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Vetigastropoda and Neritimorpha from the Lower Bajocian of Luxembourg and palaeobiogeography of Aalenian–Bajocian (Middle Jurassic) gastropods of western Europe

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ABSTRACT

Vetigastropod and neritimorph species from Lower Bajocian (Middle Jurassic) sediments of south-western Luxembourg are described. Eighteen species are recognized. Two new genera, namely *Szabotomaria* gen. nov. and *Fabercapulus* gen. nov., and four new species (*Szabotomaria ziqquratiformis* sp. nov., *Colpomphalus thuyi* sp. nov., *Colpomphalus tigratus* sp. nov. and *Fabercapulus semisculptus* sp. nov.) are erected. These species, together with other species recently described from the same strata compose a well diversified assemblage. It consists of 32 species belonging to 14 genera of six families and five superfamilies and represents the richest vetigastropod-neritimorph fauna currently known from Bajocian and sub-coeval deposits of western Europe. An analysis of the palaeoecological and palaeobiogeographical relationship of this fauna with those from other areas of the western European shelf has been performed by mean of cluster analysis and by comparison of the respective taxonomic structures. The cluster analysis detected a major cluster composed of two distinct branches, i.e. the faunas of northern Paris-Wessex Basin, including Luxembourg, and those of the southern Germany basin. These faunas share comparable taxonomic structures and occur mainly in facies represented by condensed iron ooid-rich marls and limestones deposited in lower offshore to upper offshore -shoreface settings. The close relationship between the Luxembourg and the other faunas of the Paris-Wessex Basin reflects free faunal exchange and facies similarities. Slight differences in the sedimentary context could explain the separation of the southern Germany branch from the Anglo-Paris one, whereas the affinities among Swabian and Franconian faunas most probably reflect the geographical continuity of these areas. The Early Bajocian fauna of the East Midlands Shelf comes from sediments deposited in a shallow water, oolitic barrier complex and is definitely different from the others of western Europe both in species composition and taxonomic structure.

Key words: Gastropoda; systematics; Middle Jurassic; western Europe; Luxembourg; palaeobiogeography

Introduction

The Paris Basin is an intracratonic sedimentary basin which was covered for most of the Mesozoic by an epicontinental sea extending over a large part of the north-western Europe at tropical to subtropical latitude (Mégnien 1980). During the Jurassic, its sedimentary history was greatly affected by the major tectonic events that involved the western part of the Eurasian Plate, such as the early stage of the central Atlantic rifting, the evolution of the Ligurian Tehtys and the North Sea thermal doming (Contini & Mangold 1980; Thierry 2000; Guillocheau *et al.* 2000, 2002 and references therein). The latitudinal position of the basin and the reduced extension of surrounding emerged lands favoured the periodic development of carbonate platforms where oolitic/skeletal facies alternated with mixed carbonate/terrigenous sediments in response to both local and regional tectonic impulses (Guillocheau *et al.* 2000, 2002; Brigaud *et al.* 2009, 2014). At its north-eastern part, the Paris Basin was connected to the German region and the North Sea via the Luxembourg Basin, a seaway open between two eroded Hercynian basement structures, the Ardennes high and the Rhenish Massif (Lucius 1948; Bintz *et al.* 1973). In the Lower and Middle Jurassic, the Luxembourg Basin was subjected to a shallow water sedimentary regime and conditions for well diversified benthic molluscan faunas established during Hettangian (Chapuis & Dewalque 1853; Monari *et al*, 2011) and Early Bajocian times. While the Middle Jurassic gastropods of the main Paris Basin have been extensively studied since the pioneering works by Eudes-Deslongchamps (1843a, b, c, d, e, f, 1849) and d'Orbigny (1851–1860), their coeval counterparts from the Luxembourg basin have long been neglected. Recently, a detailed study of a rich collection of Early Bajocian gastropods from southern Luxembourg localities was undertaken by the present authors in order to reconstruct the diversity and trace the recovery of these molluscs after the extinctions associated with the Toarcian Anoxic Event (Jenkyns 1988; Caruthers *et al.* 2013; Gatto *et al.* 2015a and references therein). The first outcomes of this research were the revisions of the pleurotomariid genera *Pleurotomaria* Defrance, 1826 (Monari & Gatto 2013), *Leptomaria* Eudes-Deslongchamps, 1864 (Monari & Gatto 2014), and *Laevitomaria* Conti & Szabó, 1987 (Gatto *et al.* 2015b). The present paper concludes the review of the vetigastropods and describes the neritimorph gastropods from the studied area. Relationships with other of Upper Aalenian-Bajocian faunas of western Europe are also investigated by qualitative and quantitative methods of comparisons.

Geological setting

The Jurassic sediments cropping out in the central and southern part of the Grand Duchy of Luxembourg (Gutland) range in age from the Hettangian to the Early Bajocian. They are represented by a marine succession of alternating and laterally discontinuous, more or less shallow water facies, whose deposition was for some time under the direct influence of the nearby emerged lowlands of the Ardennes (Lucius 1948; Bintz *et al.* 1973). Starting from the Late Toarcian, with the deposition of the cross-bedded oolitic ironstones and sandy limestone of the 'Minette' Formation, sedimentation became rather uniform throughout the Luxembourg Basin and the nearby French Lorraine (Guillocheau *et al.* 2002; Fayard *et al.* 2005). In this area, an important stratigraphic hiatus occurs at the top of the 'Minette' (Guillocheau *et al.* 2002; Weis & Mariotti 2008). This gap decreases from the Differdange-Longwy sub-basin at NW, where it spans the Late Toarcian–Aalenian, to the Esch-Ottange sub-basin at SE where it encompasses only the early part of the Late Aalenian (Guillocheau *et al.* 2002; Guérin-Franiatte & Weis 2010). According to Guillocheau *et al.* (2002; see also Brigaud *et al.* 2014) this erosional surface is a local expression of the mid-Cimmerian unconformity (Ziegler 1990) and was caused by a compressive deformation, presumably linked with the onset of the North Sea thermal doming (Guillocheau *et al.* 2000) and the emersion of the London-Brabant massif (Brigaud *et al.* 2014). In the Early Bajocian, the drowning of the continental domain of the Ardennes triggered a major palaeogeographical reorganization of the eastern Paris Basin, which caused a reversal of its depocentre from S to N (Thiry-Bastien 2002; Guillocheau *et al.* 2002). In this renewed palaeogeographical context, the eastern Paris Basin and its Luxembourg branch witnessed a shallowing trend and the establishment of a carbonate platform that persisted until the Humphriesianum Zone, when scleractinian coral bioherms became widespread ("plate-forme marine peu profonde à hauts fonds multiples" in Guillocheau *et al.* 2002; "flat-topped platform with coral buildups" in Brigaud *et al.* 2014).

The studied gastropods come from Lower Bajocian sediments exposed in the south-eastern Luxembourg along the current border with France (Fig. 1A). In this area, as described by Köwius (1977), the Lower Bajocian succession (Fig. 1B) starts with the unit of the *Marnes micacées* (Discites Zone) which consists of blue-green slightly calcareous, silty to sandy argillites with intercalations of phosphorite nodules. A thin, few decimetres thick unit separates the *Marnes micacées* from the overlying *Couches à Sonninia*. This unit, informally named *Conglomérat à Sonninia* (condensed Discites Zone–Laeviuscula Zone, Ovalis Subzone; Sadki *et al.* 2015) is represented by one or two closely spaced, conglomeratic beds of grey-yellowish marly limestones frequently with iron ooids, rich in bio-eroded and bio-encrusted pebbles coated with iron oxides. Locally, these beds are highly fossiliferous and contain an abundant and well-diversified invertebrate fauna including brachiopods, bivalves, gastropods (Monari & Gatto 2013, 2014; Gatto *et al.* 2015b), cephalopods (Weis & Mariotti 2008; Sadki *et al.* 2015), echinoids (Thuy 2010), solitary corals and sponges. The *Couches à Sonninia* (known also as *Calcaire d'Ottange*; Laeviuscula Zone, Trigonalis–Laeviuscula Subzones, Sadki *et al.* 2015) are represented by a sequence of blue-green (yellowish, if weathered) bioarenitic limestone alternated with green-brown marl. This unit is followed by the *Calcaire de Haut-Pont* (Propinquans Zone), a crinoidal limestone, and the *Calcaire d'Audun-le-Tiche* (Humphriesianum Zone), a bioclastic limestone with associated reefal facies corresponding to the *Calcaire à polypiers inférieur* of the French Lorraine. The sequence continues with the *Marnes d'Audun-le-Tiche*, represented by an alternation of silty limestones and marls rich in cephalopod remains (Weis 2006), and ends with the limestones of the *Calcaire de Nondkeil* (both Humphriesianum Zone). Based on the sequence stratigraphic analysis proposed by Brigaud *et al.* (2014), the described succession would indicate a change in sedimentary environment from lower offshore (*Marnes micacées*) to upper offshore-shoreface (*Calcaire d'Audun-le-Tiche*) conditions.

Material and methods

The present study is based on the extensive collection (about 600 specimens) of Early Bajocian gastropods of the Musée national d'histoire naturelle du Luxembourg, Grand-Duchy of Luxembourg. The collection was gathered through the decades-long research effort of the museum staff. Almost all the material here described was recovered from the *Conglomérat à Sonninia* beds exposed in two large abandoned iron ore open-pit named "Giele Botter" (also referred as "Prënzebierg") and "Rollesbierg", respectively north and south of Differdange, south-western Luxembourg. A few specimens come from the same levels cropping out near Longwy, north-eastern France, and from the *Calcaire d'Audun-le-Tiche* exposed in the large Ottange-Rumelange quarry located across the France-Luxembourg border (Fayard *et al.* 2005). For comparative purposes the following collections have also been examined: type material of Goldfuss (1844), Sieberer (1907) and Kuhn (1936) in the Bayerische Staatssammlung für Paläontologie und Geologie, Munich (Germany); type material of Riche (1904), Riche & Roman (1921), Roman (1935) and Marzloff *et al*. (1936) in the Collections de géologie of the Université Claude Bernard Lyon 1, Lyon (France); collections of the Palaeontological Museum of the University 'La Sapienza', Rome (Italy). The on-line catalogues of type specimens of the Muséum national d’Histoire naturelle de Paris (France) (https://science.mnhn.fr) and of the British collections of the GB3D Type Fossils Online project (United Kingdom) (http://www.3d-fossils.ac.uk) have also been accessed.

The most representative specimens have been measured and illustrated. Measurements are listed in Online Supplemental Material Tables S1 and S2. The abbreviations for the dimensions and their explanations are reported in Fig. 2. Most of the morphological terms used in the systematic descriptions follows Cox (1960a). The stratigraphic scheme for the Jurassic is that of Ogg & Hinnov (2012).

The palaeogeographical relationship of the Lower Bajocian vetigastropod and neritimorph fauna of Luxembourg with other faunas of the western European shelf has been investigated by multivariate analysis of a comprehensive presence-absence, species-level dataset compiled from the revision of relevant literature and personal observations (see final section for details). A Q-mode cluster analysis has been performed with PAST 3.12 software (Hammer *et al*. 2001; Hammer 2016) applying the unweighted pair-group method using arithmetic average (UPGMA) and based on Simpson, Dice and Jaccard similarity coefficients.

Institutional abbreviations

MNHNL: Musée national d'histoire naturelle du Luxembourg; **BSPG**: Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **UCBL**: Collections de géologie, Université Claude Bernard Lyon 1, Lyon, France; **ANSP**: Invertebrate Paleontology Collection, Academy of Natural Sciences of Philadelphia, Pennsylvania, USA.

Systematic palaeontology

Subclass **Vetigastropoda** Salvini-Plawen, 1980

Suborder **Pleurotomariina** Cox & Knight, 1960

Superfamily **Pleurotomarioidea** Swainson, 1840

Family **Pleurotomariidae** Swainson, 1840

Genus ***Bathrotomaria*** Cox, 1956

Type species. *Trochus reticulatus* Sowerby, 1821, Kimmeridgian, Dorset (England), by original designation.

Bathrotomaria subreticulata (d'Orbigny, 1850)

(Fig. 3A–V)

1849 *Pleurotomaria reticulata* Eudes-Deslongchamps: 64, pl. 9, fig. 3a–c.

* 1850 *Pleurotomaria subreticulata* d'Orbigny: 268.

1856 *Pleurotomaria subreticulata* d'Orb.; d'Orbigny: 494, pl. 392, figs 1–5.

1873 *Pleurotomaria subreticulata* d'Orbigny; Tawney: 46, pl. 3, fig. 7.

1895 *Pleurotomaria subreticulata* d'Orbigny; Hudleston: 422, pl. 36, figs 6, 7.

1907 *Pleurotomaria subornata* Goldfuss; Sieberer: 48, text-fig. 19, pl. 3, fig. 2a, b.

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

1938 *Pleurotomaria subornata* var. *adoxa* Sieberer; Kuhn: 150, pl. 5, fig.11.

1990 *Bathrotomaria subornata* (Goldfuss); Kästle: 89, pl. 12, fig. 5 (erroneously reported as fig. 6 in text and plate explanation).

1997 *Bathrotomaria reticulata* (Eudes-Deslongchamps); Fischer & Weber: 186, pl. 33, fig. 3a–b.

pars 2003 *Bathrotomaria subornata* (Münster in Goldfuss); Gründel: 53, pl. 3, figs 8–9, non figs 4–7.

2012 *Bathrotomaria subornata* (Münster in Goldfuss); Gründel *et al*.: 10, pl. 2, figs 5–10.

Material. 106 specimens. Rollesbierg: MNHNL BU103, MNHNL BU111, MNHNL BU131, MNHNL BU137A1, MNHNL BU137A2, MNHNL RB005C1, MNHNL RB005C2, MNHNL RB008A, MNHNL RB034A, MNHNL RB038, MNHNL RB046A, MNHNL RB049, MNHNL RB059, MNHNL RB065D, MNHNL RB105A, MNHNL RB108, MNHNL RB117, MNHNL RB119A, MNHNL RB132A, MNHNL RB178A, MNHNL RB181A, MNHNL RB181B, MNHNL RB189A, MNHNL RB203A1, MNHNL B203A2, MNHNL RB305B, MNHNL RB311D, MNHNL RB312A, MNHNL RB312B, MNHNL RB313A1, MNHNL B313A2, MNHNL RB317, MNHNL RB348A, MNHNL RB350A, MNHNL RB376D1–RB376D12, MNHNL RB376I, MNHNL RB384, MNHNL ZS102B, MNHNL ZS150C, MNHNL ZS175A, MNHNL ZS176B, MNHNL ZS588A, MNHNL ZS588B. Giele Botter: MNHNL BU164A, MNHNL BU164B, MNHNL MDB163A, MNHNL MDB246A, MNHNL MDB246B, MNHNL MDB336A, MNHNL ZS167B, MNHNL ZS252, MNHNL ZS274B, MNHNL ZS255A, MNHNL ZS297A, MNHNL ZS309B, MNHNL ZS312, MNHNL ZS313, MNHNL ZS368B, MNHNL ZS396B, MNHNL ZS412A, MNHNL ZS419B, MNHNL ZS531, MNHNL ZS589A, MNHNL ZS607, MNHNL ZS630A. Differdange area: MNHNL BU185A, MNHNL MDB164, MNHNL MDB220, MNHNL MDB229, MNHNL

MDB238, MNHNL MDB249H1–MDB249H4, MNHNL MDB250, MNHNL MDB260A, MNHNL MDB260B, MNHNL MDB276, MNHNL MDB308B, MNHNL MDB321B, MNHNL MDB330, MNHNL RB272B, MNHNL ZS152B, MNHNL ZS154, MNHNL ZS189A, MNHNL ZS254A1, MNHNL ZS254A2, MNHNL ZS391A, MNHNL ZS425A, MNHNL ZS494G, MNHNL ZS494H, MNHNL ZS494K, MNHNL ZS494T, MNHNL ZS522B, MNHNL ZS525. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S1.

Description. The shell is trochiform and composed of about seven whorls. The outline of the spire is conoidal to strongly cyrtoconoidal. The early whorls are almost rounded and separated by an impressed suture. They have a very narrow, convex ramp and almost flat outer face. Later whorls have an obtuse angulation separating a steep, flat to feebly convex ramp from a slightly narrower, almost flat outer face. The outer face is delimited abapically by a roundedly angular periphery. The periphery is barely covered by suture on early and subadult whorls, partially or totally exposed on later whorls. The selenizone is narrow and concave on early whorls. It runs below ramp and is marked by prominent and rather spaced lunulae. During the growth, the selenizone moves to the upper angulation and a central spiral thread appears on it; sometimes one, rarely two, further threads appear in addition to the first one. These threads thicken progressively, making the selenizone a sharply delimited, prominent, rounded cord. The base is slightly flattened, with surface faintly convex, anomphalous. The aperture is rhomboidal, rounded at peripheral angulation. The parietal lip is covered by a thin shelly film. The inner lip is sub-vertical, reinforced by a moderately strong callus and slightly reflected towards axis. The basal lip is subhorizontal and sharp. The slit is slightly less than one-fourth of last whorl deep.

The ornamentation of the early whorls is regularly reticulate, resulting from the crossing of several sharp, spiral threads (three on the ramp and three to four on the outer face) and equally sharp collabral threads; the threads bear small granules at the intersections. Four to six spiral threads run also on the peripheral angulation. During the growth, the spiral threads strengthen and increase in number on the ramp (up to eight), and the collabral threads become sharp riblets. Secondary collabral riblets appear between them making the pattern more dense and irregular. The spiral threads tend to predominate on the fully adult part of the shell and the collabral riblets become strong and packed growth striae making sharp wrinkles on the shell surface. Granules at the intersection between the spiral and collabral elements are present on the whole shell surface except the base. The base is sculptured with thin spiral threads separated by interspaces as wide as the threads thickness; the threads are slightly more robust on the adaxial region. Thin collabral threads cross the spiral ones, making them granulate and composing a fine reticulate pattern. The growth striae are prosocline and prosocyrt on the ramp, opisthocline and prosocyrt below the selenizone; on the base they are widely opisthocyrt, becoming prosocyrt on the adaxial region.

Remarks. The species is highly variable, especially in the incremental angle of the fully adult part of the shell. Consequently, the shape of the shell ranges from conoidal to almost pupiform. The angulation of the whorl bearing the selenizone may appear at different growth stages and be more or less distinct, making the shells obtusely to definitely gradate. The selenizone of the fully adult part of the shell is variably prominent and sharp. Its median lira appears at slightly different stages during the early growth and in some specimens it persists up to the last growth stage. In other specimens it loses definition and disappears, while the selenizone becomes gradually more prominent and strongly wrinkled by the growth striae. In the fully adult part of some shells the median lira is flanked by a lower spiral thread which increases in strength during the growth and confers a bisected aspect to the selenizone. One specimen shows a cord-shaped selenizone with three, partly amalgamated spiral threads (Fig. 3U). The variation of the sculpture mainly affects the rate of ontogenetic change and the strength of the ornament elements. The early shell is always ornamented by a sharp and regular network of spiral and collabral threads, whereas this network is slightly irregular to rough on the fully adult part of the shell, with variably prominent granules at the intersection points. Commonly, on the last whorls the collabral threads are denser and irregularly sized, and the spiral ornament becomes dominant over the collabral one. The rate at which these changes appear during the growth is somewhat variable among individuals.

D’Orbigny (1850) recognized the secondary homonymy between *Pleurotomaria reticulata* Eudes-Deslongchamps, 1849 and *Pleurotomaria reticulata* (Sowerby, 1821) (= *Trochus reticulatus*) (Sowerby 1821, p. 128, pl. 272, fig. 2; Woodward 1885, p. 437, pl. 9, fig. 2; Cox 1960b, p. I219, fig. 131,3) a Kimmeridgian species from England. Thus, he renamed the first taxon as *Pleurotomaria subreticulata*. Fischer & Weber (1997, p. 186) reintroduced Eudes-Deslongchamps's name, claiming that *T. reticulatus* Sowerby does not belong either to *Pleurotomaria* Defrance, 1826 or to *Bathrotomaria* Cox, 1956. However, there is no doubt that *T. reticulatus* belongs to *Bathrotomaria* since it is its type species by original designation (Cox 1956). Moreover, Eudes-Deslongchamps's name is permanently invalid being a secondary homonym replaced before 1961 and with a substitute name in use (ICZN 1999, art. 59.3). More recently, Das *et al.* (2005) regarded *B. subreticulata* as a synonym of Sowerby's *T. reticulatus* apparently on the wrong assumption that Fischer & Weber (1997) had synonymized the two taxa.

The high variability of *Bathrotomaria subreticulata* (d'Orbigny, 1850) was already implied by Hudleston (1895), who tentatively assigned to the species a specimen with a "wider spiral angle and less bicarinate whorls" (Hudleston 1895, pl. 36, fig. 7). Specimens with this morphology are rather common in the material described here.

Fischer & Weber (1997) suggested that this species might be a junior synonym of *Bathrotomaria scrobinula* (Eudes-Deslongchamps, 1849) (p. 60, pl. 9, fig. 4a–c; Fischer & Weber 1997, p. 186, 189, 190, pl. 33, figs 5–8), but they could not ascertain this relationship due to the scarcity of material at their disposition. The rich material from Luxembourg here described indicates that *B. subreticulata* is a distinct species, albeit highly variable. As already observed by Fischer & Weber (1997), it differs from *B. scrobinula* in that it has constantly much smaller size (almost one third), less acute spire angle, less gradate shell due to a more convex ramp, and collabral ornament persisting, even if attenuate, on the last whorls.

Gründel (2003) dubitatively placed *B. subreticulata* (as *P. reticulata* Eudes-Deslongchamps) in the synonymy of *Bathrotomaria subornata* (Münster in Goldfuss, 1844) (p. 74, pl. 186, fig. 5). The direct examination of the figured type of *B. subornata* (BSPG AS VII 1466) from the Middle Jurassic of Thurnau (Franconia, southern Germany) excludes this relationship. Münster's taxon differs from *B. subreticulata* in several characters. The shape is low-trochiform, almost subdiscoidal, the selenizone is placed on outer face and the spiral threads of the sutural ramp are thicker than those of the outer face.

The material from the Bajocian of Nievre (France) ascribed by Cossmann (1919) to *Pleurotomaria* (*Leptomaria*) *amyntas* d'Orbigny, 1850 is very close to the more conoidal specimens of *B. subreticulata* and is here dubitatively included in the synonymy of the last species. Das *et al.* *(*2005) described as *B. reticulata* (Sowerby) some specimens from the Upper Bathonian of Kutch (India) that by might also be referred to *B. subreticulata*.

Distribution of the species. Upper Lower Bajocian and Upper Bajocian, Dorset (south-western England); undifferentiated Aalenian–Bajocian, Somerset (south-western England); Lower Bajocian, Lincolnshire (eastern England); upper Lower Bajocian and Upper Bajocian, Calvados (northern France); undifferentiated Bajocian, Nievre (central France); Lower Bajocian, south-western Luxembourg; Lower Bajocian, Baden-Württemberg (southern Germany); uppermost Lower Bajocian–Upper Bajocian, Franconia (southern Germany).

Genus ***Szabotomaria*** gen. nov.

Type *species*. *Pleurotomaria ziqquratiformis* sp. nov. (see below). Lower Bajocian, south-western Luxembourg.

Diagnosis. Shell trochiform to subconoidal. Early spire markedly gradate, subtelescopical in outline, with narrow and subhorizontal ramp and slightly bulged shoulder. Ramp becoming wider and oblique on fully adult whorls and shoulder gradually attenuating or vanishing. Selenizone moderately wide, running below shoulder, almost at middle of outer face, concave on early whorls and convex on fully adult whorls. Base phaneromphalous, with convex to slightly funnel-shaped axial region. Inner lip provided with strong callus. Slit somewhat short. Ornamentation reticulate on early whorls, mainly spiral on adult whorls.

Derivation of name. Dedicated to János Szabó, palaeontologist of the Department of Geology and Palaeontology, National Natural History Museum of Budapest (Hungary).

