "*Pleurotomaria allica* d'Orbigny"; Quenstedt 1858: 415, pl. 57: 10, as "*Pleurotomaria elongata* Sowerby"; Quenstedt 1884: 349, pl. 198: 42, as "*Pleurotomaria elongata* Sowerby"; Hudleston 1895: 419, pl. 36: 4, 4a, as "*Pleurotomaria transilis* d'Orbigny"; Hudleston 1895: 422, pl. 36: 5, 5a, as "*Pleurotomaria allica* d'Orbigny"; Sieberer 1907: 34, pl. 2: 14, as "*Pleurotomaria elongata* Sowerby"; Fischer and Weber 1997: 175, 176, 181, 182, 185, pl. 32: 3–7; Gründel 2003: 50, pl. 1: 12–14	Early–Late Bajocian (*Stephanoceras humphriesianum* Zone–*Parkinsonia parkinsoni* Zone), Calvados (northern France); Early Bajocian, south-western England; Bajocian (probably latest Early Bajocian), Lorraine (eastern France); Late Bajocian, Franconia (southern Germany)

Conclusions

Several analogies are recognizable between the biogeographical and evolutionary history of *Laevitomaria* and that of *Pleurotomaria*. According to Monari and Gatto (2013), *Pleurotomaria* occurred in the western European shelf since the beginning of the Jurassic. In the Late Sinemurian, *Pleurotomaria* appeared also in those areas of the central region of western Tethys which were drowned by the Neotethyan rifting, concomitantly with the first appearance, early radiation and pronounced geographical expansion of *Laevitomaria* in these areas. From there, *Pleurotomaria* disappeared at the end of Pliensbachian, presumably as an effect of the Early Toarcian anoxic event. The Toarcian corresponds also to an abrupt decline of diversity of *Laevitomaria* in the central part of western Tethys and to the appearance of the genus in the western European shelf.

Similarities between the history of *Laevitomaria* and that of *Pleurotomaria* are also evident in the early Middle Jurassic. In fact, during the Aalenian–Early Bajocian, both genera underwent a major radiation in the western European epicontinental shelf and suffered a subsequent collapse of diversity. In post-Bajocian times their histories diverged. *Laevitomaria* disappeared from the European shelf and moved to the south-eastern Tethys, whereas the European shelf continued to be the preferential area of distribution of *Pleurotomaria* up to the Early Cretaceous.

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