Description. The shell is medium-sized, trochiform to subconoidal and composed of about seven whorls. The height of the last whorl is one-half to more than two-thirds of the shell height. The early spire is markedly gradate due to the presence of a narrow, subhorizontal ramp and a vertical to slightly inclined outer face. The ramp is narrowly concave and its outer shoulder is slightly bulged. The suture is distinctly incised. The outer face is concave to flat. On the fully adult whorls the ramp becomes slightly convex to flat and variably inclined. The shoulder gradually attenuates or becomes very obtuse. It vanishes on the last whorl, so that the whorl becomes flat to convex and the suture almost flush. The selenizone of the early shell is moderately wide, concave and runs just below the angulation of the whorls. It is edged by spiral threads and ornamented by sharp and evenly spaced lunulae. During the growth, the selenizone shifts towards the middle of the outer face. On the fully adult shell, it becomes feebly convex to slightly cord-like and is placed at or slightly below the mid-line of the whorl. The periphery is roundedly angulated to distinctly bulged. The base is somewhat flat to slightly swollen, phaneromphalous and with convex to slightly funnel-shaped axial region. The umbilicus is quite narrow to moderately wide. The periumbilical margin is rounded. The aperture is subpentagonal to trapezoidal. The peristome is moderately prosocline and subangulated at the periphery of the outer lip. The parietal lip is covered by a thin shelly film. The inner lip is almost vertical to slightly inclined and provided by a variably strong callus which is bordered by a sharp outer rim. The junction between the inner lip and the basal lip can be angulated or smoothly arched. The slit is moderately wide and short, being extended from one-sixth to one-eighth of the last whorl. The early shell is ornamented by a sharp and regular network of evenly spaced and sized collabral riblets and thin spiral threads. On the surface of the adult whorls the collabral riblets become thinner and indistinguishable from the growth lines. In contrast, the spiral threads increase in number and size so that the last whorls are ornamented only by spiral elements. These are quite variable in size and strength both at inter- and intraspecific level. The selenizone of the earliest whorls is ornamented only by sharp lunulae. Subsequently, a median lira appears that becomes stronger during the growth and contributes to make the selenizone slightly convex. On the last whorls the lunulae fade out and only dense and marked growth lines cross the selenizone. The base is ornamented by obscure to distinct spiral threads that sometimes weaken or disappear in the adaxial band. The growth striae are prosocline and weakly prosocyrt above the selenizone, prosocyrt below it. The base bears widely sinuous growth striae, that are opisthocyrt on its abaxial half and prosocyrt on its adaxial half.

Remarks. *Szabotomaria* gen. nov. is reminiscent of *Anodomaria* Szabó, 1980 especially in the gradate, subtelescopical early spire and in the position of the selenizone on the outer face. However, in *Anodomaria* the shell is higher, the ramp is steeper and persists on the fully adult shell. Moreover, on the last whorls the selenizone is concave and the ornament is reticulate. The selenizone on the outer face is a character that the new genus shares also with *Pleurotomaria* Defrance, 1826. The latter is readily distinguished by the presence of tubercles on the whorls shoulder. It also has a more convex base, a wider ramp and a noticeably better defined shoulder (see Monari & Gatto 2013 for further details).

The new genus bears a superficial resemblance also with other Jurassic pleurotomariids, namely *Bathrotomaria* Cox, 1956, *Leptomaria* Eudes-Deslongchamps, 1864 and *Laevitomaria* Conti & Szabó, 1987. *Bathrotomaria* differs from *Szabotomaria* in that the selenizone is placed on the angulation of the whorls, although in *Szabotomaria* a very obtuse angulation at the selenizone appears occasionally on the final part of the last whorl. *Leptomaria*, as defined by Monari & Gatto (2014), has a much narrower selenizone and deeper slit, and the whorls lack a distinct ramp. In *Laevitomaria*, the spire is higher, the periphery is sharper and the ramp is absent (Gatto *et al.* 2015b).

Included species and distribution. The genus is distributed from Pliensbachian to Lower Bajocian of France, Luxembourg, England and Germany. It includes the following species, in stratigraphical order:

Pleurotomaria subdecorata Münster in Goldfuss, 1844 (p. 71, pl. 185, fig. 3a, b, figured syntype BSPG AS VII 1455; Kuhn 1936, p. 274, pl. 8, fig. 15, non pl. 9, fig. 18 and pl. 13, fig. 16? =

Costataphrus sp. 1, according to Gründel 2014a). Upper Pliensbachian, Franconia (southern Germany). Sieberer (1907, p. 21) reported the species without illustrations from the Upper Toarcian of Baden-Württemberg (southern Germany). The species is also recorded, but not illustrated, by Dumortier (1869) from the Lower Pliensbachian deposits of Ain (France).

Pleurotomaria subornata Münster in Goldfuss, 1844 (p. 74, pl. 186, fig. 5, figured syntype BSPG AS VII 1466). Middle Jurassic, Franconia (southern Germany).

Pleurotomaria subtilis Münster in Goldfuss, 1844 (p. 71, pl. 185, fig. 4; Kuhn 1935, p. 129, pl. 9, fig. 27, pl. 10, figs 15, 41, figured type BSPG 1936 Vi 24). Lower Aalenian, Franconia (southern Germany).

Pleurotomaria depereti Riche, 1904 (p. 124, pl. 3, figs 6a–c; fig. 6a is erroneously labelled as 7, *fide* Riche 1904, p. 253, figured syntypes UCBL 26889–91). Upper Aalenian, Mont d'Or Lyonnais (Rhone, France).

Pleurotomaria araris Riche, 1904 (p. 122, pl. 3, fig. 5, figured syntype UCBL 26888). Upper Aalenian, Mont d'Or Lyonnais (Rhone, France).

Pleurotomaria vaffieri Riche, 1904 (p. 126, pl. 3, fig. 8, figured syntype UCBL 26904). Upper Aalenian, Mont d'Or Lyonnais (Rhone, France).

Pleurotomaria ziqquratiformis sp. nov. (type species, see below). Lower Bajocian, south-western Luxembourg.

Szabotomaria ziqquratiformis sp. nov.

(Fig. 4A–X)

Diagnosis. Shell medium-sized, conoidal-trochiform. Ramp distinct and horizontal on early spire, disappearing on last whorls. Base somewhat flat and slightly funnel shaped in axial region. Umbilicus narrow. Periphery rounded to slightly bulged. Collabral ornament vanishing on last whorls. Fully adult part of the shell and base ornamented by variably sized, numerous spiral threads or cords.

Derivation of name. Referred to the shape of the shell that reminds a *ziqqurat*, the ancient Mesopotamian religious stepped pyramid.

Holotype. MNHNL BU122, Rollesbierg, Fig. 4E–H.

Type locality. Rollesbierg (Differdange, south-western Luxembourg).

Type level. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone),

Paratypes. Rollesbierg: MNHNL RB245B, MNHNL RB255. Giele Botter: MNHNL ZS367. Differdange area: MNHNL MDB230, MNHNL MDB255, MNHNL ZS494S2. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Other Material. 19 specimens. Rollesbierg: MNHNL BU122, MNHNL MDB161, MNHNL RB033A, MNHNL RB128, MNHNL RB171A, MNHNL RB171B, MNHNL RB181C, MNHNL RB190, MNHNL RB245A, MNHNL RB311E, MNHNL ZS101C, MNHNL ZS403. Giele Botter: MNHNL ZS162 MNHNL ZS309A. Differdange area: MNHNL MDB305B, MNHNL MDB347, MNHNL ZS586, MNHNL ZS587, MNHNL ZS590A, MNHNL ZS590B. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S1.

Description. The shell is conoidal-trochiform and composed of six to seven whorls. The early whorls are provided with an almost horizontal, narrow ramp and a slightly concave outer face giving to the spire a markedly gradate, subtelescopical outline. The ramp attenuates during the growth and the whorl becomes flat to convex and rather steeply inclined. The suture is deep on early whorls, almost flush on adult whorls. In some specimens, the final half of the last whorl becomes slightly angulated at the selenizone and feebly concave above the selenizone. The selenizone of the early shell is placed almost on the mid-line of the outer face. It is moderately wide, concave, edged by sharp spiral threads and ornamented by prominent and evenly spaced lunulae. During the growth the selenizone becomes flat and a median lira appears almost at the transition between the second and the third teleoconch whorls. On the fully adult shell the median lira and the lunulae fade out whereas the selenizone becomes feebly convex to cord-like and is crossed only by dense and marked growth lines. The periphery is distinctly rounded to very slightly bulged. The base is flat, variably depressed and tends to become funnel-shaped on its axial region. The umbilicus is narrow. The aperture is low and asymmetrically subpentagonal. The peristome is prosocline, subangulated at the periphery of the outer lip and obtusely angulated at the junction of the inner lip with the basal lip. The parietal lip has a thin shelly covering. The inner lip is strongly thickened by a callus which is delimited by a sharp and evident outer rim and becomes thinner passing into the basal lip. The slit is moderately wide and extended about one-eighth of the last whorl from the termination of the suture.

The ornamentation of the early shell consists of a regular network of collabral riblets and spiral threads. The collabral riblets are sharp, evenly spaced and sized. The spiral threads are also sharp and thin. About four spiral threads run above the selenizone and two spiral threads below it. During the growth, the spiral threads increase in number by intercalation. They become wider whereas the interspaces become narrower. The bands immediately above and below the selenizone commonly bear spiral threads thinner and sharper than the others. On the ramp of the adult shell, the collabral riblets are wider, irregularly distributed and vanish before reaching the selenizone. They can make small and sharp granulae at the intersection with the spiral threads. On the last whorls the collabral ornament disappears. The last whorl is ornamented by about 12, variably sized spiral threads separated by thin interspaces. The ornament of the base is composed of evenly spaced and sized spiral threads. On the adult spire and on the base, marked growth striae make the ornament slightly rough. They can form irregular and weak wrinkles especially on the periumbilical margin. The growth striae are slightly prosocline and prosocyrt above the selenizone, orthocline and prosocyrt below it. They are opisthocyrt on the abaxial half of the base, prosocyrt on its adaxial half and straight on the umbilical wall.

Remarks. The species is rather variable, mainly in the rate of ontogenetic changes affecting shell shape, ornament and details of the selenizone. A narrow ramp is always present in the juvenile shell but is variably persistent during the adult growth. The outline of the adult whorls above the selenizone varies from convex to almost flat. Consequently, the shape of the shell ranges from subtrochiform to conoidal. The angulation which sometimes appears at the selenizone on the final part of the last whorl is occasionally rather strong and accompanied by a moderately marked concavity of the adapical whorl surface. The adult selenizone varies from slightly convex to cord-shaped. The axial concavity of the base, though always distinguishable, can be more or less marked. The collabral riblets on the ramp and the granulae at the intersection with the spiral threads vary in size and persistence during the growth. Some adult shells lack spiral elements immediately above and below the selenizone so that the selenizone runs within a smooth band, which makes the selenizone more evident.

Szabotomaria depereti (Riche, 1904), from the Upper Aalenian of the Rhone Basin (southern France) is the species most similar to *Szabotomaria ziqquratiformis* sp. nov. It differs in being smaller, more cyrtoconoidal and with a wider spire angle, and in having a higher last whorl and a more convex base. The slit is twice as deep as in the new species and the inner lip less stout.

Szabotomaria subdecorata (Münster in Goldfuss, 1844) (p. 71, pl. 185, figs 3a, b; Kuhn 1936, p. 274, pl. 8 fig. 15) from the Upper Pliensbachian of Franconia (southern Germany) has a more acute early spire, and a distinctly more convex and higher base. The ramp of the early whorls becomes wider and somewhat inclined during the growth, so that it forms an obtuse angulation on the last whorls. In contrast, in *S. ziqquratiformis* the ramp disappears on the fully adult shell. The specimen assigned by Tawney (1873, p. 44) and Hudleston (1895, p. 421, pl. 36, fig. 10) to *Pleurotomaria subdecorata* Münster in Goldfuss, 1844, from the lower Middle Jurassic of England, and the shell from the Upper Aalenian of Rhone (southern France) ascribed to the same species by Riche (1904, p. 125, pl. 3, fig. 7, erroneously labelled 6a, see errata corrige in Riche 1904, p. 253, specimen UCBL 26900) might belong instead to *S. ziqquratiformis*. The specimen from England has more rounded adult whorls and its umbilicus seems wider than in *S. ziqquratiformis*. Riche's specimen has a more prominent peripheral bulge.

Distribution of the species. Lower Bajocian, south-western Luxembourg.

Genus ***Obornella*** Cox, 1959

Type species. *Pleurotomaria plicopunctata* Eudes-Deslongchamps, 1849, Bajocian, Calvados (northern France), by original designation.

Obornella granulata (Sowerby, 1818)
(Fig. 5A–G)

pars* 1818 *Trochus granulatus* Sowerby: 37, pl. 220, fig. 2 (left).
1849 *Pleurotomaria granulata* var. c *reticulata*, Eudes-Deslongchamps: 101, pl. 16, fig. 6a–c.
1895 *Pleurotomaria granulata* Sowerby; Hudleston: 440, pl. 39, fig. 10a–c, pl. 40, fig. 1, 1a.
1907 *Pleurotomaria granulata* Sowerby; Sieberer: 42, pl. 3, fig. 4a, b.
1997 *Obornella granulata* (Sowerby); Fischer & Weber: 177, pl. 37, fig. 2–4.
2003 *Obornella granulata* (Sowerby); Hägele: 116, fig. 11C.

Material. BU229. Piedmont (Longwy, Meurthe-et-Moselle, Lorraine, north-eastern France), Lower Bajocian.

Measurements. See Online Supplemental Material Table S1.

Description. The shell is medium-sized, trochiform-lenticular, with slightly coeloconoidal spire. The teleoconch is composed of about six whorls. The apical spire is slightly coeloconoidal and subgradate in outline and formed by definitely convex whorls. During the growth the whorl becomes obtusely angulated, with a wide and flat ramp and a narrow outer face. The selenizone is placed at the abapical edge of the ramp. On the early teleoconch it corresponds to a sharp spiral cord bearing subnodose lunulae. On the fully adult shell it becomes a prominent bulge crossed by strong and packed growth striae. The periphery is swollen and partly covered by the suture on the spire, becoming almost completely exposed on the final half of the penultimate whorl. The base is strongly convex and swollen, with a moderately wide umbilicus. The aperture is not preserved.
The ornamentation consists of spiral threads and collabral riblets. The spiral threads are five to six on the first preserved whorls and increase in number to about ten on the last whorls. They are crossed by dense collabral riblets which make low nodes at the intersection points. The outer face and the periphery are sculptured by some cord-like spiral threads bearing nodes by intersection with collabral riblets. These riblets slightly extend to the base disappearing on its peripheral band. On the final part of the last whorl the spiral threads of the ramp tend to disappear and the collabral riblets become dense wrinkles. The peripheral band of the base is ornamented by few weak and wide spiral threads. The growth striae are prosocline and prosocyrt on the surface of the whorls, orthocline and strongly prosocyrt on the periphery. On the base the growth striae form dense, widely opisthocyrt wrinkles that revert to prosocyrt towards the umbilical region.

Remarks. Fischer & Weber (1997) and Hägele (2003) reported a detailed history of how *Obornella granulata* (Sowerby, 1818) was interpreted by previous authors. In synthesis, Eudes-Deslongchamps (1849) recognized five varieties of *Pleurotomaria granulata* Sowerby, 1818, namely *reticulata*, *plicopunctata*, *coelata*, *lentiformis* and *laevigata*. Subsequently, d'Orbigny (1850, 1855) maintained that Sowerby's species includes only the varieties *reticulata*, *plicopunctata* and *coelata* and instituted *Pleurotomaria palemon* d'Orbigny, 1850 based on the varieties *lentiformis* and *laevigata*. Hudleston (1895) raised the variety *plicopunctata* to specific rank and instituted two other species, *Pleurotomaria phylax* Hudleston, 1895 and *Pleurotomaria trapezia* Hudleston, 1895, emphasizing their transitional features to *P. palemon*. In contrast, Sieberer (1907) adopted d'Orbigny's interpretation and distinguished three other varieties of *P. palemon*, namely *serpentina*, *suevica* and *wurttembergensis*. On the basis of an extensive analysis of numerous specimens, Fischer & Weber (1997) observed that the varieties identified by Eudes-Deslongchamps (1849) are connected by morphological continuity and concluded that they belong to the same highly variable species. Gründel (2003) substantially shared Fischer & Weber's (1997) opinion. Moreover, he included the variety *suevica* in the synonymy of *Obornella montreuilensis* (Hébert & Eudes-Deslongchamps, 1860). Jaitly *et al.* (2000) e Das *et al.* (2005) treated the variety *wurttembergensis* as a distinct species. Hägele (2003) proposed an interpretation diametrically opposite to that of Fischer & Weber (1997). He attributed the rank of distinct species to all the varieties of the previous authors and accepted the species erected by Hudleston (1895). The only specimen available prevents to take a position on this matter. For this reason the above synonymy list includes only citations concerning material morphologically close to the specimen described here, which is characterized by a relatively high spire, periphery not bulging the surface of the base, moderately open umbilicus, moderately marked ornament of the spire and comparatively obscure ornament of the base. The material figured by Hudleston (1895) is the most similar to the specimen described here.

Distribution of the species. Undifferentiated Aalenian-Bajocian, Somerset (south-western England); middle Lower Bajocian, Dorset (south-western England); Lower and Upper Bajocian, Calvados (northern France); Lower Bajocian, Longwy (Meurthe-et-Moselle, Lorraine, north-eastern France); upper Lower Bajocian to lower Upper Bajocian, (Baden-Württemberg, southern Germany).

Genus ***Pyrgotrochus*** Fischer, 1885

Type species. *Pleurotomaria bitorquata* Eudes-Deslongchamps, 1849, Upper Pliensbachian, Calvados (northern France) (*fide* Fischer & Weber, 1997), by monotypy.

Pyrgotrochus punctatus (Sowerby, 1818)

(Fig 6A–Z)

* 1818 *Trochus punctatus* Sowerby: 211, pl. 193, fig. 1.

v non 1844 *Pleurotomaria punctata* Sow.; Goldfuss: 74, pl. 186, fig. 6.

1850 *Pleurotomaria punctata* Sow.; d'Orbigny: 267.

1856 *Pleurotomaria punctata* d'Orb.; d'Orbigny: 513, pl. 399, figs 11–13.

non 1858 *Pleurotomaria punctata* Sowerby; Quenstedt: 415, pl. 57, fig. 8.

1874 *Pleurotomaria geometrica* Dumortier: 286, pl. 59, fig. 8–9.

1895 *Pleurotomaria punctata* Sowerby; Hudleston: 396, pl. 33, figs 1, 2.

v 1904 *Pleurotomaria sub-Grasi* Riche: 118, pl. 3, fig. 1.

v 1904 *Pleurotomaria subgeometrica* Riche: 120, pl. 3, fig. 3a, b.

1904 *Pleurotomaria punctata* Sow.; Riche: 121, pl. 3, fig. 4.

non 1907 *Pleurotomaria punctata* Sowerby; Sieberer: 36, pl. 2, fig. 9.

v 1921 *Pleurotomaria subgeometrica* Riche; Roman in Riche & Roman: 110, pl. 4, fig. 10.

v 1921 *Pleurotomaria sub-Grasi* Riche; Roman in Riche & Roman: 110, pl. 4, figs 11, 11a, 12.

1997 *Pyrgotrochus punctatus* (Sowerby); Fischer & Weber: 192, pl. 34, fig. 15.

non 2012 *Leptomaria punctata* (Sowerby); Gründel *et al*.: 12, pl. 2, figs 11–15, pl. 3, figs 1–5.

Material. 35 specimens. Rollesbierg: MNHNL BU120A, MNHNL BU120B, MNHNL MDB248, MNHNL RB421A, MNHNL RB106, MNHNL RB018B, MNHNL RB168, MNHNL RB226A, MNHNL RB226B, MNHNL RB291, MNHNL RB298, MNHNL RB311F, MNHNL RB353, MNHNL ZS163, MNHNL ZS174, MNHNL ZS175B, MNHNL ZS179, MNHNL ZS259. Giele Botter: MNHNL ZS168A, MNHNL ZS204, MNHNL ZS233A, MNHNL ZS258, MNHNL ZS291, MNHNL ZS299B, MNHNL ZS380, MNHNL ZS624. Differdange area: MNHNL MDB156, MNHNL MDB162, MNHNL MDB206, MNHNL MDB208, MNHNL MDB218, MNHNL MDB223, MNHNL MDB305C, MNHNL ZS321C, MNHNL ZS510. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S1.

Description. The shell is conoidal and composed of about 12, low whorls. The early spire is conoidal to slightly coeloconoidal. The fully adult part of the shell is conoidal to feebly cyrtoconoidal, The whorls are almost flat. The periphery is somewhat sharp and the suture runs next to it. The periphery is weakly prominent on the early spire, indistinct to slightly prominent on the fully adult part of the shell. The suture is flush and easily recognizable only on specimens with a prominent periphery. The selenizone is moderately wide and runs slightly below the mid-line of the whorl. On the earliest spire, the selenizone is almost flat to slightly concave, bordered by sharp marginal threads and ornamented by strong, evenly and somewhat widely spaced lunulae. During the early growth, a median lira appears which makes the lunulae slightly scaly. On the adult part of the shell, a spiral thread appears above the median lira, or on both sides of it. These threads and the median lira increase in thickness forming a cord-like, variably prominent, spirally bi- or trisected selenizone, whereas the lunulae become less distinct. The base is anomphalous and flat, except for a widely concave axial region. The aperture is low, asymmetrically subquadrangular. The peristome is prosocline and with parietal lip covered by a thin shelly film. The columellar lip is short, subvertical on the subadult specimens, slightly arched and more inclined on the spire axis on the fully adult shell. It is provided with a robust callus which strengthens during the growth and is limited by a sharp, variably prominent, widely arched and opisthocyrt outer rim. The callus is abruptly interrupted at its lower end, before reaching the basal lip. Therein, it forms a prominent plica on its apertural side. The basal lip is almost orthogonal to the spire axis and joins the outer lip with a sharp peripheral angulation.

The ornament of the early-subadult spire is composed of a fine and regular network of sharp and thin spiral threads (two to four above the selenizone) and collabral threads bearing very small granules at their intersection. During the growth, the spiral threads increase in number and become irregularly thinner and variable in size. On the subadult whorls, about six spiral threads are present both above and below the selenizone, whereas the last whorls bear about twenty spiral threads above the selenizone and about ten below it. The collabral threads tend to persist on the subsutural and peripheral bands. On the remaining part of the surface they change in denser, strong striae which partly or fully granulate the spiral threads. The peripheral band is commonly ornamented by two or three spiral threads which are more marked than the others. The base is ornamented by spiral threads as strong as those of the spire, evenly spaced and sized. They sometimes attenuate on the axial part of the base. The growth striae are moderately prosocline and prosocyrt above the selenizone, feebly opisthocline and prosocyrt below the selenizone, opisthocyrt on the base and slightly prosocyrt on its axial region.

Remarks. The material shows a rather high variability. The outline of the adult shell is slightly variable and the spire angle ranges from 42° to 53°. The periphery is commonly indistinct, being marked only by thicker spiral threads. A slightly prominent, cord-like periphery is present only in few specimens. The morphology of the selenizone is highly variable. In most of the specimens the selenizone is convex and conspicuous on the adult shell, otherwise it is scarcely prominent and hardly distinguishable from the spiral ornaments. It can bear one to three, somewhat distinct to obscure spiral threads. The fully adult shell frequently shows a smooth, cord-like selenizone owing to the disappearance of its spiral ornament. The variation of the other sculptural elements concerns the distribution of the spiral threads, their alternation in size, the rate of attenuation of the granulae on the middle of the whorls during the growth, and their prominence on the subsutural and peripheral bands. The concavity of the axial region of the base is also more or less developed.

The morphological variability of *Pyrgotrochus punctatus* (Sowerby, 1818) resulting from the study of the rich material from Luxembourg suggests to consider *Pleurotomaria geometrica*

Dumortier, 1874 and *Pleurotomaria subgeometrica* Riche, 1904 as younger synonyms of Sowerby's species. The differences listed by Dumortier (1874), concerning the general shape of the shell and the height of the whorls are not sufficient to separate his species from *P. punctatus*. According to Riche (1904), *P. subgeometrica* has the selenizone ornamented by three spiral threads, whereas in *P. punctatus* the selenizone is smooth. However, as described above the selenizone sculpture is very variable and cannot be used alone as a distinctive character.

Distribution of the species. Middle Aalenian, Upper Aalenian and upper Lower Bajocian, Dorset (south-western England); undifferentiated Aalenian-Bajocian, Somerset (south-western England); undifferentiated Upper Toarcian-Middle Aalenian, Isère (southern France); Upper Aalenian, Mont d'Or Lyonnais and Ardeche (southern France); Lower Bajocian, south-western Luxembourg.

Pyrgotrochus elongatus (Sowerby, 1818)

(Fig: 7A–V)

* 1818 *Trochus elongatus* Sowerby: 211, pl. 193 fig. 2–4

1818 *Trochus abbreviatus* Sowerby: 212, pl. 193, fig. 5.

1831 *Pleurotomaria conoidea* Deshayes: 181, pl. 4, fig. 4.

1837 *Pleurotomaria conoidea* Desh.; Bronn: 387, pl. 21, fig. 1a, b.

1849 *Pleurotomaria mutabilis* Eudes-Deslongchamps: 104.

1849 *Pleurotomaria mutabilis* var. a *corrugata*, Eudes-Deslongchamps: 108, pl. 10, fig. 18a–c.

1849 *Pleurotomaria mutabilis* var. b *coelata*, Eudes-Deslongchamps: 109, pl. 10, fig. 17a, b.

1849 *Pleurotomaria mutabilis* var. c *abbreviata*, Eudes-Deslongchamps: 109, pl. 10, fig. 13a–c.

? 1849 *Pleurotomaria mutabilis* var. d *patula*, Eudes-Deslongchamps: 111, pl. 10, fig. 12a–c.

1849 *Pleurotomaria mutabilis* var. e *circumsulcata*, Eudes-Deslongchamps: 112, pl. 11, fig. 2a–c.

1849 *Pleurotomaria mutabilis* var. f *ambigua*, Eudes-Deslongchamps: 113, pl. 11, fig. 1a–c.

1849 *Pleurotomaria mutabilis* var. g *mutica*, Eudes-Deslongchamps: 113, pl. 10, fig. 14a–c.

1849 *Pleurotomaria mutabilis* var. h *elongata*, Eudes-Deslongchamps: 114, pl. 10, fig. 15a–c.

1849 *Pleurotomaria mutabilis* var. i *turrita*, Eudes-Deslongchamps: 115, pl. 10, fig. 16a–b.

1850 *Pleurotomaria conoidea* Desh.; d'Orbigny: 268.

1850 *Pleurotomaria subconoidea* d'Orb., d'Orbigny: 268.

1850 *Pleurotomaria Agatha* d'Orbigny: 268.

1850 *Pleurotomaria subelongata* d'Orbigny: 268.

1850 *Pleurotomaria mutabilis* d'Orb.; d'Orbigny: 269.

1853 *Pleurotomaria mutabilis* Eudes-Deslongchamps; Chapuis & Dewalque: 102, pl. 14, fig. 3.

? 1855 *Pleurotomaria Bessina* d'Orbigny: 460, pl. 376, figs 1–4.

1855 *Pleurotomaria circumsulcata* d'Orbigny: 470, pl. 381, figs 6–10.

1855 *Pleurotomaria conoidea* Deshayes; d'Orbigny: 472, pl. 382, figs 1–5.

1855 *Pleurotomaria Agatha* d'Orb.; d'Orbigny: 474, pl. 383, figs 1–3.

1855 *Pleurotomaria subelongata* d'Orb.; d'Orbigny: 477, pl. 383, figs 8–10.

1855 *Pleurotomaria mutabilis* Deslongch.; d'Orbigny: 479, pl. 384, figs 6–8.

1856 *Pleurotomaria Ebrayana* d'Orbigny: 483, pl. 387, figs 1–5.

1856 *Pleurotomaria Pictaviensis* d'Orbigny: 510, pl. 399, figs 1–5.

1858 *Pleurotomaria elongata* Sw.; Quenstedt: 385, pl. 52, fig. 3.

non 1858 *Pleurotomaria elongata* Sw.; Quenstedt: 415, pl. 57, fig. 10.

1874 *Pleurotomaria rhodanica* Dumortier: 288, pl. 59, figs 13–14.

1884 *Pleurotomaria conoidea* Deshayes; Quenstedt: 342, pl. 198, figs 22–25, ?27.

? 1884 *Pleurotomaria Bessina* D'Orbigny; Quenstedt: 343, pl. 198, fig. 26.

non 1884 *Pleurotomaria elongata* Sw.; Quenstedt: 349, pl. 198, fig. 42.

1895 *Pleurotomaria bicingulata* Hudleston: 398. pl. 33, fig. 3.

1895 *Pleurotomaria elongata* Sowerby; Hudleston: 399, pl. 33, figs 4–7, pl. 34, fig. 8.

1895 *Pleurotomaria abbreviata* Sowerby; Hudleston: 401, pl. 33, figs 8–9.

1895 *Pleurotomaria Agatha* d'Orbigny; Hudleston: 402, pl. 33, fig. 12a, b, pl. 34, fig. 6.

1895*Pleurotomaria circumsulcata* d'Orbigny; Hudleston: 404, pl. 33, figs 10–11, pl. 34, fig. 3.

1895 *Pleurotomaria obornensis* Hudleston: 404, pl. 34, fig. 9.

? 1895 *Pleurotomaria Bessina* d'Orbigny; Hudleston: 406, pl. 34, figs 4–5.

v 1904 *Pleurotomaria subrhodanica* Riche: 119, pl. 3, fig. 2a, b.

non 1907 *Pleurotomaria elongata* Sowerby; Sieberer: 34, pl. 2, fig. 14.

1907 *Pleurotomaria elongata* var. *conoidea* d'Orbigny; Sieberer: 35, pl. 2, figs 15.

? v 1907 *Pleurotomaria Bessina* d'Orbigny; Sieberer: 37, pl. 4, fig. 2.

v 1912 *Pleurotomaria elongata* Sow.; Roman & Gennevaux: 274, pl. 2, fig. 2.

v 1935 *Pleurotomaria subrhodanica* Riche; Roman: 34, pl. 5, fig. 3.

v 1935 *Pleurotomaria* cf. *ebrayi* (sic) d'Orbigny; Roman: 34, pl. 5, fig. 8.

? 1997 *Pyrgotrochus elongatus* (Sowerby) morphe *patulus*, Fischer & Weber: 174, pl. 35, figs 9–10, pl. 36, fig. 1.

1997 *Pyrgotrochus elongatus* (Sowerby) morphe *abbreviatus*, Fischer & Weber: 178, 180, 181, pl. 35, figs 5–8.

1997 *Pyrgotrochus elongatus* (Sowerby); Fischer & Weber: 179, 183, 192, pl. 35, figs 1, 3–4.

1997 *Pyrgotrochus elongatus* (Sowerby) morphe *turritus*, Fischer & Weber: 180, pl. 35, figs 2a, b.

v 2001 *Pyrgotrochus* cf. *elongatus* (Sowerby); Conti & Monari: 188, Fig. 5.2–3.

2003 *Pyrgotrochus elongatus* (Sowerby); Gründel: 52, pl. 3, figs 1–3, ? pl. 2, figs 11–14.

2010 *Pyrgotrochus elongata* (sic) (Sowerby); Lindström & Peel: 544, fig. 2C.

2010 *Pyrgotrochus* sp., Lindström & Peel: 544, fig. 2E, G.

2012 *Pyrgotrochus elongatus* (Sowerby); Gründel *et al*.: 12, pl. 3, figs 6–9.

Material. 122 specimens. Rollesbierg: MNHNL BU101A, MNHNL MDB155A, MNHNL MDB213, MNHNL RB009, MNHNL RB010, MNHNL RB016, MNHNL RB019, MNHNL RB034B, MNHNL RB036, MNHNL RB040, MNHNL RB041A, MNHNL RB041B, MNHNL RB048, MNHNL RB055A, MNHNL RB055B, MNHNL RB065A, MNHNL RB065B, MNHNL RB068B, MNHNL RB069B1–RB069B3, MNHNL RB095, MNHNL RB119B, MNHNL RB122A, MNHNL RB126, MNHNL RB127, MNHNL RB132B, MNHNL RB139, MNHNL RB150, MNHNL RB169, MNHNL RB189B, MNHNL RB193B, MNHNL RB203B1–RB203B6, MNHNL RB312C, MNHNL RB316, MNHNL RB350B, MNHNL RB354, MNHNL RB376G1–RB376G14, MNHNL RB388, MNHNL ZS102A, MNHNL ZS150D1, MNHNL ZS150D2, MNHNL ZS159, MNHNL ZS161A, MNHNL ZS172A, MNHNL ZS173A. Giele Botter: MNHNL RB244, MNHNL MDB278, MNHNL MDB396A, MNHNL MDB396B, MNHNL ZS623A, MNHNL ZS157, MNHNL ZS187A, MNHNL ZS187B, MNHNL ZS203A, MNHNL ZS219, MNHNL ZS224, MNHNL ZS230, MNHNL ZS233B, MNHNL ZS240, MNHNL ZS247A, MNHNL ZS253A, MNHNL ZS299A, MNHNL ZS320, MNHNL ZS322, MNHNL ZS333A, MNHNL ZS365B, MNHNL ZS424A, MNHNL ZS480, MNHNL ZS488A, MNHNL ZS626A. Differdange area: MNHNL BU172, MNHNL MDB159, MNHNL MDB202A, MNHNL MDB205, MNHNL MDB207, MNHNL MDB214, MNHNL MDB233, MNHNL MDB249D1, MNHNL MDB249D2, MNHNL MDB260D, MNHNL MDB263B, MNHNL MDB308A, MNHNL MDB321A, MNHNL MDB353, MNHNL MDB397A, MNHNL MDB397B, MNHNL ZS151, MNHNL ZS283, MNHNL ZS286, MNHNL ZS321A, MNHNL ZS321B, MNHNL ZS324, MNHNL ZS376, MNHNL ZS379, MNHNL ZS385, MNHNL ZS391B, MNHNL ZS425B, MNHNL ZS494A, MNHNL ZS494E,

MNHNL ZS494R, MNHNL ZS519R, MNHNL ZS522A, MNHNL ZS529. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is slightly cyrtoconoidal to moderately coeloconoidal. The spire is composed of about 12 low whorls. The apical shell is feebly cyrtoconoidal and formed by weakly convex whorls. During the earliest growth, the whorls become concave and their periphery prominent. The periphery is cord-like and not covered by the suture on the spire. The selenizone is placed almost in the middle of the abapical half of the whorl. On the early spire the selenizone is slightly incised, moderately wide, limited by strong and sharp threads, and ornamented by sharp and spaced lunulae. On the subadult spire, the selenizone becomes flat and bears a median lira which makes small scales at its intersection with the lunulae. The selenizone of the fully adult shell is somewhat wide, flat to convex or almost cord-like. It is commonly ornamented by a prominent and wide median lira with a sharp to obscure spiral thread on each side of it. The base is flat and anomphalous, with a feebly convex surface, sometimes very slightly concave in the axial region. The aperture is low and asymmetrically subquadrangular, quite strongly angulated at the termination of the periphery on the peristome. The parietal lip is covered by a very thin shelly film. The inner lip is short and somewhat arched. The columella has a strong callus which strengthens during the growth and ends abruptly before reaching the basal lip. The columellar callus extends on the axial region of the base as a smooth shelly coating. The outer rim of the callus is sharp, widely opisthocyrt and passes smoothly into the basal lip.

The surface of the early whorls above the selenizone is ornamented by two to three spiral threads, commonly placed towards the adapical suture. They intersect densely spaced growth threads making a network pattern. Quite strong and short collabral ribs cross the subsutural band and vanish before reaching the selenizone. They make moderately strong and somewhat regularly distributed granules on the spiral threads. The peripheral cord bears two to four spiral threads crossed by collabral riblets that are thinner than those of the subsutural region and make smaller granules at the intersection with the spiral ornament. During the adult growth, thin and irregular spiral threads appear above and below the selenizone, while the collabral ribs and the corresponding granules of the subsutural band attenuate and loose regularity. The spiral threads of the peripheral cord become weaker and tend to disappear on the last whorls, whereas the granules become fused to each other in collabral direction forming short, strong, densely and evenly spaced prosocyrt ribs. During the last growth stages these ribs can lose their regularity changing in dense growth striae and wrinkles that make the peripheral cord rough. The base of the juvenile shell is ornamented by numerous, thin, evenly spaced and sized spiral threads. On the adult shell they are thinner and more irregularly sized, especially on the axial and peripheral regions of the base. The growth striae are strongly prosocline and widely prosocyrt above the selenizone, feebly opisthocline and prosocyrt below it, opisthocyrt on the base and prosocyrt on its axial region.

Remarks. The rich material here described displays high intraspecific variability. The general shape of the adult shell is highly variable, ranging from slightly cyrtoconoidal to strongly coeloconoidal. The periphery is feebly prominent on the early shell, whereas on the adult shell it is moderately prominent to strongly projected. In some specimens, the last whorl becomes slightly convex though it maintains a slightly concave subsututal band. The axial region of the base is moderately concave to flat. The variability also concerns the persistence and regularity in size and spacing of the subsutural granulae, the rate of ontogenetic changes of the sculptural elements of the periphery, and the number and spacing of the spiral threads on the adult spire. As described above, some of the characters of the selenizone are also rather variable on the adult shell. On the last whorls of some specimens the median lira tends to strengthen making the selenizone almost cord-like (Fig. 7E). In other specimens the spiral threads beside the median lira are almost obscure, and the selenizone is slightly prominent to flat (Fig. 7R).

The high variation of the material described here supports the interpretation proposed by Fischer & Weber (1997) who considered *Pyrgotrochus elongatus* (Sowerby, 1818) as an extremely variable species. Most of the specimens from Luxembourg are morphologically similar to *Pleurotomaria agatha* d'Orbigny, 1855, *Pleurotomaria mutabilis* var. *ambigua* Eudes-Deslongchamps, 1849 and their transitional forms. Specimens with a wider spire angle and a more coeloconoidal shell are intermediate in shape and ornament between *Pleurotomaria mutabilis* var. *circumsulcata* Eudes-Deslongchamps, 1849 and the form named by Fischer & Weber (1997) as *varieté large*, i.e. part of the material assigned by d'Orbigny (1855) to *Pleurotomaria conoidea* Deshayes, 1831. In the material from Luxembourg there are no shells characterized by a very wide spire angle like that seen in *Pleurotomaria mutabilis* var. *patula* Eudes-Deslongchamps, 1849 (=*Pleurotomaria bessina* d'Orbigny, 1855). For this reason, these taxa are dubitatively included into the synonymy list.

Pleurotomaria subrhodanica Riche, 1904 is close to *P. elongatus* in the shape of the spire, the size of the whorls and the shape of the base. It differs in having a less prominent ornament. However, the ornament pattern is comparable to that of *P. elongata* and the difference in strength of the ornament is not sufficient to consider *P. subrhodanica* as a distinct species.

In comparison with *Pyrgotrochus punctatus* (Sowerby, 1818), *Pyrgotrochus elongatus* has a rougher and less uniform network of spiral threads and collabral riblets in the early teleoconch, a prominent periphery and strong axial ribs below the suture. The adult shell of *P. elongatus* tends to be coeloconoidal whereas it is cyrtoconoidal in *P. punctatus*. Moreover, the selenizone, which is always distinct, is wider and slightly lower on the whorl surface, and the base is less excavated on its axial region.

Pleurotomaria sandersii Tawney, 1873 (p. 39, pl 3, fig. 1) considered by Hudleston (1895, p. 403, pl. 34, fig. 7.) as a variety of *P. agatha*, differs from *P. elongatus* in having evidently convex whorls and base.

The specimen from Brauner Jura δ of Baden-Württemberg (southern Germany) described by Quenstedt (1858, p. 415, pl. 57, fig. 10; 1884, p. 349, pl. 198, fig. 42) as *P. elongata*, which most probably is the same figured by Sieberer (1907, p. 34, pl. 2, fig. 14), shows higher and more convex whorls. According to Gründel (2003), it belongs to *Leptomaria gyroplata* (Eudes-Deslongchamps, 1849).

Distribution of the species. Undifferentiated Aalenian-Bajocian and uppermost Bajocian, Somerset (south-western England); Lower to Upper Aalenian, Lower Bajocian and uppermost Bajocian, Dorset (south-western England); uppermost Bajocian, Hampshire (southern England); undifferentiated Middle to Upper Aalenian, Vendée (western France); Upper Aalenian, Ardeche (southern France); undifferentiated Bajocian, French Jura (eastern France) and Deux-Sèvres (western France); condensed uppermost Lower Bajocian-middle Upper Bajocian, Hérault (southern France); Undifferentiated Bajocian and Upper Bajocian, Calvados (northern France); (?Upper) Bajocian, Meurthe-et-Moselle (Lorraine, north-eastern France); undifferentiated Upper Toarcian - Middle Aalenian, Isère (southern France); Lower Bajocian, south-western Luxembourg; Lower Bajocian, Baden-Württemberg (southern Germany); Upper Bajocian, Franconia (southern Germany); ? Lower Bajocian, Central High Atlas (Morocco). The occurrence of the species in post-Bajocian sediments is uncertain.

Family **Trochotomidae** Cox, 1960b

Genus ***Trochotoma*** Eudes-Deslongchamps, 1843

Type species. *Trochotoma conuloides* Eudes-Deslongchamps, 1842, Upper Bathonian, Calvados (northern France), by subsequent designation (Woodward, 1851).

Trochotoma affinis Eudes-Deslongchamps, 1843
(Fig. 8A–P)

* 1843 *Trochotoma affinis* Eudes-Deslongchamps: 106, pl. 8, fig. 8–10.
1850 *Ditremaria affinis* d'Orb., d'Orbigny: 267.
1850 *Trochotoma carinata* Lycett: 417.
1853 *Ditremaria affinis* d'Orb.; d'Orbigny: 381, pl. 341, figs 1–3.
1855 *Trochotoma affinis* Deslongchamps; Pictet: 180, pl. 63, fig. 18.
1857 *Trochotoma carinata* Lyc.; Lycett: 64, pl. 4, fig. 5.
? 1866a *Trochotoma Schlumbergeri* Eudes-Deslongchamps: 63, pl. 8, fig. 5a, b.
1866a *Trochotoma affinis* (Desl.); Eudes-Deslongchamps: 64, pl. 8, fig. 6a, b.
? 1868 *Trochotoma Schlumbergeri* (Eug. Desl.); Eudes-Deslongchamps: 219, pl. 8, fig. 5a, b.
1868 *Trochotoma affinis* (Desl.); Eudes-Deslongchamps: 220, pl. 8, fig. 6a, b.
? 1871 *Pleurotomaria* (*Trochotoma*) *Schlumbergeri* Mayer, Mayer: 239, pl. 8, fig. 5.
1877 *Trochotoma Schlumbergeri* Eug. Desl.; Hermite: 690, pl. 14, figs 1–3.
1896 *Trochotoma affinis* Deslongchamps; Hudleston: 447, pl. 41, fig. 4.
1896 *Trochotoma gradus* Deslongchamps; Hudleston: 447, pl. 41, figs 2, 3.
1934 *Ditremaria* (*Ditremaria*) *affinis* (Deslongchamps); Haber: 326.
1997 *Trochotoma affinis* Eudes-Deslongchamps; Fischer & Weber: 151, pl. 24, fig. 6a–c.
2015 *Trochotoma affinis* E.-Deslongchamps; Ferrari *et al*.: 332, fig. 5.5–6.

Material. 17 specimens. Rollesbierg: MNHNL RB166, MNHNL RB167, MNHNL RB236, MNHNL RB237, MNHNL RB311G, MNHNL RB342, MNHNL RB370, MNHNL ZS106, MNHNL ZS369. Giele Botter: MNHNL ZS168B, MNHNL ZS488B. Differdange area: MNHNL MDB157, MNHNL MDB210, MNHNL MDB236, MNHNL ZS363, MNHNL ZS373, MNHNL ZS511. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is trochiform, sharply gradate, and composed of about six whorls. The first preserved whorls are somewhat high and with a distinct, narrow ramp that widens progressively during the adult growth. The ramp is flat, horizontal and limited by a sharp outer angulation. The outer face is flat and subvertical. The fully adult shell is slightly coeloconoidal and formed by sharply angulated whorls. The peripheral band is marked by a prominent and rounded swelling partly exposed on the spire, the abapical suture being placed almost in its middle. The last whorl is expanded and slightly downward inflected before the last peristome. In this region, the peripheral band is slightly projected off and the angulation of the whorl surface becomes obtuse. Consequently, the ramp passes almost smoothly into the outer face. The selenizone is narrow and ornamented by moderately spaced lunulae. It is provided with a median, cord-like spiral thread running almost exactly on the angulation of the whorl. The end of selenizone is marked by a wide, spirally elongated exhalant hole (trema) on the final part of the last whorl. A shell seam occurs between the trema and the peristome. The base is low, widely concave and funnel-shaped, with a deep axial cavity. The last peristome is strongly prosocline. The outer lip is sharp, widely curved and passing smoothly into a short basal lip. The parietal lip is provided with a moderately thick and smooth shelly film which expands on the base covering a great part of its adaxial half. The columellar part of inner lip is long, slightly thickened and strongly inclined on the spire axis. It extends up to the centre of the funnel-like axial cavity and forms an obtuse angle with the basal lip.

The first preserved whorls are ornamented by evenly spaced and sized spiral threads. They are three to four on the outer face and two to three, lighter and almost obscure on the ramp. The spiral threads are granulated by intersection with narrower and dense collabral riblets which are well visible on the intervals between the spiral threads. The exposed part of the peripheral swelling on the spire is densely granulated by the collabral threads. During the growth of the last whorl, the spiral threads on the ramp and on the adapical half of the outer face become obscure or vanish. The peripheral swelling of the last whorls is sculptured by moderately strong and widely spaced spiral threads that ornament also the abaxial band of the base. The remaining surface of the base is ornamented by faint, thin and evenly spaced spiral threads. The growth striae are strongly prosocline and widely prosocyrt on the ramp, strongly prosocyrt on the upper half of the outer face, straight and strongly prosocline on its lower half, slightly and widely opisthocyrt on the base.

Remarks. The material shows a low variability. The spire angle varies from 89° to 100°. The vanishing of the spiral ornament on the ramp and on the adapical half of the outer face can occur at slightly different growth stages. According to Hudleston (1885, 1896) *Trochotoma calix* (Phillips, 1829) (p. 157, pl. 11, fig. 30; Hudleston 1885, p. 156, pl. 4, fig. 6; 1896, p. 445, pl. 41, figs 1, 6, 7), *Trochotoma gradus* Eudes-Deslongchamps, 1843 (p. 106, pl. 8, figs 4–7; Fischer & Weber 1997, p. 150, pl. 24, fig. 5a–c) and *Trochotoma affinis* Eudes-Deslongchamps, 1843 might represent varieties of the same species. However, *T. calix* differs from *T. affinis* in its smaller size and more prominent spiral ornament, and *T. gradus* is a Late Pliensbachian species showing a more obtuse spire and more marked spiral elements on the ramp. According to Eudes-Deslongchamps (1866a, 1868), *Trochotoma schlumbergeri* Eudes-Deslongchamps, 1866 differs from *T. affinis* in having a smaller size, more acute spire and less expanded last whorl. The type illustrated by that author and the specimen assigned by Mayer (1871) to the same species show also a stronger spiral ornament. These traits characterize also the not fully adult shell of *T. affinis* and this suggest that *T. schlumbergeri* may represent only juveniles of the first species. The shell illustrated by Hermite (1877) as *T. schlumbergeri* does not show differences that justify its distinction from *T. affinis*.

Distribution of the species. Middle Aalenian and Lower Bajocian, Somerset (south-western England); Lower Bajocian, Gloucestershire (south-western England); Middle Aalenian and Lower Bajocian, Meurthe-et-Moselle (Lorraine, north-eastern France); Lower Bajocian, Calvados (northern France); Lower Bajocian, south-western Luxembourg.

Suborder **Trochomorpha** Naef, 1911

Superfamily **Turbinoidea** Rafinesque, 1815

Family **Ataphridae** Cossmann, 1915

Subfamily **Ataphrinae** Cossmann, 1915

Genus ***Ataphrus*** Gabb, 1869

Type species. *Ataphrus crassus* Gabb, 1869, Upper Cretaceous (Maastrichtian)?, California (USA), by monotypy.

Remarks. Kaim *et al*. (2014) considered *Ataphrus* Gabb, 1869 a *nomen dubium* because of the bad state of preservation and the uncertain stratigraphic position and geographic provenance of the type material of *Ataphrus crassus* Gabb, 1869. However, this view does not seem justified. The figured and only existing type specimen of *A. crassus* (ANSP IP4243, see also Stewart 1926, p. 313, pl. 24, fig. 12, 12a), although not perfectly preserved, is congruent with the probably doctored original illustration presented by Gabb (1869, p. 171, pl. 28, fig. 54; digital images of ANSP IP4243 have been provided for the present study by P. Callomon, Malacology Department, Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA). The uncertainty about the origin of the type material does not affect the taxon availability. Therefore, the original diagnosis of the genus, subsequently revised by Gabb (1877) with details of the columellar lip, does seem based on a valid species. Kaim *et al*. (2014) also noted that many Jurassic and Cretaceous species ascribed to *Ataphrus* by past authors might belong to different genera. This could be due to the scarcity of morphological characters defining the genus, which makes difficult to assess its interspecific variability.

Ataphrus acmon (d'Orbigny, 1850)

(Fig. 9A–Y)

1844 *Monodonta laevigata* Münster in Goldfuss: 101, pl. 195, fig. 5a, b.

* 1850 *Trochus Acmon* d'Orbigny: 265.

1853 *Trochus Acmon* d'Orb.; d'Orbigny: 278, pl. 314, figs 1–4.

non 1867 *Chrysostoma acmon* d'Orbigny; Laube: 13, pl. 3, fig. 2. (= *Ataphrus baraboshkini* Gerasimov, 1992, *fide* Gründel, 2012).

1885 *Turbo* (*Monodonta*) *laevigatus* Sowerby var. *bellulata* Bean; Hudleston: 53, pl. 2, fig. 4, 4a, 4b.

non 1885 *Ataphrus Acmon* d'Orbigny; Cossmann, 281, pl. 7, figs 9–10 (= *Ataphrus labadyei* d'Archiac, 1843).

1894 *Ataphrus Labadyei* d'Archiac; Hudleston: 350, pl. 29, figs 9, 10.

1894 *Ataphrus Acmon* d'Orbigny; Hudleston: 351, pl. 29, figs 11–13.

v 1904 *Ataphrus Labadyei* d'Arch.; Riche: 99, pl. 2, fig. 14a–e.

v 1904 *Ataphrus Acmon* d'Orb.; Riche: 100, pl. 2, fig. 15a, b.

v 1904 *Ataphrus Hudlestoni* Riche: 101, pl. 2, fig. 16a–d.

1909 *Chrysostoma ovulatum* Hébert and Deslongchamps; Brösamlen: 225, pl. 18, fig. 34a, b.

1918 *Ataphrus Acmon* (d'Orbigny); Cossmann: 41, pl. 1, figs 22, 23.

1938 *Ataphrus* (aff.) *acmon* d'Orb.; Kuhn: 157.

1938 *Ataphrus belus* d'Orb.; Kuhn: 157, pl. 3, fig. 3.

1990 ?*Crossostoma discoideum* Morris and Lycett; Kästle: 91, fig. 60, pl. 13, fig. 3a–c.

1997 *Ataphrus acmon* (d'Orbigny); Fischer & Weber: 109, pl. 20, fig. 14.

2003 *Ataphrus acmon* (d'Orbigny); Gründel: 69, pl. 8, figs 1–3.

2004 *Ataphrus acmon* (d'Orbigny); Hägele: 620, fig. 1B, 1C2–C5, 1E.

2012 *Ataphrus acmon* (d'Orbigny); Gründel *et al*.: 32, pl. 7, figs 12–15.

Material. 21 specimens. Rollesbierg: MNHNL BU137B2–BU137B5, MNHNL MDB374A, MNHNL RB004E, MNHNL RB101, MNHNL RB311M, MNHNL RB376C1, MNHNL RB376C2, MNHNL RB381, MNHNL ZS113B, MNHNL ZS172B, MNHNL ZS228. Giele Botter: MNHNL ZS405C, MNHNL ZS589B1, MNHNL ZS589B2. Differdange area: MNHNL MDB231, MNHNL

MDB249F, MNHNL ZS254D, MNHNL ZS494X. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is turbiniform, variably high. Its outline is distinctly cyrtoconoidal, especially on the early spire that shows a blunt apex. The protoconch is composed of a globular nucleus followed by slightly less than one volution which passes smoothly to the teleoconch. The teleoconch consists of five whorls. The first teleoconch whorl is strongly convex and delimited by an impressed suture. The subsequent whorls become less convex and with a distinctly pendent outline. The last whorls are moderately to slightly convex apart for a weakly concave subsutural band. The periphery has a smooth outline and the suture runs slightly below it. The suture of the adult shell is linear, feebly impressed and shifts slightly downwards, especially during the growth of the last whorl. The last whorl is variably high, approximately 80% of the height of the shell, and passes to the base through an almost obscure angulation. The base is moderately convex and anomphalous. The aperture is suborbicular, almost drop-shaped. The peristome is prosocline and lies nearly in one plane. The parietal lip is thickened at the sutural corner and at the junction with the columellar lip. The outer lip is sharp and passes to the basal lip through an acutely rounded to almost circular curve. The columellar lip is reinforced by an adapical, short and moderately prominent tubercle-like swelling. The abapical part of the columellar lip is enlarged to form a somewhat wide, comma-shaped, excavated outer face. The outer rim of this excavation is sharply prominent and thin. It draws a semi-circular curve and reaches the parietal lip passing along the external edge of the columellar tubercle.

The protoconch is smooth. The early teleoconch whorls bear strong growth lines and one or two incised spiral striae, especially in the suprasutural band. The adult teleoconch is smooth or, rarely ornamented by obscure, densely distributed spiral lines. The growth lines are sharp and very thin. They are prosocline, straight to gently prosocyrt on the whorl surface and on the peripheral band, widely and evenly opisthocyrt on the base and slightly sinuous on its axial region.

Remarks. The material shows a rather high large variability in shell shape. Specimens with prominent spire, more convex whorls and almost obscure peribasal angulation are common. They are comparable to the lectotype of *Ataphrus acmon* (d'Orbigny, 1850) (see Fischer & Weber 1997), *Ataphrus hudlestoni* (Riche, 1904) and to the specimens described by Hudleston (1894) as *Ataphrus labadyei* (D'Archiac, 1843). Other more globose specimens, with wider spire angle, lower spire, and a more evident peribasal angulation are very similar to the shells of *A. acmon* illustrated by Hudleston (1894), Riche (1904), Gründel (2003) and Gründel *et al.* (2012), and to the specimen illustrated by Brösamlen (1909) as *Chrysostoma ovulatum* (Hébert & Eudes-Deslongchamps, 1860). The wide variability of *A. acmon* was already demonstrated by Hägele (2004), who included in its synonymy also *Ataphrus acis* (d'Orbigny, 1850) (p. 265; d'Orbigny 1853, p. 277, pl. 313, figs 13–16; Hudleston 1894, p. 352, pl. 29, fig. 14; Fischer & Weber 1997, p. 109, pl. 20, fig. 13; Hägele 2004, p. 618, fig. 1A, 1C1, 1F), a species with an even more acute shell. In the material here described there are no shells comparable to *A. acis*.

Monodonta laevigata Münster in Goldfuss, 1844 does not seem to be significantly different from *A. acmon*, as also suggested by Kuhn (1938). Based on the dates of institution, Münster's species should have the priority, but its name is invalid because currently a younger secondary homonym of *Ataphrus laevigatus* (Sowerby, 1818).

Distribution of the species. Lower Aalenian, Yorkshire (eastern England); (?Upper) Aalenian, Dorset and Somerset (south-western England); Upper Bajocian, Dorset (south-western England) and Oxfordshire (southern England); Upper Aalenian (Concavum), Mont d'Or Lyonnais (southern France); undifferentiated Bajocian and Upper Bajocian, Calvados (northern France); Lower Bajocian, south-western Luxembourg; upper Lower Bajocian and Upper Bajocian, Franconia (southern Germany); middle Lower Bajocian to lower Upper Bajocian, Baden-Württemberg (southern Germany).

Ataphrus obtortus Hudleston,1894

(Fig. 10A–E)

* 1894 *Ataphrus obtortus* Hudleston: 350, pl. 29, fig. 7, 8.

Material. One specimen, MNHNL BU137B6. Rollesbierg, Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is turbiniform-globose, slightly wider than high, with distinctly cyrtoconoidal spire and moderately blunt apex. The protoconch passes smoothly to the teleoconch. The teleoconch consists of five whorls. The height of the last whorl is almost 90% of the shell height. The first teleoconch whorl is somewhat rounded and edged by an incised suture. The second whorl is slightly convex and strongly pendent. The suture becomes weakly impressed and runs above the periphery. The periphery corresponds to the maximum convexity of the whorl. The base is rather convex and anomphalous. The aperture is ovate. The peristome is moderately prosocline and discontinuous on the parietal lip. The columellar lip has a strong subvertical pillar in its upper and median part. Below this structure, the columellar lip has a comma-shaped, strong excavation which is bordered by a sharp outer edge and by an evenly concave apertural inner rim. The outer lip is sharp and simple. The shell is smooth. The growth lines are thin. They are prosocline and prosocyrt on the whorl surface, and slightly opisthocyrt on the peripheral band and on the base.

Remarks. *Ataphrus obtortus* Hudleston, 1894 differs from *Ataphrus acmon* (d'Orbigny, 1850) in having a more globose shell, more depressed spire and higher last whorl. Moreover, the suture does not shift downward during the growth. The columellar thickening is represented by a sharp, subvertical pillar whereas in *A. acmon* it is a rounded, arched and more expanded tubercle. Hudleston (1894) stated that the less depressed shells of *A. obtortus* are difficult to distinguish from the more depressed shells of *A. acmon*, admitting implicitly that the former species could be a simple variation of d'Orbigny's species. Although the synonymy between these two taxa cannot be excluded, the specimen described here is clearly distinct morphologically from the specimens above assigned to *A. acmon*.

Distribution of the species. Undifferentiated Aalenian-Bajocian, Dorset (south-western England); Lower Bajocian, south-western Luxembourg.

Ataphrus laevigatus (Sowerby, 1818)

(Fig. 10F–O)

* 1818 *Nerita laevigata* Sowerby: 31, pl. 217, fig. 1.

1885 *Turbo* (*Monodonta*) *laevigatus* Sowerby; Hudleston: 52, pl. 2, fig. 6, 6a.

1894 *Ataphrus laevigatus* Sowerby; Hudleston: 349, pl. 29, figs 5, 6.

v 1904 *Ataphrus laevigatus* Sow.; Riche: 98, pl. 2, fig. 13a–d.

v 1921 *Ataphrus laevigatus* Sow.; Roman in Riche & Roman: 109, pl. 3, figs 13, 14.

v 1936 *Ataphrus laevigatus* Sowerby; Marzloff *et al*.: 77, pl. 8, fig. 48, 48a.

non 1938 *Ataphrus laevigatus* Sow.; Kuhn: 157, pl. 3, fig. 4.

Material. Two specimens, MNHNL RB041C and MNHNL RB055C. Rollesbierg, Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is turbiniform-sublenticular, slightly wider than high, with a feebly cyrtoconoidal spire. The teleoconch is composed of five gently convex whorls. The suture is almost flush and runs on the periphery of the preceding whorl. The last whorl is about 90% of the height of the shell. The base is rather convex, almost swollen, and anomphalous. The peristome is prosocline, and seemingly lies on one plane. The parietal region is covered by a shelly layer that thickens the sutural corner and the junction with the columella lip, and gives a circular outline to the apertural rim of the parietal lip. The outer side of the columellar lip is reinforced by a somewhat wide and strong swelling. The shell is smooth and the growth lines are very thin, almost obscure. They are prosocline and feebly prosocyrt on the whorl surface and on the peripheral band, widely and evenly opisthocyrt on the base.

Remarks. *Ataphrus laevigatus* (Sowerby, 1818) differs from *Ataphrus acmon* (d'Orbigny, 1850) in having a proportionally lower shell, wider spiral angle, less cyrtoconoidal spire and less convex whorls. In *A. acmon* the suture shifts downwards on the fully adult spire and the abaxial band of the base is subangulated. Conversely, in *A. laevigatus* the suture draws a regular spiral line and the base is regularly convex. *Ataphrus obtortus* (Hudleston, 1894) differs from *A. laevigatus* in having a lower, more cyrtoconoidal outline, with a more pendent whorl profile. In *A. laevigatus* the columellar tubercle is wider and arched, whereas in *A. obtortus* it consists of a sharp, subvertical pillar.

The specimen from the Bajocian deposits of Franconia (southern Germany) described by Kuhn (1938) as *A. laevigatus* shows a higher and more acute spire and does not seem to belong to that species. Gründel (2003) tentatively included it into the synonymy of his *Ataphrus*? sp. 2.

Distribution of the species. Lower Aalenian, Yorkshire (eastern England); undifferentiated Aalenian-Bajocian, Somerset (south-western England); Upper Aalenian, Dorset (south-western England); Lower Bajocian, Lincolnshire (eastern England); Upper Aalenian and Upper Bajocian, Mont d'Or Lyonnais (southern France); Upper Aalenian, Ardèche (southern France); Lower Bajocian, south-western Luxembourg.

Superfamily **Eucycloidea** Koken, 1896a

Family **Eucyclidae** Koken, 1896a

Genus ***Ambercyclus*** Ferrari, Kaim & Damborenea, 2014

Type species. *Amberleya orbignyana* Hudleston, 1892 (= *Purpurina ornata* d'Orbigny, 1853, *non* Sowerby, 1819), Upper Bajocian, Dorset (south-western England), by original designation.

Ambercyclus orbignyanus (Hudleston, 1892)

(Fig. 11A–D)

1850 *Turbo ornatus* Sow.; d'Orbigny: 265.

1853 *Purpurina ornata* d'Orb.; d'Orbigny, pl. 330, figs 4–5.

* 1892 *Amberleya Orbignyana* Hudleston: 285, pl. 22, figs 7, 8.

1898 *Amberleya Orbignyana* Hudleston; Greppin: 43, pl. 5, fig. 1, 1a.

1909 *Eucyclus Orbignyanus* Hudleston; Brösamlen: 262, pl. 20, fig. 16.

v 1912 *Amberleya Murchisoni* Münster; Roman & Gennevaux: 273, pl. 2, fig. 5.

non 1919 *Eucyclus Orbignyanus* Hudleston; Couffon: 149, pl. 10, fig. 18, 18a–e.

1938 *Eucyclus orbignyanus* Hudl.; Kuhn: 153, pl. 3, fig. 8.

1946 *Amberleya orbignyana* Hudleston; Gardet & Gérard: 36, pl. 3, figs 16–18.

1997 *Amberleya* (*Eucyclus*) *orbinyana* Hudleston; Fischer & Weber: 137, pl. 21, figs 13–14.

2003 *Eucycloscala orbignyana* (Hudleston); Gründel: 62, figs 12–14.

2005 *Amberleya* (*Eucyclus*) *jugata* (Quenstedt); Meiers: 52, text-figs without number.

Material. One specimen, MNHNL BM382. Ottange-Rumelange Quarry, Lower Bajocian (*Stephanoceras humphriesianum* zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is pagodiform and slightly coeloconoidal. The whorls are rather high, their width being two times their height. The last whorl is almost half the height of the shell. The teleoconch whorls are biangulated. On the early whorls, the adapical angulation runs slightly below mid-whorl and the abapical angulation just above the suture. The periphery corresponds to both angulations. During the growth, the adapical angulation moves distinctly below mid-whorl. It becomes more prominent and peripheral, whereas the abapical angulation becomes more obtuse. The outer face, delimited by the angulations, is narrow and concave. The ramp is wide, rather steep and slightly concave. The base is quite convex, high and anomphalous.

The main ornament elements of the spire consist of two spiral keels at the angulations of the whorl surface. On the first three preserved whorls, these keels bear nodes at the intersection with strong and regularly distributed collabral ribs. The subsutural band is marked by a spiral row of small and pointed nodes. On the subsequent whorls, the nodes of the adapical keel become progressively more prominent, more acute, more widely spaced and elongated in spiral direction. Eighteen nodes are present on the penultimate whorl and about fifteen on the last whorl. Swollen collabral ribs start from the nodes and cross the ramp. They become weaker towards the adapical suture and vanish before reaching it. On the last whorl the collabral ribs are even shorter, disappearing in the middle of the ramp. The nodes of the abapical keel remain densely distributed and become smaller than the nodes of the adapical keel. The row of subsutural nodes attenuate on the penultimate whorl and seemingly disappears on the last whorl. The base is ornamented by six strong and nodose spiral cords. The growth striae form thin and faint thread-like lines. They are prosocline, straight to slightly opisthocyrt on the ramp, not observable on the remaining part of the shell.

Remarks. The poor preservation of the specimen allows observation of the details of the ornament only on some parts of the shell. Moreover, the shell lacks the apical part and most of the peristome. Hudleston (1892) included both *Turbo ornatus* Sowerby, 1819 and *Purpurina ornata* d'Orbigny, 1853 in the genus *Amberleya*, making the last taxon a secondary homonym of the first. He therefore introduced a new name, *Amberleya orbignyiana* Hudleston, 1892, for *P. ornata*. That species has been recently selected by Ferrari *et al.* (2014) as type species of the genus *Ambercyclus* Ferrari, Kaim & Damborenea, 2014.

According to Hudleston (1892), *Eucyclus goniatus* Eudes-Deslongchamps, 1860 (p. 146, pl. 9, fig. 6; Hudleston, 1892, p. 284, pl. 22, fig. 6), from the Bajocian sediments of Calvados (northern France) and Dorset (south-western England), and *A. orbignyanus* most probably represent only varieties of the same species. However, *Ambercyclus goniatus* has a more prominent peripheral keel and lacks a distinct abapical angulation. The nodes of the peripheral keel are less numerous, more widely spaced and more acute, and the collabral ribs are more marked and less elongated on the ramp of the last whorl.

Distribution of the species. Undifferentiated Aalenian-Bajocian, upper Lower Bajocian and Upper Bajocian, Somerset (south-western England); upper Lower Bajocian and Upper Bajocian, Dorset (south-western England); Upper Bajocian, Calvados (northern France); Upper Bajocian, Hérault (southern France); upper Lower Bajocian, south-western Luxembourg; upper Lower Bajocian, Swiss Jura (Switzerland); undifferentiated upper Lower Bajocian to lower Upper Bajocian, undifferentiated Lower Bathonian to lower Upper Bathonian, Franconia (southern Germany); undifferentiated Bathonian, Baden-Württemberg (southern Germany); undifferentiated Bajocian, Middle Atlas (Morocco).

Ambercyclus ornatus (Sowerby, 1819)

(Fig. 11E–U)

* 1819 *Turbo ornatus* Sowerby: 69, pl. 240, figs 1, 2.

non 1844 *Turbo ornatus* Sowerby; Goldfuss: 97, pl. 194, fig. 2a, b.

1844 *Turbo spinulosus* Münster in Goldfuss: 98, pl. 194, fig. 3.

non 1850 *Turbo ornatus* Sow.; d'Orbigny: 265 [= *Ambercyclus orbignyanus* (Hudleston, 1892)].

1850 *Turbo bathis* d'Orbigny: 266.

1853 *Purpurina bathis* d'Orbigny; d'Orbigny, pl. 330, figs 6–8.

non 1858 *Turbo ornatus* Sow.; Quenstedt p. 416, pl. 57, fig. 11–13.

1873 *Amberleya ornata* Sowerby; Tawney: 27, pl. 1, fig. 9.

non 1884 *Turbo ornatus* Sow.; Quenstedt: 431, pl. 202, figs 9, 10.

1892 *Amberleya ornata* Sowerby; Hudleston: 279, pl. 21, figs 13, 14.

1892 *Amberleya ornata* var. *spinulosa* Munster; Hudleston: 279, pl. 21, fig. 15.

1892 *Amberleya ornata* var. *abbas*, Hudleston: 279, pl. 21, figs 16–18, pl. 22, fig. 1.

1892 *Amberleya ornata* var. *horrida*, Hudleston: 281, pl. 22, fig. 2.

v 1904 *Amberleya murchisoni* Münst.; Riche: 112, pl. 2, fig. 25.

1909 *Turbo bathis* d'Orb.; Thèvenin: 70, pl. 16, figs 5–7.

1916 *Eucyclus bathis* (d'Orbigny); Cossmann: 52, pl. 3, fig. 1.

1935 *Eucyclus ornatus* Sow. var. *abbas* Hudleston; Roman: 33, pl. 6, fig. 3a.

? 1936 *Eucyclus ornatus* Sowerby; Marzloff *et al.*: 75, pl. 8, fig. 43.

1938 *Eucyclus spinulosus* Münst.; Kuhn: 153, pl. 3, fig. 7.

1990 *Amberleya ornata* var. *abbas* Hudleston; Hickman & McLean: 76, figs 38A, 39.

1997 *Amberleya (Eucyclus) ornata* (Sowerby); Fischer & Weber: 137.

v 2001 *Eucyclus ornatus* (Sowerby); Conti & Monari: 196, figs 6.6–12.

2014 *Ambercyclus ornatus* (Sowerby); Ferrari *et al*.: 1117, fig. 2.9 (original illustration by Sowerby, 1819).

Material. 79 specimens. Rollesbierg: MNHNL BU167A, MNHNL BU167B, MNHNL MDB247, MNHNL RB002, MNHNL RB004B–RB004D, MNHNL RB005A, MNHNL RB008B, MNHNL RB033B, MNHNL RB051, MNHNL RB061, MNHNL RB068A, MNHNL RB069A1, MNHNL RB069A2, MNHNL RB097, MNHNL RB105B1, MNHNL RB105B2, MNHNL RB109, MNHNL RB123, MNHNL RB144, MNHNL RB198, MNHNL RB217B1, MNHNL RB217B2, MNHNL RB281, MNHNL RB304B, MNHNL RB311J, MNHNL RB311K, MNHNL RB376A1–RB376A5, MNHNL RB376F, MNHNL ZS101A, MNHNL ZS150B, MNHNL ZS166C, MNHNL ZS173B, MNHNL ZS257A, MNHNL ZS257B. Giele Botter: MNHNL MDB245, MNHNL ZS160B1–ZS160B5, MNHNL ZS193, MNHNL ZS245B, MNHNL ZS249B, MNHNL ZS250, MNHNL ZS292, MNHNL ZS297B, MNHNL ZS305, MNHNL ZS396A1, MNHNL ZS396A2, MNHNL ZS430A1, MNHNL ZS430A2, MNHNL ZS630B, MNHNL ZS636A1, MNHNL ZS636A2. Differdange area: MNHNL MDB216, MNHNL MDB235, MNHNL MDB239, MNHNL MDB249A–MDB249C, MNHNL MDB305A, MNHNL MDB313A, MNHNL MDB324, MNHNL ZS184B1, MNHNL ZS184B2, MNHNL ZS215A1–ZS215A3, MNHNL ZS234, MNHNL ZS254C, MNHNL ZS452, MNHNL ZS494M. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone). Piedmont (Longwy): MNHNL BU230. Lower Bajocian.

Measurements. See Online Supplemental Material Table S2.

Description. The shell is turbiniform, gradate, slightly coeloconoidal and composed of eight whorls. The height of the last whorl is two-thirds of the height of the shell. The teleoconch whorls are biangulated. The adapical angulation is placed at mid-whorl or slightly below it and represents the outer edge of a slightly concave, rather sloping ramp. The abapical angulation runs slightly above the suture. The narrow spiral band between this angulation and the abapical suture is slightly concave. The outer face, delimited by the two angulations, is concave and slightly narrower than the ramp. On the adult shell the periphery of the whorls corresponds to both the angulations or to the abapical angulation. During the adult growth, at different stages in different specimens, a third obtuse angulation appears on the adapical half of the ramp and forms the edge of a rather steep sutural shelf. The suture runs in a wide channel between the abapical angulation and the sutural shelf. The base is rather convex and anomphalous. It is somewhat elongated in axial direction. The aperture is widely elliptical, drop-shaped. The peristome is slightly prosocline. The parietal lip is covered by a very thin callus. The columellar lip is robust, almost straight, subvertical and covered by a smooth callus. The outer lip is sharp, simple and evenly arched. The basal lip meets the columellar lip through a rounded angulation.

The early four teleoconch whorls are ornamented by a strong and wide network made by intersection of two spiral cords, each marking the respective angulations of the whorl, and strong, regularly spaced collabral ribs. The collabral ribs have almost the same size as the spiral cords. Prominent nodes mark the intersection points. On the subsequent whorls, the collabral ribs weaken and gradually vanish, while densely distributed collabral riblets appear. The nodes of the spiral keels become more acute and pointed, while a spiral cord with acute nodes appears marking the onset of the angulation at the edge of the sutural shelf. This keel becomes more and more prominent but commonly does not reach the size of the other keels. Most of the collabral ribs branches from each node in groups of two or three. They are roughly undulated and some of them are also bifurcated. The base is sculptured by six or seven, strong spiral cords which bear small but distinct nodes at the intersection with dense collabral riblets. The most abapical of these spiral cords is covered by the suture on the spire and becomes partially exposed only on the last two whorls. The growth lines are prosocline, almost straight on the ramp, very slightly and widely opisthocyrt on the peripheral band, more distinctly opisthocyrt on the base.

Remarks. The analysis of the very rich material from Luxembourg confirms the considerable variability of *Ambercyclus ornatus* (Sowerby, 1819) described by Hudleston (1892). The morphology and ornament pattern of numerous specimens, characterized by strong spiral keels bearing prominent nodes, are comparable to those described Hudleston (1892) in *Amberleya ornata* var. *horrida* (Hudleston, 1892). Other specimens show thinner spiral keels and smaller nodes. They are more similar to the typical morphology illustrated by Sowerby (1819) and to the variety described by Hudleston (1892) as *Amberleya ornata* var. *abbas* (Hudleston, 1892).

Distribution of the species. Undifferentiated Aalenian-Bajocian, Lower Bajocian, Somerset (south-western England); Middle to Upper Aalenian, Dorset (south-western England); undifferentiated Bajocian, Calvados (northern France), Vendée and Deux-Sèvres (north-western France) and Ardèche (southern France); ? Upper Bajocian, Mont d'Or Lyonnais (southern France); Lower Bajocian, south-western Luxembourg; undifferentiated upper Lower Bajocian to lower Upper Bajocian, Franconia (southern Germany); Upper Aalenian and Lower Bajocian, Central High Atlas (Morocco).

Ambercyclus praetor (Goldfuss, 1844)

(Fig. 11V–Z)

* v 1844 *Turbo praetor* Goldfuss: 99, pl. 194, fig. 8a, b.

1844*Turbo ornatus* Sow.; Goldfuss: 97, pl. 194, fig. 2a, b.

1858 *Turbo ornatus* Sow.; Quenstedt: 416, pl. 57, figs 11, 12, ?13.

1892 *Littorina* (*Echinella*) *praetor* Goldfuss; Hudleston: 294, pl. 24, fig. 8.

? 1898 *Littorina praetor* Goldfuss; Greppin: 46, pl. 5, fig. 4, 4a.

1909 *Litorina ornata* Quenstedt; Brösamlen: 253, pl. 19, fig. 49a, b, pl. 20, fig. 1.

1909 *Litorina praetor* Goldfuss; Brösamlen: 254, pl. 20, figs 2–3.

1909 *Eucyclus trijugatus* Brösamlen: 259, pl. 20, fig. 12.

1938 *Eucyclus ornatosculptus* Kuhn: 154, pl. 5, fig. 12.

1938 *Littorina praetor* Münst.; Kuhn: 155, pl. 5, fig. 18, pl. 6, fig. 27.

1990 *Eucyclus ornatus* (Sowerby); Kästle: 91, pl. 13, fig. 7.

pars 2003 *Eucycloscala praetor* (Goldfuss); Gründel: 62, pl. 5, figs 7–9, non figs 1–6.

2012 *Eucycloscala praetor* (Goldfuss); Gründel *et al.*: 18, pl. 5, figs 4–12.

Material. One specimen, MNHNL RB376E. Rollesbierg, Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is moderately gradate and composed of about six whorls. The spire is conoidal and the fully adult part of the shell is slightly coeloconoidal. The last whorl is rather high, being about two-thirds of the height of the shell. The teleoconch whorls are biangulated. The adapical angulation runs slightly below the mid-whorl and corresponds to the edge of a wide and steep ramp. It is quite obtuse on the early teleoconch and becomes sharper on the last whorls. The abapical angulation is sharp and placed in peripheral position slightly above the suture. The spiral band of the whorl surface between this angulation and the abapical suture is very narrow. The outer face between the angulations is concave and narrower than the ramp. It is inclined upwards toward the spire axis on the spire and becomes almost vertical on the last two whorls. The suture runs in a deep channel bordered by the abapical angulation and a strong subsutural spiral cord. The base is convex, anomphalous and elongated axially. The aperture is seemingly elliptical or semicircular.

The parietal lip is covered by a thin shelly film. The columellar lip is strong, almost straight, and coated by a smooth callus.

The earliest preserved whorl of the teleoconch is sculptured by a strong and quite regular network of three equally spaced spiral cords and collabral ribs. On the subsequent whorl, two spiral cords correspond to the adapical and abapical angulations, respectively. A third spiral cord runs in subsutural position. A fourth narrower spiral cord appears in the middle of the ramp. This pattern persists on the adult whorls where the cords at the angulations are the strongest. The collabral ribs of the early teleoconch are prosocline, straight, regularly distributed and equally sized. They are about twenty per whorl and form prominent nodes at the intersection with the spiral cords. On the last two whorls, the collabral ribs become thinner on the ramp, whereas they remain somewhat strong on the outer face. The nodes are rather prominent and pointed. The base is ornamented by six, well spaced spiral cords with neat, secondary spiral threads intercalated between them. The prolongation of the collabral ribs on the base makes strong tubercles on the spiral cords and waves the secondary spiral threads. The growth lines are sharp and make the shell surface rough. They are slightly prosocline, almost straight to very feebly opisthocyrt on the ramp, and widely opisthocyrt on the peripheral band and on the base.

Remarks. The specimen is well preserved, although the apical spire and the peristome are incomplete. *Ambercyclus praetor* (Goldfuss, 1844) has been described and discussed in detail by Gründel *et al.* (2012) to which paper the reader is referred for further information. Those authors treated *Turbo phillipsii* Morris & Lycett, 1851 (p. 117, pl. 15, fig. 12, 12a, b) as a junior synonym of *A. praetor*, claiming that the two species differ only in the height of the spire. However, *T. phillipsii* is the type species of the genus *Ooliticia* Cossmann, 1893, a taxon characterized by the presence of a weak swelling on the adapical part of the columellar lip. This swelling is absent in *A. praetor*.

Ambercyclus ornatus (Sowerby, 1819) differs from *Ambercyclus praetor* (Goldfuss, 1844) in having a more acute and gradate shell with sharper spiral keels, and dense collabral riblets characteristically collated at the nodes. Moreover, *A. praetor* has an additional, strong spiral cord in subsutural position that is absent in *A. ornatus*, and the spiral cords of the base are intercalated with secondary spiral threads.

Distribution of the species. Middle Aalenian, Dorset (south-western England); Lower Bajocian, south-western Luxembourg; undifferentiated upper Lower Bajocian to Upper Bajocian, undifferentiated Bathonian, Franconia (southern Germany); middle and upper Lower Bajocian, undifferentiated upper Lower Bajocian to Upper Bajocian, undifferentiated Bathonian, Baden-Württemberg (southern Germany). ? upper Lower Bajocian, Swiss Jura.

Genus ***Ooliticia*** Cossmann, 1893

Type species. *Turbo phillipsi* Morris & Lycett, 1851, Lower Bajocian, Northamptonshire (northern England), by monotypy.

Ooliticia polytimeta (Hudleston, 1892)

(Fig. 12A–J)

? 1871 *Turbo ditissimus* Mayer: 239, pl. 8, fig. 6.

* 1892 *Littorina* (*Tectarius* or *Echinella*) *polytimeta* Hudleston: 295, pl. 23, figs 12, 13.

1898 *Littorina polytimeta* Hudleston; Greppin: 46, pl. 5, fig. 8, 8a.

v 1904 *Littorina polytimeta* Hudl.; Riche: 108, pl. 2, fig. 22a, b.

Material. 10 specimens. Rollesbierg: MNHNL BU137C2, MNHNL RB005B, MNHNL RB087, MNHNL RB311H1, MNHNL RB313B, MNHNL ZS150E. Giele Botter: MNHNL ZS260B, MNHNL ZS384. Differdange area: MNHNL ZS391C, MNHNL MDB395. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is turbiniform-conoidal, composed of about seven whorls, with a conoidal to slightly cyrtoconoidal spire. The width of the whorls is slightly more than two and a half times their height. The last whorl is slightly swollen and its height is about 80% of the shell height. The earliest whorls are convex, seemingly with an angulated periphery lying just above the suture. The whorls are almost flat on the middle part of the teleoconch. The last two whorls are slightly convex and with an evenly rounded periphery. The suture runs in a deep and distinct channel bordered by the peripheral and subsutural cords of the spiral ornament. The base is rather convex, slightly swollen and anomphalous. The aperture is circular, slightly drop-shaped. The peristome is prosocline. A thin shelly film covers the parietal lip. It smoothly passes to the columellar lip and extends to the axial part of the base adhering to its surface. The columellar lip is robust, almost straight. The uppermost part of its inner rim, near to the junction with the parietal lip, is provided with a tooth-like tubercle. The outer lip is sharp and evenly arched. The basal lip is gently elongated downward.

The early whorls are ornamented by strong prosocline collabral riblets crossed by three weak spiral cords that become stronger during the growth. The adapical cord is subsutural in position and the abapical one is suprasutural and peripheral. The median cord lies almost at mid-whorl. The peripheral cord is slightly stronger than the others. The spiral interspaces are almost as wide as the cords. The collabral ribs overlap the spiral cords making strong, closely packed and collabrally elongated nodes. They become sharper during the growth and gradually change in prominent ridges that are well distinguishable on the spiral interspaces. The base is sculptured by six or seven, very strong spiral cords densely tuberculated by the overlapping collabral ridges. The spiral cord below the periphery is covered by the suture or partly exposed on the spire. Occasionally, it becomes completely exposed on the penultimate whorl. The growth lines are somewhat prosocline, almost straight on the adapical part of the whorl surface, and opisthocyrt on the peripheral band and on the base.

Remarks. The shape of the spire is not very variable, ranging from conoidal to slightly cyrtoconoidal. The spire angle and the convexity of the base are also slightly variable. The ornament pattern is quite constant. The columellar lip is provided with a distinct inner tooth-like swelling which is one of the main diagnostic characters of the genus *Ooliticia* Cossmann, 1893. The material from Luxembourg conforms perfectly to the type material of *Ooliticia polytimeta* (Hudleston, 1892) and to the specimens illustrated by Riche (1904), although these come from slightly older stratigraphical levels.

Turbo ditissimus Mayer, 1871, from the Lower Bajocian deposits of Meurthe-et-Moselle (Lorraine, north-western France) is very similar to *O. polytimeta* and the two taxa could be conspecific. In this case Mayer's name should have the priority. However, Mayer (1871) did not describe in detail the morphology of the columellar lip.

Distribution of the species. Upper Aalenian, Dorset (south-western England); Upper Aalenian, Mont d'Or Lyonnais (Rhone, France); ? lower part of Lower Bajocian, Meurthe-et-Moselle (Lorraine, north-western France). Lower Bajocian, south-western Luxembourg; upper Lower Bajocian, Swiss Jura (Greppin);

Ooliticia recteplanata (Tawney, 1873)

(Fig. 12K–Y)

* 1873 *Littorina recte-planata* Tawney: 26, pl. 2, fig. 6.

1892 *Littorina recteplanata* Tawney; Hudleston: 300, pl. 24, figs 6, 7.

v 1904 *Littorina recteplanata* Tawney; Riche: 109, pl. 2, fig. 23a–c.

Material. 23 specimens. Rollesbierg: MNHNL BU137C1, MNHNL RB005G, MNHNL RB057B, MNHNL RB311H2–RB311H4, MNHNL RB376B, MNHNL RB394. Giele Botter: MNHNL MDB277, MNHNL ZS167A, MNHNL ZS260A, MNHNL ZS333B, MNHNL ZS405B, MNHNL ZS420, MNHNL ZS421A, MNHNL ZS421B. Differdange area: MNHNL MDB211, MNHNL MDB249E, MNHNL MDB307A, MNHNL ZS145A, MNHNL ZS254B1, MNHNL ZS254B2, MNHNL ZS391D. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is turbiniform, conoidal to very slightly cyrtoconoidal, composed of about seven whorls. The width of the whorls is two and a half times its height and the last whorl is two-thirds of the height of the shell. The earliest teleoconch whorls are moderately and evenly convex, whereas the adult whorls are almost flat to very slightly convex. The suture runs in a distinct channel between the spiral elements of the ornament. The periphery lies slightly above the suture. It is smoothly angulated on the early teleoconch and becomes rounded on the last whorls. The base is rather convex and anomphalous. The aperture is wide, circular, slightly drop-shaped. The peristome is prosocline and its parietal lip is covered by a thin callus. The columellar lip is robust, straight and bears a very weak, tubercle-like swelling on its abapical part, slightly inside the aperture. The columellar lip forms a distinct angle with the parietal lip and passes to the basal lip through a smooth but evident angulation. The outer face of the columellar lip bears a somewhat wide and smooth callosity which is reflected outward and adheres to the axial region of the base. The outer lip is prosocline and evenly arched.

The first teleoconch whorl is ornamented by collabral riblets which rapidly become strong ribs. Subsequently, three equally spaced spiral cords appear making a strong network with the collabral ribs. The intersection points are marked by closely repeating nodes. From about the third whorl another nodose spiral cord arises in subsutural position so that the adult teleoconch is ornamented by four, equally distributed and densely nodose spiral cords. Rarely, an additional fifth cord appears abapically on the whorl surface. The most abapical cord, corresponding to the periphery, is commonly stronger than the others, especially on the early teleoconch. The spiral interspaces are about as wide as the cords. They commonly widen on the last whorl while the spiral cords become thinner. The collabral ribs of the early teleoconch progressively become sharp riblets connecting the nodes in a prosocline direction. On the last two whorls, the collabral riblets changes in thin ridges. These are variously bifurcated or collated at the nodes and form a somewhat irregularly braided texture on the spiral intervals. The base is ornamented by eight or nine strong and densely nodose spiral cords, whose interspaces are crossed by collabral ridges forming the same braided texture described above. The spiral cord below the periphery can become partially exposed on the penultimate whorl. The growth lines are prosocline, almost straight on the adapical half of the whorl surface, widely opisthocyrt on its abapical half and on the base.

Remarks. Some variability can be seen in the ornament of *Ooliticia recteplanata* (Tawney, 1873). Commonly, four spiral cords ornament the adult whorls, but few specimens show five cords which appear early during the teleoconch growth. The braided texture of the collabral ridges of the fully adult shell can be partially developed and with a patchy distribution. The spire is commonly conoidal, more rarely very slightly cyrtoconoidal, and slightly variable in height.

Littorina elongata Brösamlen, 1909, from the Brauner Jura ε of Baden-Württemberg (southern Germany) is a possible junior synonym of *O. recteplanata* from which it only differs in having a more acute spire angle. *Ooliticia polytimeta* (Hudleston, 1892) differs from *O. recteplanata* in its slightly bigger shell, more swollen shape and spiral ornament made by only three spiral cords. In addition, the collabral ribs are not bifurcated at the nodes and do not form a braided texture.

Distribution of the species. Undifferentiated Aalenian–Bajocian, Somerset (south-western England); Middle Aalenian, Gloucestershire (south-western England); Upper Aalenian, Mont d'Or Lyonnais (Rhone, France); Lower Bajocian, south-western Luxembourg.

Superfamily **Discohelicoidea** Schröder, 1995

Family **Discohelicidae** Schröder, 1995

Genus ***Colpomphalus*** Cossmann, 1916

Type species. *Straparollus altus* d'Orbigny, 1853, Upper Bathonian, Calvados (northern France), by original designation.

Colpomphalus thuyi sp. nov.

(Fig. 13A–E)

Diagnosis. Shell globose, Spire moderately prominent for the genus. Spire whorls very low, concave between bulge-shaped outer angulation and distinct subsutural bulge. Lateral surface of last whorl rather convex. Periphery rounded, placed below outer angulation. Umbilicus very wide, with sharply angulated outer edge. Aperture slightly pendent in outline. Peristome with thick parietal lip. Subsutural bulge, outer angulation and periumbilical edge bearing strong nodes. Nodes densely distributed on outer angulation and on subsutural bulge, much stronger, more widely spaced and less numerous on periumbilical edge. Lateral whorl surface ornamented by fine, feeble and dense spiral striae.

Derivation of name. Dedicated to Ben Thuy, palaeontologist of the National Museum of Natural History of Luxembourg.

Holotype. MNHNL ZS124B, Fig. 13A–E.

Type locality. Rollesbierg (Differdange, south-western Luxembourg, Grand-Duchy of Luxembourg).

Type level. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Other Material. The material is represented only by the holotype.

Measurements. See Online Supplemental Material Table S2.

Description. The shell is globose, with an obtuse, cyrtoconoidal spire, and is composed of about six whorls. The shell width is slightly more than one and a half times its height and the last whorl is about 85% of the shell height. The surface of the whorls exposed on the spire is somewhat narrow and distinctly concave. It is bordered by a bulge-shaped outer angulation and a subsutural cord, both strongly nodose. The suture is incised between these spiral elements. The lateral surface of the last whorl is somewhat convex and passes smoothly to the base. The periphery is rounded and placed well above the mid-line of the lateral surface. The base is very widely phaneromphalous. The umbilicus is deep and its width is almost two-thirds of the shell width. The periumbilical edge is sharply angulated and strongly nodose. The aperture is semicircular, with a slightly pendent outline.

It is obtusely angulated in correspondence to the outer angulation and more acutely angulated at the periumbilical angulation. The peristome is slightly prosocline, continuous on the parietal lip where it is provided with a thick callus. The outer lip is seemingly simple.

The main ornament elements of the fully adult shell are represented by nodose keels marking the subsutural cord, the outer angulation and the periumbilical edge. On the outer angulation and on the subsutural cord, the nodes are densely distributed and almost equal in size. On the penultimate whorl, each keel bears slightly less than forty nodes. On the last whorls the nodes of the outer angulation tend to become smaller and slightly more widely spaced, whereas the nodes of the subsutural bulge become slightly larger. About fifteen very strong and prominent nodes separated by slightly narrower intervals ornament the periumbilical edge of the last whorl. The lateral surface of the last whorl bears about twenty, evenly spaced, fine and feeble spiral striae. They intersect the growth lines making a thin, almost obscure network. The growth lines are prosocline and almost straight on the spiral side of whorl surface, slightly prosocline and widely opisthocyrt on the lateral surface, prosocline and almost straight on the umbilical wall.

Remarks. The specimen is somewhat well preserved. Although the apical spire is slightly eroded, the spiral bulge marking the outer angulation and the subsutural cord on the early whorls seem to be smooth. The nodes probably appear gradually during the growth. *Colpomphalus crussoliensis* (Riche & Roman, 1921) (p. 102, pl. 3, fig. 5, 5a, figured syntype UCBL 26823), from the Upper Aalenian of Ardèche (southern France) resembles *Colpomphalus thuyi* sp. nov. in having the spiral surface of the whorls concave between the subsutural and outer angulations. However it has a higher and slightly coeloconoidal spire, with a more inclined whorl surface and a more obtuse outer angulation. In addition, the nodes are smaller and the spiral sculpture consists of marked spiral threads, whereas in *C. thuyi* it is composed of spiral striae. The umbilicus is also wider and surrounded by a sharper angulation bearing smaller and more numerous nodes.

Distribution of the species. Lower Bajocian, south-western Luxembourg.

Colpomphalus tigratus sp. nov.

(Fig. 13F–J)

Diagnosis. Shell discoidal. Spire moderately prominent for the genus. Whorls subtrapezoidal in cross section. Lateral side of whorls about twice the spiral side, moderately oblique and slightly convex. Nodes on adapical angulation strong and densely distributed. Subsutural band bulge-shaped and with small and dense nodes. Spiral side of whorls narrow and deeply grooved between row of nodes of adapical angulation and subsutural bulge. Lateral surface of whorls sculptured by opisthocyrt collabral riblets bifurcating from nodes of angulations. Riblets extending from nodes to nodes irregularly alternated with riblets vanishing before reaching opposite angulation. Spiral ornament of threads overlapping collabral riblets.

Derivation of name. The name refers to the pattern of collabral riblets on the lateral surface of the last whorl which is reminiscent of the stripes on the coat of a tiger.

Holotype. MNHNL ZS124A, Fig. 13F–J.

Type locality. Rollesbierg (Differdange, south-western Luxembourg, Grand-Duchy of Luxembourg).

Type level. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Other Material. The material is represented only by the holotype.

Measurements. See Online Supplemental Material Table S2.

Description. The shell is small, dextral, discoidal and composed of about five whorls. The spiral side is slightly prominent and high almost one-ninth of the shell height. The umbilical side is very deep. The whorls have a subtrapezoidal cross section with narrow spiral and umbilical sides which are less than half the lateral side and meet it through sharp angulations. The umbilical angulation is more acute than the adapical angulation. The lateral surface is slightly sinuous in outline, i.e. slightly convex along the bands adjacent to the angulations and weakly concave in the middle. It is inclined downward towards the spire axis. The periphery is placed at about one quarter of the height of the lateral surface towards the adapical angulation. The aperture is subtrapezoidal. The parietal lip is covered by a thin callus.

Both the angulations are ornamented by very strong and rounded nodes. On the adapical angulation the nodes are densely repeating and separated by deep and narrow intervals. They increase both in size and number during the growth, being about 30 on the antepenultimate whorl and 35 on the last whorl. On the spiral side, the sutural band is marked by a strong spiral cord which is seemingly smooth on the early whorls. On the last two whorls, small, tightly arranged, prosocline nodes progressively appear on this cord. They increase in size during the growth but remain distinctly smaller than the nodes of the adapical angulation. The surface of the spiral side, between the adapical angulation and the sutural cord, is narrow and deeply grooved. Also the suture is confined in a narrow furrow by these spiral elements. The umbilical angulation is ornamented by subacute, prominent and collabrally elongated nodes that are more spaced and less numerous than the nodes of the adapical angulation. The lateral surface is sculptured by distinctly opisthocyrt collabral riblets starting from the nodes of the angulations and separated by narrower interspaces. Two or three riblets start from each node, sometimes bifurcating. Most of them reach the corresponding node of the opposite angulation, but some pass through the interspace between adjacent nodes vanishing before reaching the opposite angulation. The spiral ornament consists of thin threads separated by finer interspaces. Few spiral threads ornament the grooved surface of the spiral side and become waved on the nodes. The whole lateral surface is covered by numerous (about 30), dense and rather regularly distributed spiral threads separated by thinner interspaces. They overlap the collabral riblets and appear slightly thinner at mid-whorl. The growth lines are prosocline and slightly opisthocyrt on the spiral side, prosocyrt on the outer angulations, straight and almost symmetrically opisthocyrt on the lateral surface, opisthocline and prosocyrt on the umbilical side.

Remarks. The earliest spire and the outer part of the peristome are incomplete, otherwise the specimen is quite in good state of preservation. *Colpomphalus exsertus* (Hudleston, 1892)(p. 320, pl. 26, figs 3, 4), from the Middle Aalenian of Dorset and Somerset (south-western England) differs from *Colpomphalus tigratus* sp. nov. in having whorls with a wider and not deeply grooved spiral side, a more convex flank, and a less prominent ornament. The nodes of the adapical angulation are smaller and those of the sutural band are scarcely differentiated. Also the nodes of the umbilical angulation are less marked and the lateral surface lacks distinct collabral ribs. The same differences distinguish *C. tigratus* from *Straparollus dundriensis* Tawney, 1873 (p. 35, pl. 2, fig. 9; Hudleston 1892, p. 319, pl. 26, fig. 2), from the Inferior Oolite of Somerset (south-western England). Moreover, *S. dundriensis* has an almost flat spire. *Colpomphalus abrardi* Cossmann in Cossmann & Abrard, 1921 (p. 156, pl. 8, figs 22–24), from the uppermost Lower Toarcian of Morocco is quite similar to *C. tigratus* in shell shape and in some details of the ornament. It differs in having collabral ribs that cross the spiral side of the whorl surface and form smaller nodes on the outer angulation, and in lacking a nodose sutural cord. The higher spire, more convex lateral whorl surface and wider umbilicus distinguish *Colpomphalus thuyi* sp. nov. from *C. tigratus*. The two species also show clearly different ornament patterns.

Distribution of the species. Lower Bajocian, south-western Luxembourg.

Subclass **Neritimorpha** Koken, 1896b

Superorder **Cycloneritimorpha** Frýda, 1998

Superfamily **Symmetrocapuloidea** Wenz, 1938

Family **Symmetrocapulidae** Wenz, 1938

Genus ***Symmetrocapulus*** Dacqué, 1933

Type species. *Patella rugosa* Sowerby, 1816 (*non* Roeding, 1798), Bathonian, Gloucestershire (south-western England), by original designation.

Symmetrocapulus tessoni (Eudes-Deslongchamps, 1843)

(Fig. 13K–N)

* 1843 *Patella tessonii* Eudes-Deslongchamps: 113, pl. 7, figs 3, 4.

1896 *Capulus rugosus* Sowerby; Hudleston: 458, pl. 42, figs 1, 2.

1936 *Patella* (*Helcion*) *tessoni* Deslongchamps; Marzloff *et al*.: 63, pl. 9, figs 1, 1a, 2.

2003 *Symmetrocapulus rugosus* (Sowerby); Gründel: 70, pl. 8, figs 7, 8.

2005 *Symmetrocapulus tessoni* (Deslongchamps); Meiers: 52, unnumbered text-figure.

Material. MNHNL BM358. Ottange-Rumelange Quarry, Lower Bajocian (*Stephanoceras humphriesianum* zone).

Measurements. See Online Supplemental Material Table S2.

Description. The shell is medium-large in size, limpet-shaped and with somewhat anterior, seemingly down-curved apex. The shell wall is moderately thick. The height of the shell is about 40% of its length. The apex is located at the anterior fourth fifth of the shell length. The outline of the posterior slope is strongly convex. The outline of the anterior slope is markedly concave. The peristome is elliptical, slightly narrower anteriorly. The width of the peristome is about 70% of its length. The surface of the shell is ornamented by numerous, somewhat irregularly sized and spaced radial threads which increase in number by intercalation during the growth. They are less evident on the lateral surfaces of the shell and disappear on the anterior slope. The interspaces are commonly larger than the threads and sometimes bear very thin radial lines. The growth striae are strong and make the radial ornament rough. Weak, unevenly sized and spaced collabral threads ornament the apical region of the shell. During the adult growth they become indistinct from the growth striae. The whole surface of the shell is undulated by irregular, wide and very faint commarginal folds.

Remarks. Several authors (Cossmann 1885; Hudleston 1896; Haber 1932; Fischer 1969; Cox 1960b) considered *Patella tessoni* Eudes-Deslongchamps, 1843 as a synonym of *Patella rugosa* Sowerby, 1816 (p. 87, pl. 139, fig. 6; Eudes-Deslongchamps 1843, p. 112, pl. 7, figs 1, 2; Morris & Lycett 1851, p. 89, pl. 12, fig. 1a–e; Cossmann 1885, p. 349, pl. 12, figs 1–5). However, as discussed in detail by Eudes-Deslongchamps (1843), the former is distinguishable by thinner, more irregularly sized and spaced radial threads.

Distribution of the species. Lower Bajocian, Northamptonshire (England); undifferentiated Bajocian, Calvados (northern France); Upper Bajocian, Mont d'Or Lyonnais (southern France); upper Lower Bajocian, south-western Luxembourg; (?Upper) Bajocian, Franconia (southern Germany).

Genus ***Fabercapulus*** gen. nov.

Type species. *Fabercapulus semisculptus* sp. nov. (see below). Lower Bajocian, south-western Luxembourg.

Diagnosis. Limpet-shaped, moderately high shell. Apex definitely anterior. Apical shell downward pointing and dextrally coiled. Posterior profile of the shell convex. Anterior profile of the shell slightly concave. Posterior slope of adult shell corresponding to a triangular, depressed radial region edged by marginal radial folds. Peristome lying in an outward convex surface. Ornament consisting of radial riblets decussated by dense growth threads.

Derivation of name. Dedicated to Alain Faber, palaeontologist and director of the National Natural History Museum of Luxemburg. Gender masculine.

Remarks. The limpet-like shape of the adult shell and the presence of an apical region downward pointing and dextrally coiled permit to assign *Fabercapulus* gen. nov. to the family Symmetrocapulidae Wenz, 1938. *Fabercapulus* differs from *Symmetrocapulus* Dacqué, 1933 in having a depressed posterior area limited by two radial plicae.

Included species and distribution. The genus is represented only by the type species from the Lower Bajocian deposits of south-western Luxembourg.

Fabercapulus semisculptus sp. nov.

(Fig. 13O–T)

Diagnosis. Same as the genus.

Derivation of name. The name refers to the presence of a marked radial ornament on the posterior part of the shell which disappears on the anterior slope.

Holotype. MNHNL ZS101D, Fig. 13O–T.

Type locality. Rollesbierg (Differdange, south-western Luxembourg, Grand-Duchy of Luxembourg).

Type level. Lower Bajocian (*Hyperlioceras discites* Zone–*Witchellia laeviuscula* Zone).

Other Material. The material is represented only by the holotype.

Measurements. See Online Supplemental Material Table S2.

Description. The shell is medium-sized, limpet-shaped and with a quite anterior, downward oriented apical part. In anterior view the apical spire is slightly leftward bending and draws a slightly rightward curved line reflecting the presence of a dextrally coiled apical shell. The shell wall is moderately thick. The height of the shell is about one-third of its length. The apex is placed at the anterior fourth fifth of the shell length. The outline of the posterior slope is feebly convex and that of the anterior slope very slightly concave. The peristome is elliptical-subrectangular, slightly narrower posteriorly and is convex in lateral view. The width of peristome is about three-quarters of its length. The anterior peristomal margin is undulated by the presence of a light concavity. Two rounded radial folds edge a triangular, depressed region of the posterior slope and wave distinctly the posterior peristomal margin. The folds are almost indistinct on the apical area and become more and more elevated towards the posterior edge. The surface of the shell is ornamented by numerous, dense and thin collabral threads intersected by radial riblets. The radial riblets are rather wide and moderately strong on the posterior radial plicae, whereas they are weaker on the lateral areas and obscure on the anterior slope. They are separated by narrower intervals and are slightly thinner on the posterior concavity between the plicae. The surface of the shell is further ornamented by widely and irregularly spaced commarginal cords.

Remarks. Although the apical part of the shell is incomplete, some evidence shows that this part is dextrally coiled. In fact, in anterior view, the apical portion of the shell is slightly leftward inclined and the earliest part of the shell, most probably corresponding to the last whorl of the apical spire, is slightly rightward and backward curved. No species comparable to *Fabercapulus semisculptus* sp. nov. have been found.

Distribution of the species. Lower Bajocian, south-western Luxembourg.

Palaeogeographical and palaeoecological comparisons

The systematic analysis allowed recognition of 16 vetigastropod species belonging to nine genera. One genus and three species are new, namely *Szabotomaria ziqquratiformis* gen. et sp. nov., *Colpomphalus thuyi* sp. nov. and *Colpomphalus tigratus* sp. nov. In addition, two species and two genera of the neritimorph family Symmetrocapulidae have been described. One of these genera and its type species are new, namely *Fabercapulus semisculptus* gen. et sp. nov. The symmetrocapulid taxa are the only representatives of the subclass Neritimorpha presently known in the Lower Bajocian of Luxembourg. These species add to the species recently described from the same deposits by Monari & Gatto (2013, 2014) and Gatto *et al*. (2015b). The resulting list of vetigastropods and neritomorphs is reported in Online Supplemental Material Table S3. The fauna is fairly well diversified and consists of 32 species and 14 genera representing six families (Pleurotomariidae, Trochotomidae, Ataphridae, Euclyclidae, Discohelicidae and Symmetrocapulidae) and five superfamilies (Pleurotomarioidea, Turbinoidea, Eucycloidea, Discohelicoidea and Symmetrocapuloidea). *Bathrotomaria subreticulata*, *Pyrgotrochus elongatus* and *Ambercyclus ornatus* are the most frequent taxa representing 54% of the total number of specimens. *Pleurotomaria armata*, *Pleurotomaria ornata*, *Szabotomaria ziqquratiformis*, *Pyrgotrochus punctatus*, *Ataphrus acmon* and *Ooliticia recteplanata* are subordinate species with a number of specimens ranging from 4% to 7% each. This is the richest Bajocian vetigastropod-neritimorph assemblage known from a distinct stratigraphical interval and single locality or limited area of western Europe. As a comparison, 24 Lower Bajocian species were described by Gründel *et al.* (2012) from the classical locality of Kahlenberg (Baden-Württemberg, southern Germany) and 21 Upper Bajocian species from the Sengenthal-Kinding area (Franconia, southern Germany; Gründel 2003).

In order to understand the palaeobiogeographical and palaeoecological significance of this fauna, its relationship with other sub-coeval faunas from the western European shelf has been investigated by cluster analysis and by comparison of the respective taxonomic structures. It must be noted that the investigation involved a partial, though consistent sample of the gastropod communities including only the patellogastropod, vetigastropod and neritimorph groups, therefore the results have to be considered preliminary. A similar method, exclusively based on palaeobiogeografical data, has recently been used by Ferrari (2015) to analyze the distribution patterns of the Pliensbachian–Toarcian vetigastropods from Argentina. For the present study, a comprehensive faunal list of species recorded in the Upper Aalenian to Upper Bajocian deposits of western Europe have been compiled based on a critical analysis of literature sources (Sowerby J. 1812–1822; Sowerby J. de C. 1823–1835; Phillips 1829; Thorent 1838; Eudes-Deslongchamps J.C.A. 1843a, 1843b, 1849; Goldfuss 1844; d'Orbigny 1850, 1851–1860; Lycett 1850, 1853, 1857; Morris & Lycett 1851; Chapuis & Dewalque 1853; Quenstedt 1856–58, 1881–1884; Eudes-Deslongchamps E. 1860, 1864, 1866a, 1866b, 1868; Dumortier, 1860, 1874; Terquem & Jourdy 1869; Mayer 1871; Tawney 1873; Hermite 1877; Hudleston 1884, 1885, 1889, 1892, 1894, 1895 1896; Greppin, 1898; Riche 1904; Sieberer 1907; Brösamlen 1909; Thevenin 1909; Roman & Gennevaux 1912; Rollier 1918; Cossmann 1919; Riche & Roman 1921; Haber 1932, 1934; Roman 1935; Marzloff *et al*. 1936; Kuhn 1938; Gardet & Gérard 1946; Cox & Arkell 1949; Fischer 1977; Kästle 1990; Fischer & Weber 1997; Gründel 1997, 2000, 2003, 2009; Conti & Monari 2001; Hägele 2003, 2004; Meyers 2005; Lazar 2006; Gründel *et al.* 2012; Monari & Gatto 2013, 2014; Gründel & Hostettler 2014; Gatto *et al*. 2015b). The stratigraphical interval has been selected based on the average stratigraphical range of the species concerned. Only species for which systematic information was sufficient to verify their taxonomic attribution have been used and priority has been given to those records for which stratigraphical data at substage or ammonite zones level and facies information were available. Based on these assumptions, 176 species have been selected (Table 1) and their supraspecific taxonomy updated by personal observations on the original type material, or by critical evaluation of published sources. Besides the Luxembourg Basin, seven palaeogeographical units provided faunal lists with a significant number of species for a comparative study, namely the Central High Atlas (Morocco), Rhone Basin (southern France), Swabia and Franconia (southern Germany), Calvados (northern France), Wessex Basin (southern England) and East Midlands Shelf (eastern England) (Fig. 14). Other regions with known important gastropod assemblages, such as the northern Germany, the Cotswolds (southern England) and the Cleveland Basin (north-eastern England) have been excluded because the number of species in the selected stratigraphical interval was insufficient for the statistical analysis. Presence-absence matrices were obtained from the dataset of Table 1 and then treated by UPGMA cluster analysis using Simpson, Dice and Jaccard similarity coefficients. More in detail, two matrices based on different time slices have been made. The first matrix includes all the species occurring within the upper Aalenian to upper Bajocian interval, independently from the extension of their total stratigraphical range. The second matrix takes into account narrower stratigraphical intervals selected on the basis of the quality of the stratigraphical information and of the number of species represented in each areas. These are as follows: Upper Aalenian for Rhone Basin, Upper Aalenian–Lower Bajocian for Central High Atlas, Upper Aalenian–Lower Bajocian and Upper Bajocian for Wessex Basin, Lower Bajocian for Luxembourg and East Midland Shelf, Lower Bajocian–lowermost Upper Bajocian for Swabia, uppermost Lower Bajocian–Upper Bajocian for Franconia, and Upper Bajocian for Calvados.

There is a strong correspondence between the mid-Jurassic palaeogeography of western Europe and the results of the cluster analysis. All dendrograms detect a major cluster that includes two main branches: one comprises the northern Paris-Wessex Basin and the Luxembourg area, the other corresponds to the southern Germany Basin (Fig. 15). The first matrix produced Simpson, Dice and Jaccard dendrograms with the same topology. Simpson dendrogram is reported in Figure 15A. It shows clearly that the fauna of Luxembourg has the closest relationship with those of the Calvados and Wessex, i.e. the northern Paris Basin and its southern England extension. The application of the cluster analysis to the second matrix supports these results and helps to clarify some aspects of the faunal relationships (Fig. 15B, C). The dendrograms show that the close association between the Calvados and Wessex faunas is determined by the similarity between their respective Upper Bajocian components, whereas the closeness of the Lower Bajocian fauna of Luxembourg to the Calvados-Wessex cluster reflects its similarity with the sub-coeval fauna of the Wessex.

The dataset in Table 1 has also been used to reconstruct the taxonomic structure of the vetigastropod-neritimorph component of the selected faunas (Fig. 16). The Lower Bajocian fauna of Luxembourg is distinctly dominated by pleurotomariid species. The Eucycloidea and the Ataphridae are subordinate groups, and the Trochotomidae, Discohelicidae and Neritimorpha

(Symmetrocapulidae) are occasional components. The same framework is basically recognizable in the faunas of Calvados, Wessex, Swabia and Franconia, apart from local differences in the minor taxa and presence/absence of other accessory groups (e.g. Proconulidae and Cirridae). Only the family Nododelphinulidae seems to defy a simple interpretation, being well represented in Swabia and Wessex, poorly represented in Calvados and absent in Franconia and Luxembourg. The similarity in taxonomic structure of these faunas most probably reflects facies similarities. Almost all these assemblages come from condensed successions with evidences of reworking, erosion and non-deposition surfaces, such as the 'oolithe ferrugineuse de Bajeux' in the Paris Basin (Rioult *et al*. 1991; Préat *et al*. 2000), the 'ironshot' beds of the Inferior Oolite in the Wessex Basin (Gatrall 1969; Chandler & Sole 1996) and the 'Parkinsonien-Oolith' in Franconia (Callomon *et al*. 1987; Kästle 1990; Arp 2001). The dominant facies in these successions are marls and limestones with iron ooids and other ferruginous structures, such as microstromatolites, coatings and hardgrounds. Even in the successions of Swabia, where claystone and marls are the prevailing sediments, the gastropod assemblages mostly come from iron ooids-rich, more calcareous levels or lenses, e.g. the ‘Geisingen-Oolith’ (Gründel *et al.* 2011; Dietze *et al*. 2014), the ‘Humphriesi-Oolith’ and the 'Blaukalk' (Gründel *et al*. 2012; Dietze *et al*. 2009, 2013). Although the genesis of iron ooids is not yet completely understood, most authors agree that they form in moderately deep to shallow water environments during periods of sediment starvation/reworking (see review in Young 1989; Burkhalter 1995; Ferretti 2005). Favourable conditions for the deposition of iron ooid-rich sediments and other ironstones were apparently rather common in the Jurassic (Van Houten 1985; Norris & Hallam 1995) and have been linked to sea-level changes (Hallam & Bradshaw 1979; Dill 2012). Recent studies showed that, at least in the Jurassic epicontinental seas, these deposits formed frequently in relatively deep-water, open marine shelf settings, below fair-weather wave base or near to storm wave base (Fürsich *et al*. 1992; Préat *et al*. 2000; Collin *et al*. 2005; Lazăr *et al*. 2013). This picture agrees well with the already mentioned interpretation of the Lower Bajocian succession of the north-eastern Paris Basin and Luxembourg as having been deposited in offshore to shoreface zones.

Although a wide-scale interpretation of the relationship between all the faunas involved in the analysis is out of the scope of this paper, which is mainly focused on the Luxembourg fauna, some points concerning the southern Germany and East Midlands faunas deserve consideration. The Swabia-Franconia cluster most probably reflects the geographical closeness and continuity between these regions. Its separation from the Anglo-Paris branch could be explained by the slightly different sedimentary context of the southern German sea, which was influenced by a more consistent siliciclastic supply (Callomon 2003; Pieńkowski *et al*. 2008). The Lower Bajocian fauna of the East Midlands Shelf is definitely different from other western European faunas here considered. The distinctness of this fauna was already known to Hudleston (1888, p. 73) who noted:

> 'one thing must strike the most casual observer, and that is the extraordinary difference between the gasteropod fauna of Dorsetshire, and of the Lincolnshire Limestone. Some forms, it is true, are merely micromorphs of species occurring elsewhere; but even granting that, the contrasts are enormous'.

Species shared between the East Midlands Shelf and the other faunas considered are indeed very few. Consequently, the similarity coefficients are extremely low and this determines the constant position of the East Midlands fauna at the root of the dendrograms. Also the taxonomic structure is strongly different being much more complex and diversified, and composed of several groups, none of which distinctly dominant (Fig. 16). A facies control may be invoked to explain, at least in part, this striking contrast with the fauna of the relatively close Wessex basin. In Late Aalenian–Early Bajocian times, the East Midlands Shelf was a very shallow water carbonate shelf and the upper member of the Lincolnshire Limestone, which contain the gastropod assemblages here considered, was deposited in a oolitic barrier complex at the margin of a lagoon (Asthon 1980).

Finally, the relationships of the vetigastropods and neritimorphs of the Central High Atlas and of the Rhone Basin with the other faunas studied change among dendrograms, indicating that they are sensitive to the similarity coefficient used and to the stratigraphical interval considered. These results are not easily explained and deserve further investigations.

The analysis of a more complete dataset including other gastropod groups, such as the caenogastropods and heterobranchs is clearly needed to verify these preliminary results and could represent a further step in the reconstruction of the relationship between the Aalenian–Bajocian benthic communities of the western European epicontinental seas.

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CAPTIONS

Figure 1. Geographical map and Lower Bajocian stratigraphical succession cropping out in the study area. **A**, location of the outcrops; grey lines, motorways; thin double lines, national roads and main byroads ; 1, Ottange-Rumelange quarry; 2, Giele Botter; 3, Rollesbierg; 4, Piedmont (Longwy). **B**, Schematic stratigraphical succession. The numbers indicates the levels yielding gastropods and the corresponding outcrops.

Figure 2. Dimensions of the specimens reported in the systematic descriptions and in Tables 1 and 2. **A**, cap-shaped shells. **B**, trochospiral shells. H, height of the shell; HL, height of the last whorl; HA, height of the peristome; Hap, height of the apex; L, length of the shell; LP, distance of the apex from the posterior margin; W, width of the shell; WA, width of the peristome; α_{ap}, apical angle; α_{pl}, pleural angle; α_{m}, mean spiral angle.

Figure 3. *Bathrotomaria subreticulata* (d'Orbigny, 1850). **A–D**, MNHNL BU103, apertural, dorsal and basal views, and detail of the last whorl, Rollesbierg; **E–I**, MNHNL RB376I, basal, dorsal and apertural views, detail of the penultimate whorl and of the apical spire, Rollesbierg; **J–L**, MNHNL BU131, basal, dorsal and apertural views, Rollesbierg; **M, N**, MNHNL ZS154, apical and dorsal views, Differdange area; **O**, MNHNL RB105, lateral view, Rollesbierg; **P, Q**, MNHNL ZS525, dorsal and basal views, Differdange area; **R–T**, MNHNL ZS312, apertural, basal and dorsal views, Giele Botter; **U, V**, MNHNL ZS175A, detail of the last whorls and subdorsal view, Rollesbierg; Lower Bajocian.

Figure 4. *Szabotomaria ziqquratiformis* sp. nov. **A–D**, MNHNL RB245B, apertural, basal and dorsal views, and detail of the penultimate whorl, Rollesbierg; **E–H**, MNHNL BU122, dorsal, apertural, lateral and basal views, Rollesbierg; **I–L**, MNHNL MDB230, apical, apertural, basal and dorsal views, Differdange area; **M–R**, MNHNL MDB255, apertural, basal, dorsal and apical views, detail of the spire, and detail of the penultimate and last whorls, Differdange area; **S, T**, MNHNL RB255, apertural and dorsal views, Rollesbierg; **U**, MNHNL ZS367, dorsal view, Giele Botter; **V–X**, MNHNL ZS494S2, dorsal, basal and apertural views, Differdange area; Lower Bajocian.

Figure 5. *Obornella granulata* (Sowerby, 1818). **A–G**, MNHNL BU229, dorsal, apical, lateral, basal and apertural views, detail of the last whorl and of the penultimate whorl in apical view, Piedmont (Longwy, Meurthe-et-Moselle, north-eastern France); Lower Bajocian.

Figure 6. *Pyrgotrochus punctatus* (Sowerby, 1818). **A–C**, MNHNL BU120A, apertural, basal and dorsal views, Rollesbierg; **D–G**, MNHNL BU120B, apertural view, detail of the early spire, basal and dorsal views, Rollesbierg; **H–J**, MNHNL ZS233A, basal and dorsal views, and detail of the last whorl, Giele Botter; **K, L**, MNHNL ZS179, dorsal view and detail of the early spire, Rollesbierg; **M–P**, MNHNL ZS510, dorsal, apertural and basal views, and detail of the last whorl, Differdange area; **Q–T**, MNHNL ZS321C, apertural, basal and dorsal views, and detail of the penultimate whorl, Differdange area; **U**, MNHNL ZS163, apertural view, Rollesbierg; **V–Z**, MNHNL RB298, dorsal, basal and apertural views, detail of the penultimate whorl and of the inner lip, Rollesbierg; Lower Bajocian.

Figure 7. *Pyrgotrochus elongatus* (Sowerby, 1818). **A–E**, MNHNL ZS322, apertural, basal, lateral and dorsal views, and detail of the last whorl, Giele Botter; **F, G**, MNHNL RB139, dorsal view and detail of the early spire, Rollesbierg; **H–K**, MNHNL ZS494E, basal and apertural views, detail of the early spire and of the last whorl, Differdange area; **L–O**, MNHNL ZS151, basal, dorsal and apertural views, and detail of the inner lip, Differdange area; **P–S**, MNHNL ZS187A, dorsal and basal views, detail of the penultimate whorl, and apertural view, Giele Botter; **T–V**, MNHNL ZS172A, dorsal, basal and apertural views, Rollesbierg; Lower Bajocian.

Figure 8. *Trochotoma affinis* Eudes-Deslongchamps, 1843. **A–G**, MNHNL ZS106, apertural, apical, basal, lateral and dorsal views, detail of the last whorl and of the pre-peristomal region, Rollesbierg; **H, I**, MNHNL ZS488B, apertural and basal views, Giele Botter; **J–L**, MNHNL ZS373, apical, dorsal and apertural views, Differdange area; **M–P**, MNHNL RB342, apertural, basal and dorsal views, and detail of the antepenultimate and penultimate whorls, Rollesbierg; Lower Bajocian.

Figure 9. *Ataphrus acmon* (d'Orbigny, 1850). **A–C**, MNHNL BU137B2, apertural, basal and dorsal views, Rollesbierg; **D–F**, MNHNL RB376C1, basal, apertural and dorsal views, Rollesbierg; **G–K**, MNHNL RB376C2, basal, dorsal and apertural views, detail of the inner lip, and detail of the early spire and protoconch, Rollesbierg; **L–P**, MNHNL BU137B4, basal, dorsal, lateral and apertural views, and detail of the early spire, Rollesbierg; **Q–T**, MNHNL MDB249F, dorsal, lateral, basal and apertural views, Differdange area; **U–Y**, MNHNL BU137B3, apertural, basal, dorsal and apical views, and detail of the early spire and protoconch, Rollesbierg; Lower Bajocian.

Figure 10. Other species of *Ataphrus* Gabb, 1869. **A–E**, *Ataphrus obtortus* (Hudleston, 1894), MNHNL BU137B6, apertural, basal, lateral and dorsal views, and detail of the early spire and protoconch, Rollesbierg; Lower Bajocian. **F–O**, *Ataphrus laevigatus* (Sowerby, 1818); **F–J**, MNHNL RB041C, dorsal, apertural, lateral, basal and apical views, Rollesbierg; **K–O**, MNHNL RB055C, basal, apertural, apical and dorsal views, and detail of the early spire, Rollesbierg; Lower Bajocian.

Figure 11. Species of *Ambercyclus* Ferrari, Kaim & Damborenea, 2014. **A–D**, *Ambercyclus orbignyanus* (Hudleston), BM382, dorsal, apertural, basal and lateral views, Ottange-Rumelange Quarry; Lower Bajocian. **E–U**, *Ambercyclus ornatus* (Sowerby); **E–F**, MNHNL MDB249B, apertural, basal, dorsal and lateral views, Differdange area; **I, J**, MNHNL RB376A1, basal and apertural views, Rollesbierg; **K, L**, MNHNL ZS249B, subapertural view and detail of the apical spire, Giele Botter; **M, N**, MNHNL ZS292, apertural view and detail of the penultimate whorl, Giele Botter; **O–Q**, MNHNL RB376A2, dorsal, apertural and basal views, Rollesbierg; **R–U**, MNHNL RB311J, dorsal, lateral and apertural views, and detail of the last whorl, Rollesbierg; Lower Bajocian. **V–Z**, *Ambercyclus praetor* (Goldfuss), MNHNL RB376E, basal, apertural, dorsal and apical views, and detail of the penultimate whorl, Rollesbierg; Lower Bajocian.

Figure 12. Species of *Ooliticia* Cossmann, 1893. **A–J**, *Ooliticia polytimeta* (Hudleston, 1892); **A–D**, MNHNL RB311H1, apertural, basal and dorsal views, and detail of the inner lip, Rollesbierg; **E, F**, MNHNL ZS384, dorsal view and detail of the last whorl, Giele Botter; **G–J**, MNHNL BU137C2, apical, dorsal, apertural and basal views, Rollesbierg; Lower Bajocian. **K–Y**, *Ooliticia recteplanata* (Tawney, 1873); **K–O**, MNHNL BU137C1, apertural, basal and dorsal views, detail of the inner lip and of the penultimate whorl, Rollesbierg; **P–S**, MNHNL RB311H2, apertural, dorsal, lateral and basal views, Rollesbierg; **T**, MNHNL ZS391, detail of the apical spire, Differdange area; **U–X**, MNHNL MDB277, basal, apertural, lateral and dorsal views, Giele Botter; **Y**, MNHNL RB311H3 and MNHNL RB311H4, lateral views, Rollesbierg; Lower Bajocian.

Figure 13. Discohelicidae Schröder, 1995 and Symmetrocapulidae Wenz, 1938. **A–E**, *Colpomphalus thuyi* sp. nov., holotype MNHNL ZS124B, apertural, apical, dorsal and basal views, and detail of the surface of the last two whorls in apical view, Rollesbierg, Lower Bajocian. **F–J**, *Colpomphalus tigratus* sp. nov., holotype MNHNL ZS124A, apical, apertural, basal and dorsal views, and detail of the lateral surface of the last whorl, Rollesbierg; Lower Bajocian. **K–N**, *Symmetrocapulus tessoni* (Eudes-Deslongchamps, 1843), MNHNL BM358, lateral, anterior and

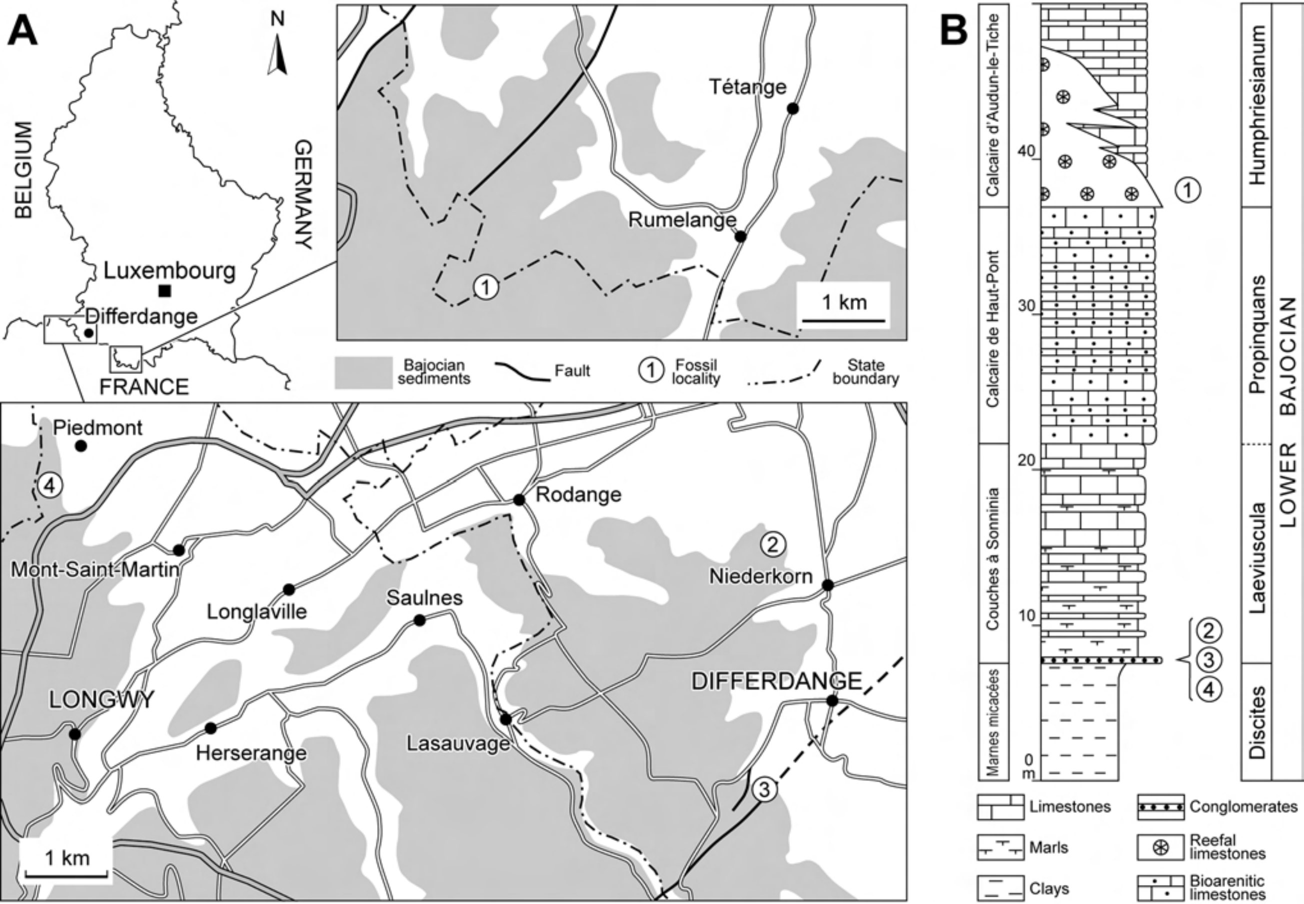
apical views, and detail of the ornament, Ottange-Rumelange Quarry; Lower Bajocian. **O–T**, *Fabercapulus semisculptus* sp. nov., holotype MNHNL ZS101D, apical, lateral, anterior and posterior views, detail of the apical part and of the ornament, Rollesbierg; Lower Bajocian.

Figure 14. Palaeogeographical map of western European epicontinental shelf during the Bajocian (Middle Jurassic) with the location of the palaeogeographical units selected for the comparative analysis. Asterisk (*) indicates the Luxembourg basin. AR, Armorica; BM, Bohemian Massif; IM Iberian Massif; IrM, Irish Massif; LBM, London-Brabant-Ardennes Landmass; MC, Massif Central; MM, Moroccan Meseta; RM, Rhenish Massif; SCM, Sardinia-Corsica Massif. Map redrawn and simplified from Ziegler (1988), Bradshaw *et al*. (1992) and Dercourt *et al*. (2000).

Figure 15. Dendrograms of Q-mode cluster analysis with the UPGMA representing the relationships among Upper Aalenian–Upper Bajocian patellogastropod, vetigastropod and neritimorph components of selected western European faunas. **A**, dendrogram based on Simpson coefficient for a matrix including all the species present within the Upper Aalenian to Upper Bajocian interval; **B**, **C**, dendrograms based on Simpson and Dice coefficients for a matrix considering selected stratigraphical intervals. See text for details. UA, Upper Aalenian; LB, Lower Bajocian; MB, uppermost Lower Bajocian to lowermost Upper Bajocian; UB, Upper Bajocian; shaded areas, major clusters discussed in the text.

Figure 16. Histograms showing the taxonomic composition at family rank of the patellogastropod, vetigastropod and neritimorph components in selected western European faunas (see text for details).

TABLE 1. Upper Aalenian–Bajocian patellogastropod, vetigastropod and neritimorph species of selected palaeobiogeographical units included in the cluster analysis and in the computation of the taxonomic structure. RB, Rhone Basin (southern France); SL, southern Luxembourg and eastern Lorraine; CA, Calvados (northern France); SW, Swabia (southern Germany); FR, Franconia (southern Germany); WB, Wessex Basin (southern England); EM, East Midlands Shelf (eastern England); HA, central High Atlas (Morocco); UA, Upper Aalenian; LB, Lower Bajocian; MB, undifferentiated uppermost Lower Bajocian–lowermost Upper Bajocian; mBj, Bajocian, condensed Humphriesianum-Garantiana Zones; UB, Upper Bajocian; UnBj, undifferentiated Bajocian. See text for details.



A
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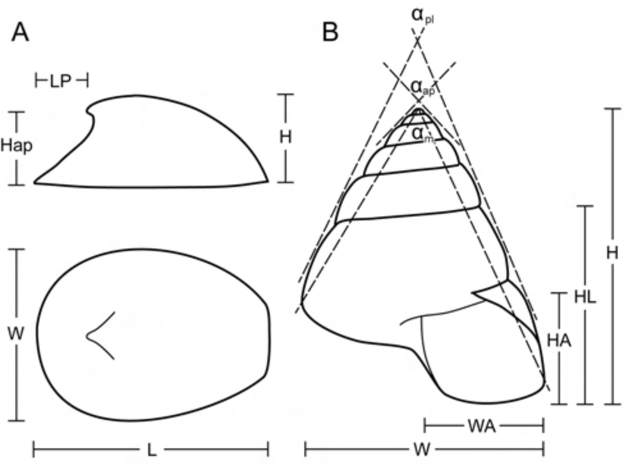
BELGIUM
GERMANY
FRANCE
Luxembourg
Differdange
Tétange
Rumelange
1 km
Bajocian sediments
Fault
Fossil locality
State boundary
Piedmont
Rodange
Mont-Saint-Martin
Longlaville
Saulnes
Niederkorn
DIFFERDANGE
LONGWY
Herserange
Lasauvage
Calcaire d'Audun-le-Tiche
Calcaire de Haut-Pont
Couches à Sonninia
Marnes micacées
Humphriesianum
Propinquans
Laeviuscula
Discites
LOWER BAJOCIAN
0 m
10
20
30
40
Limestones
Marls
Clays
Conglomerates
Reefal limestones
Bioarenitic limestones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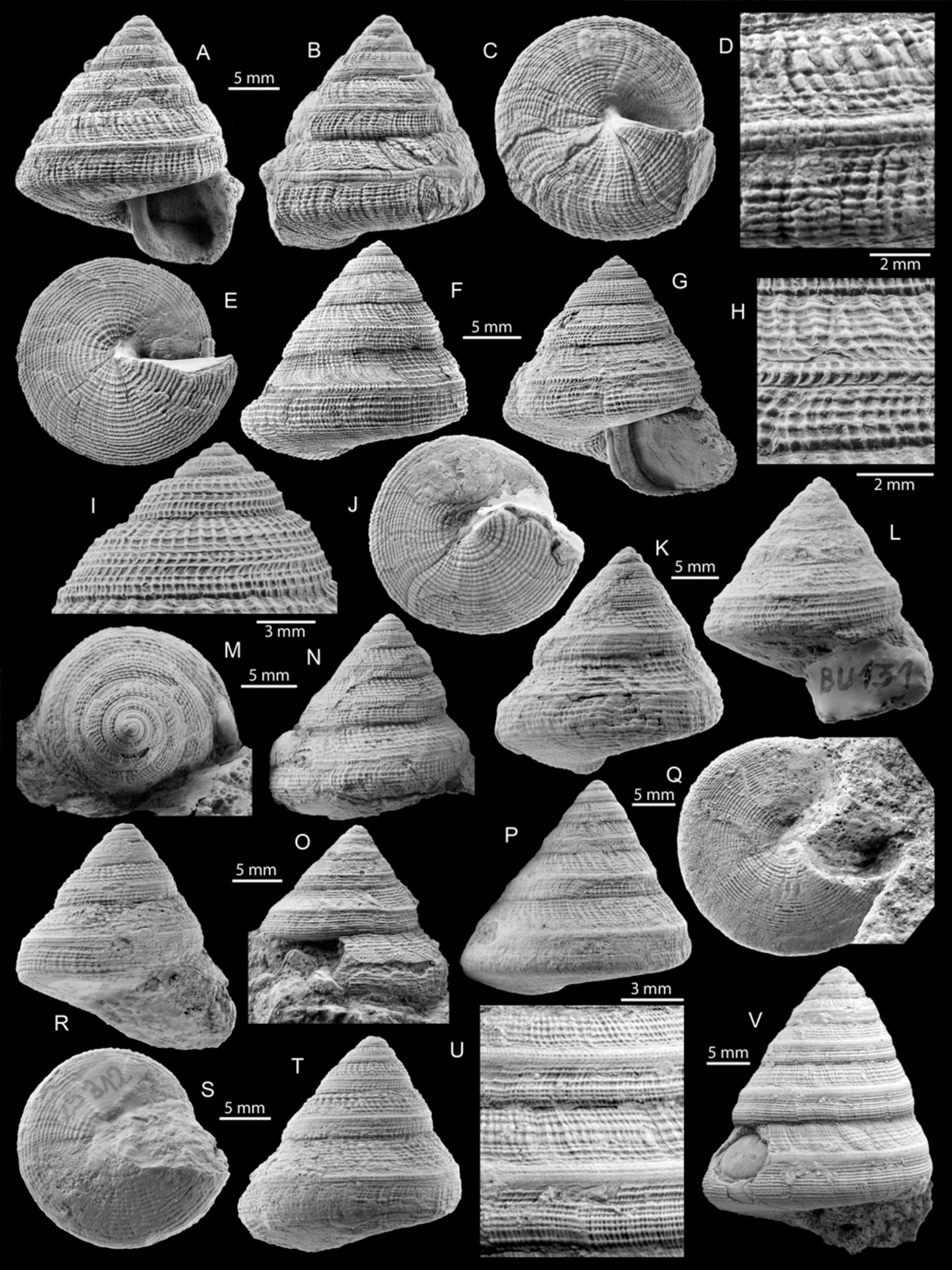
αpl
αap
αm
H
HL
HA
WA
W



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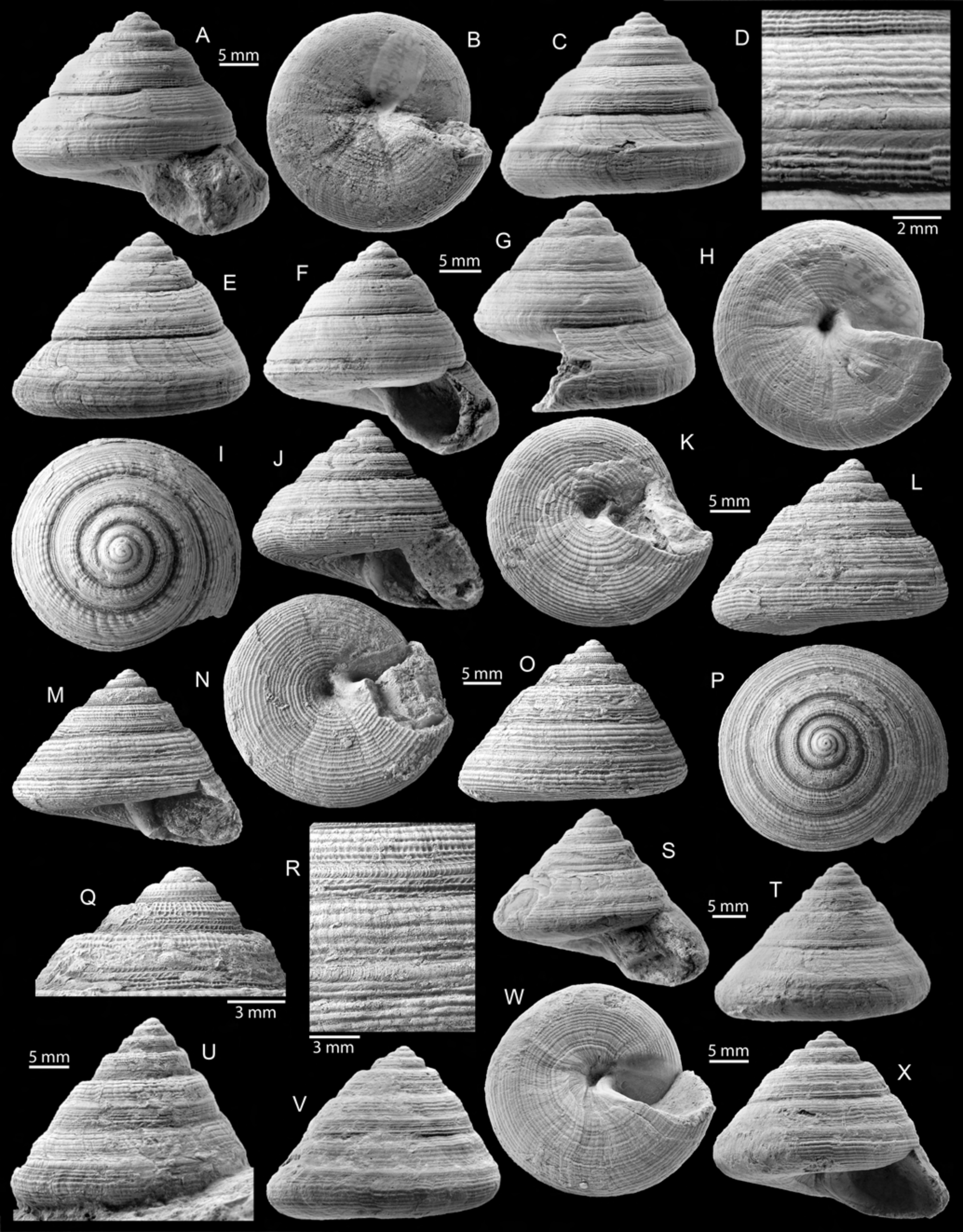
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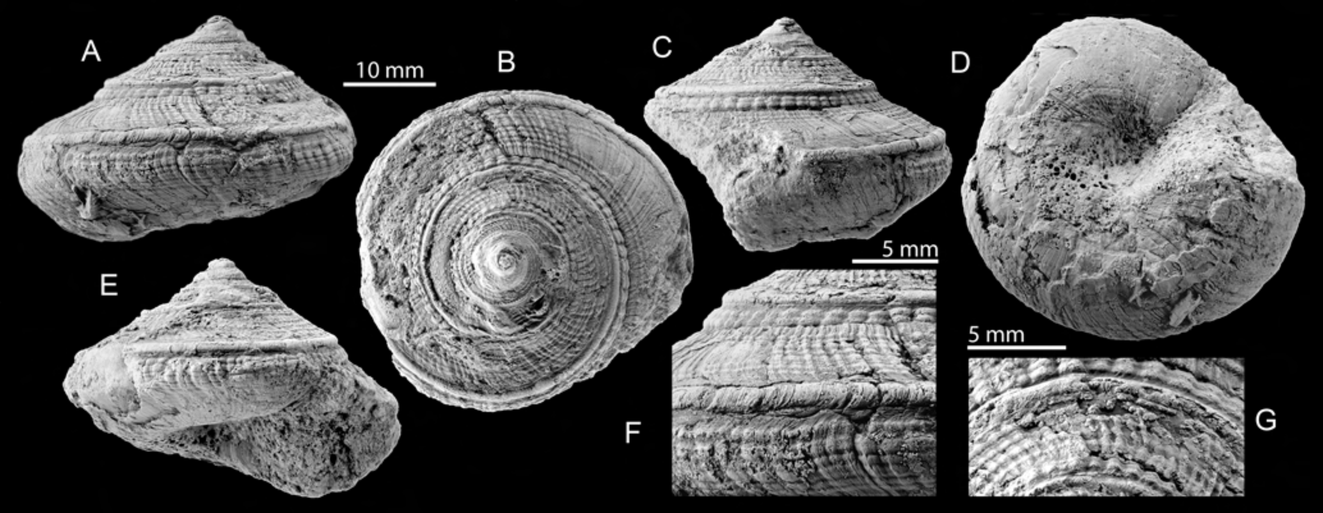
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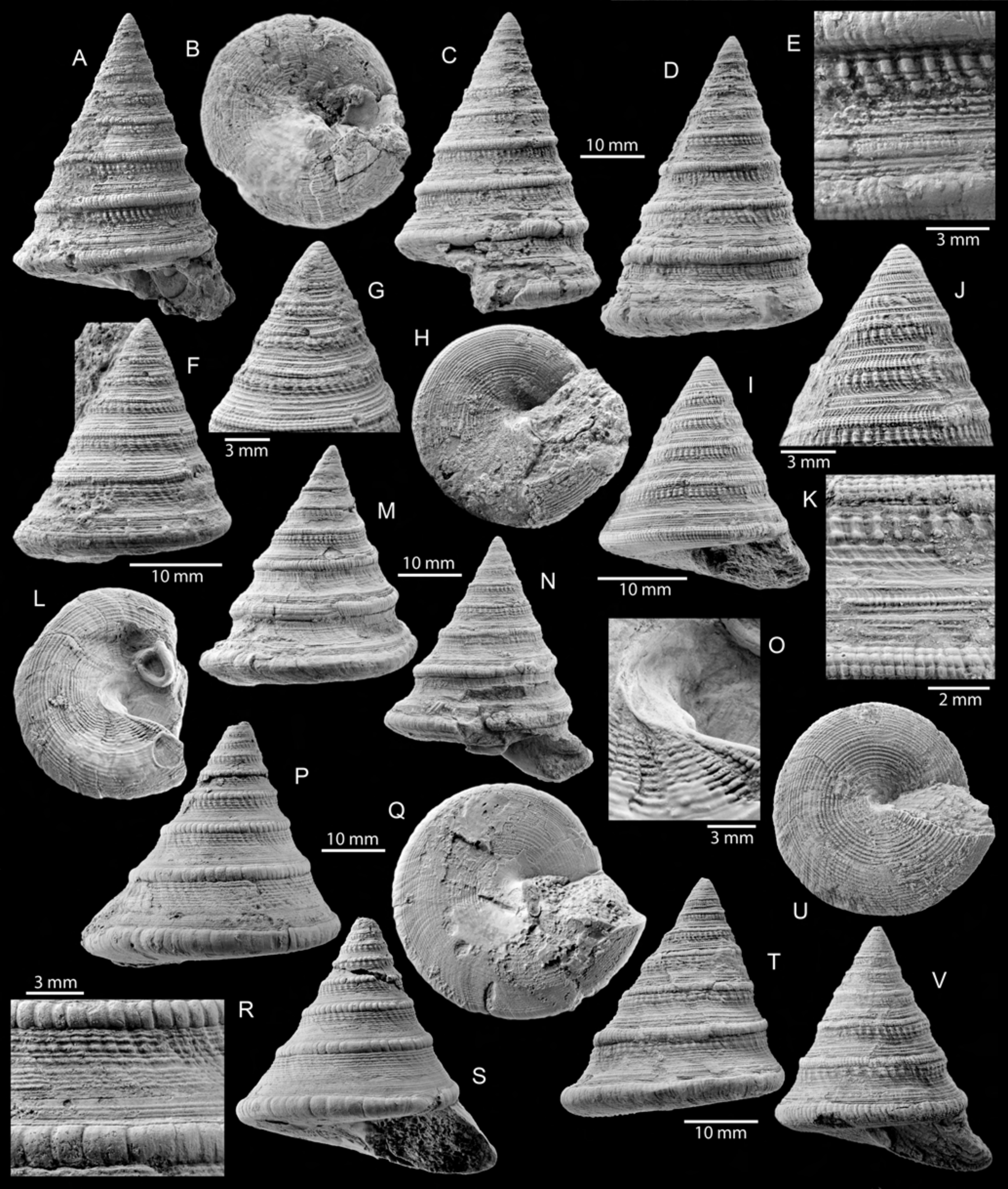
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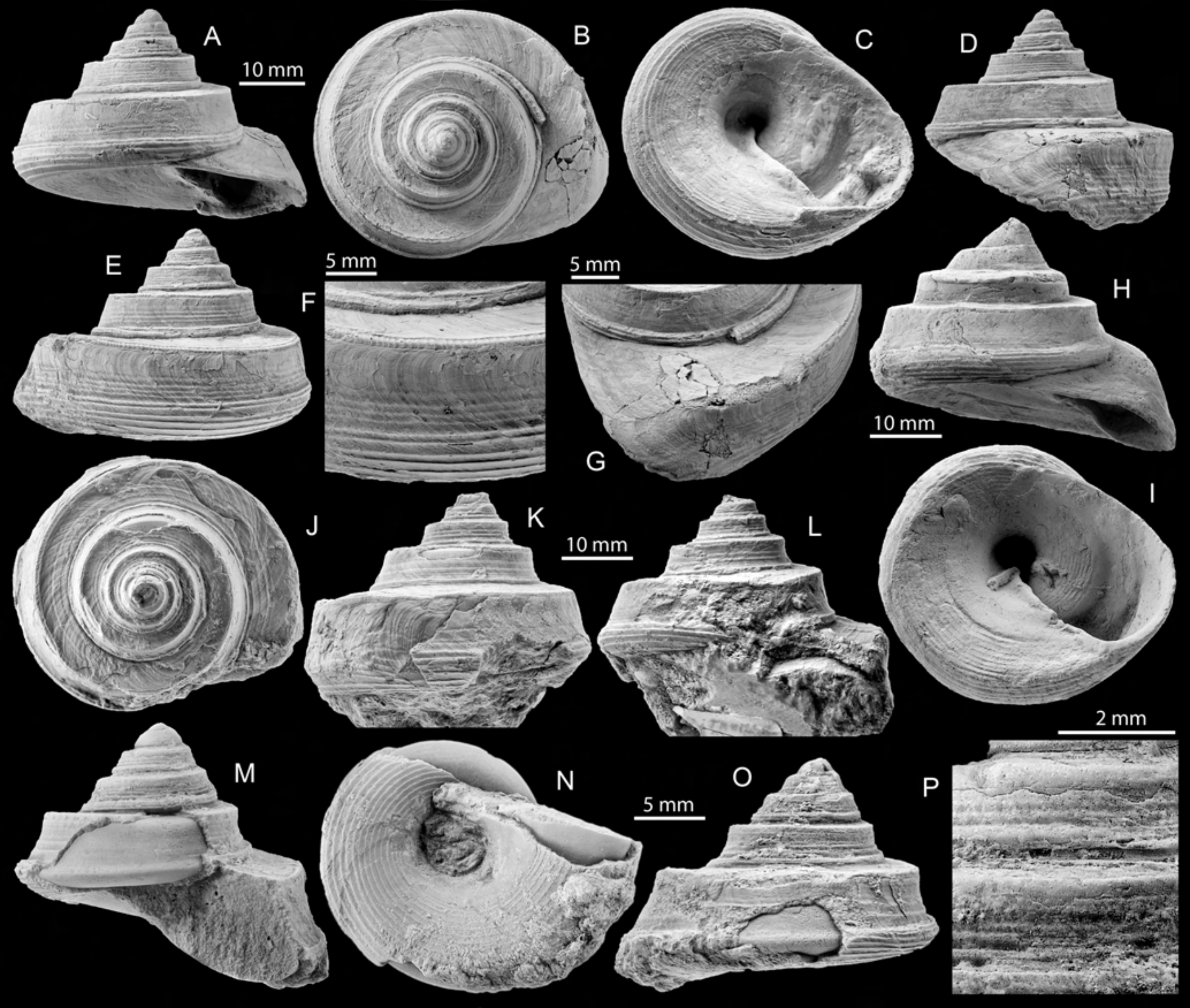
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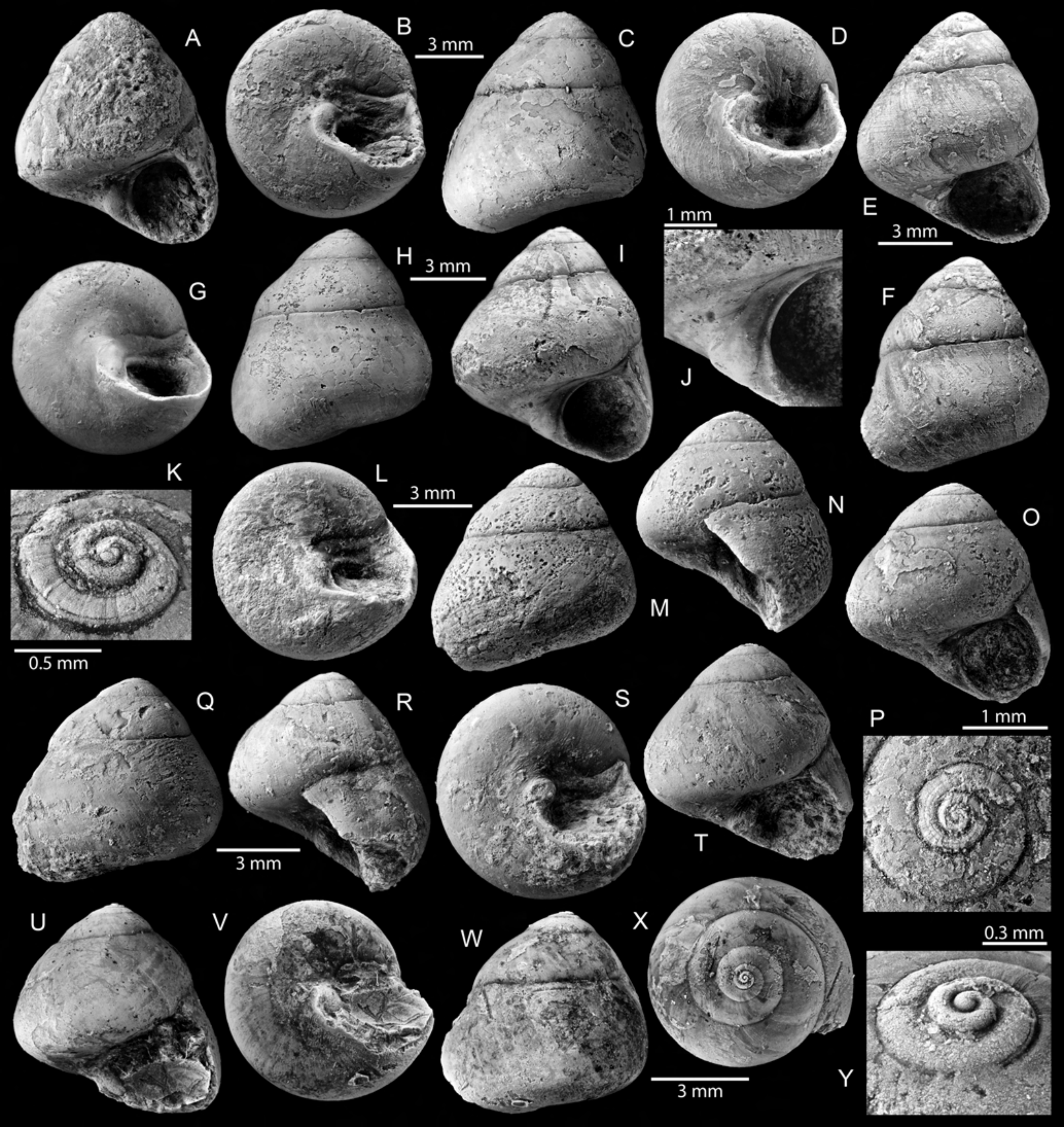
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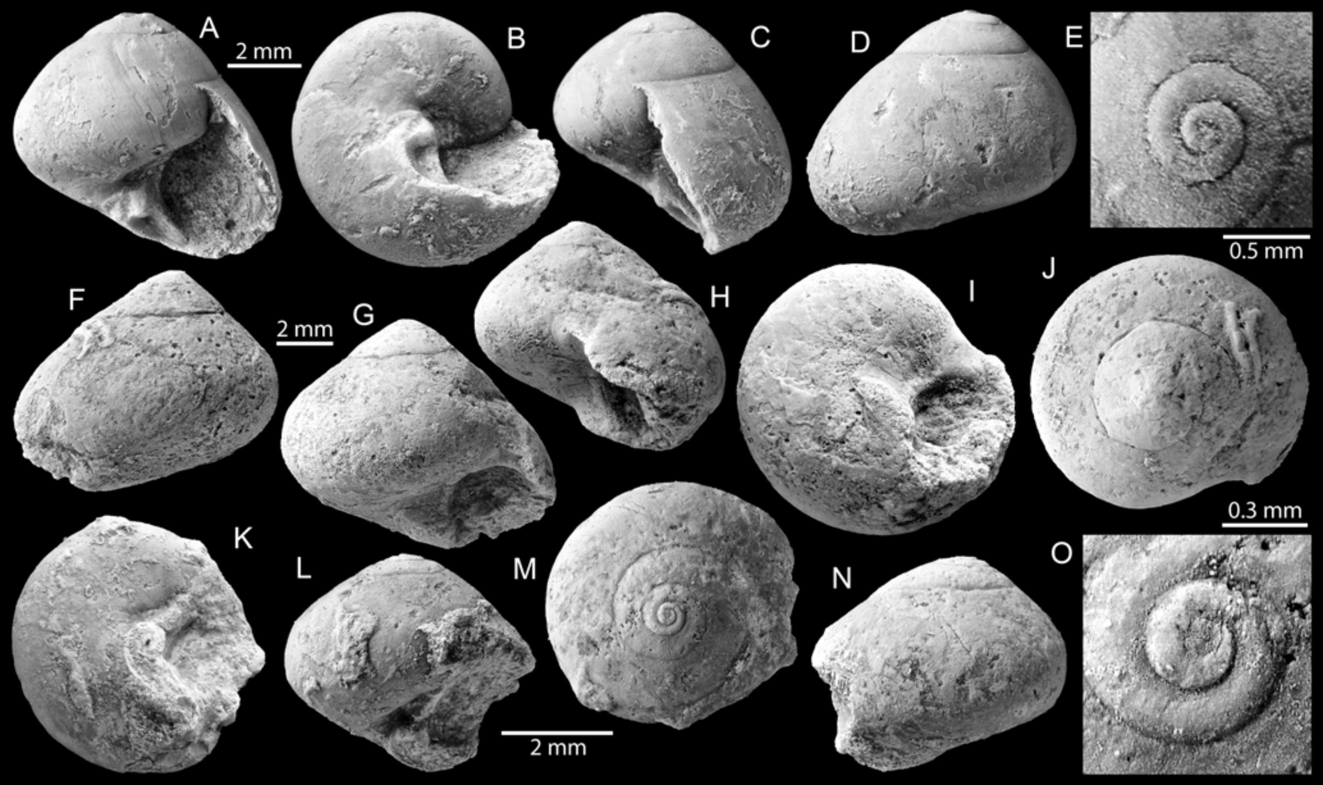
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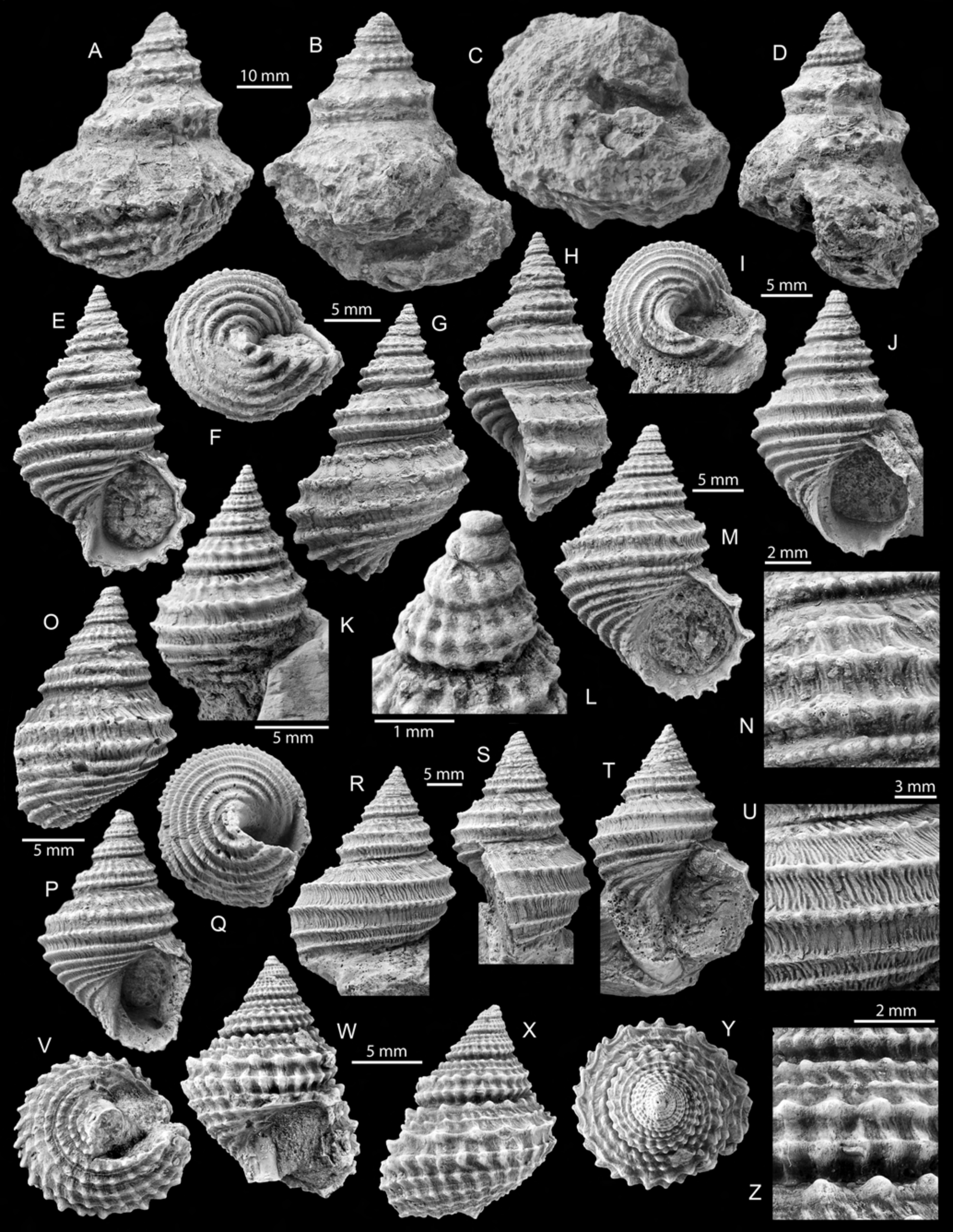

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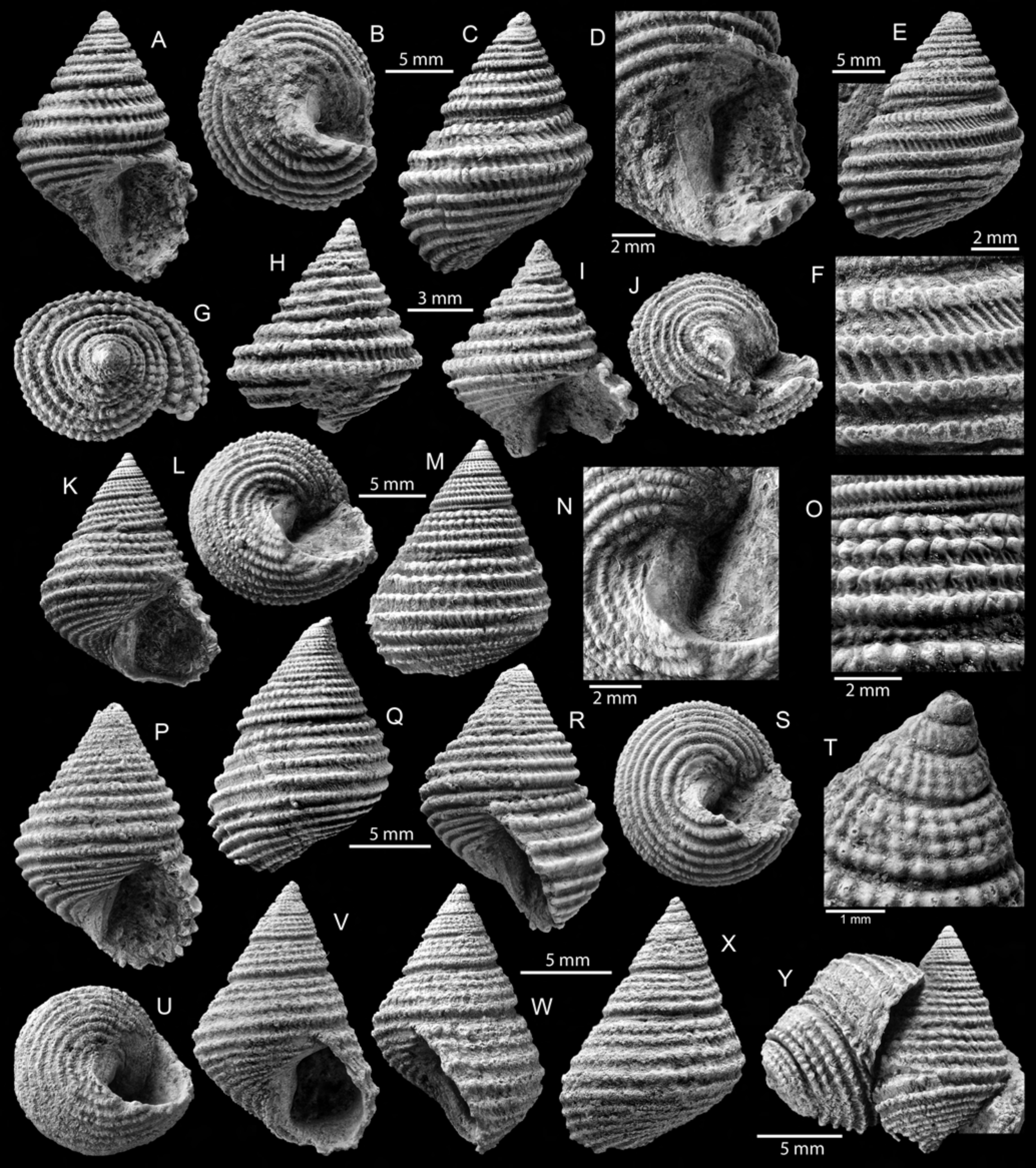

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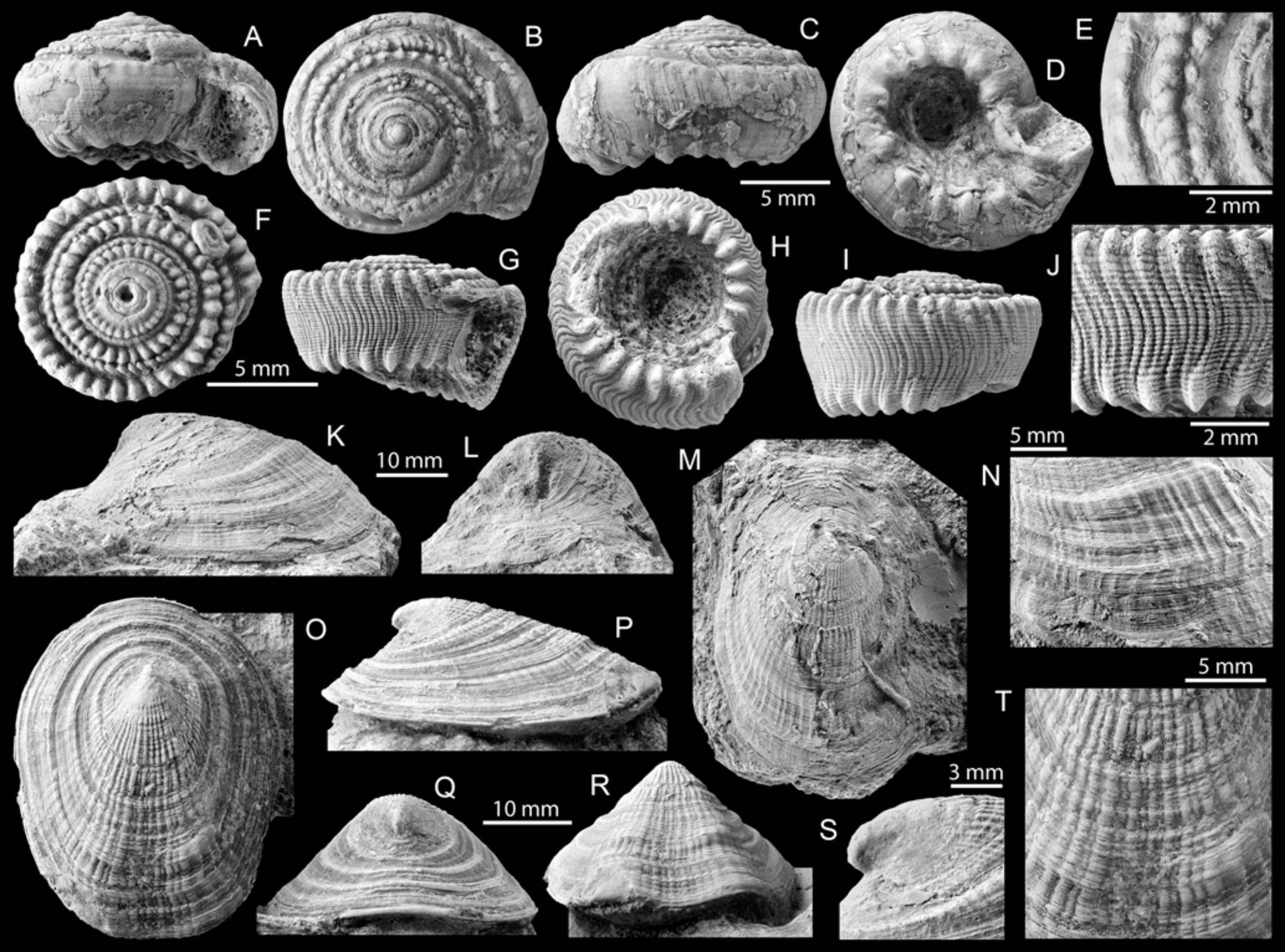
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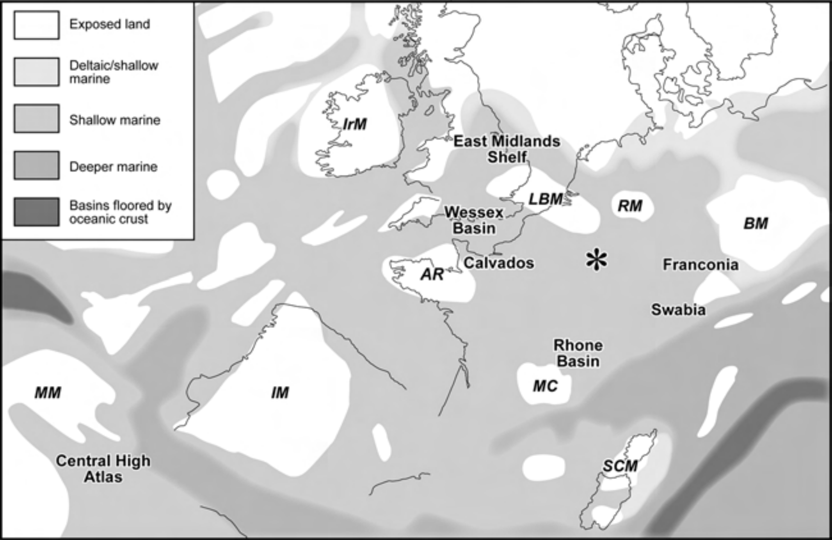
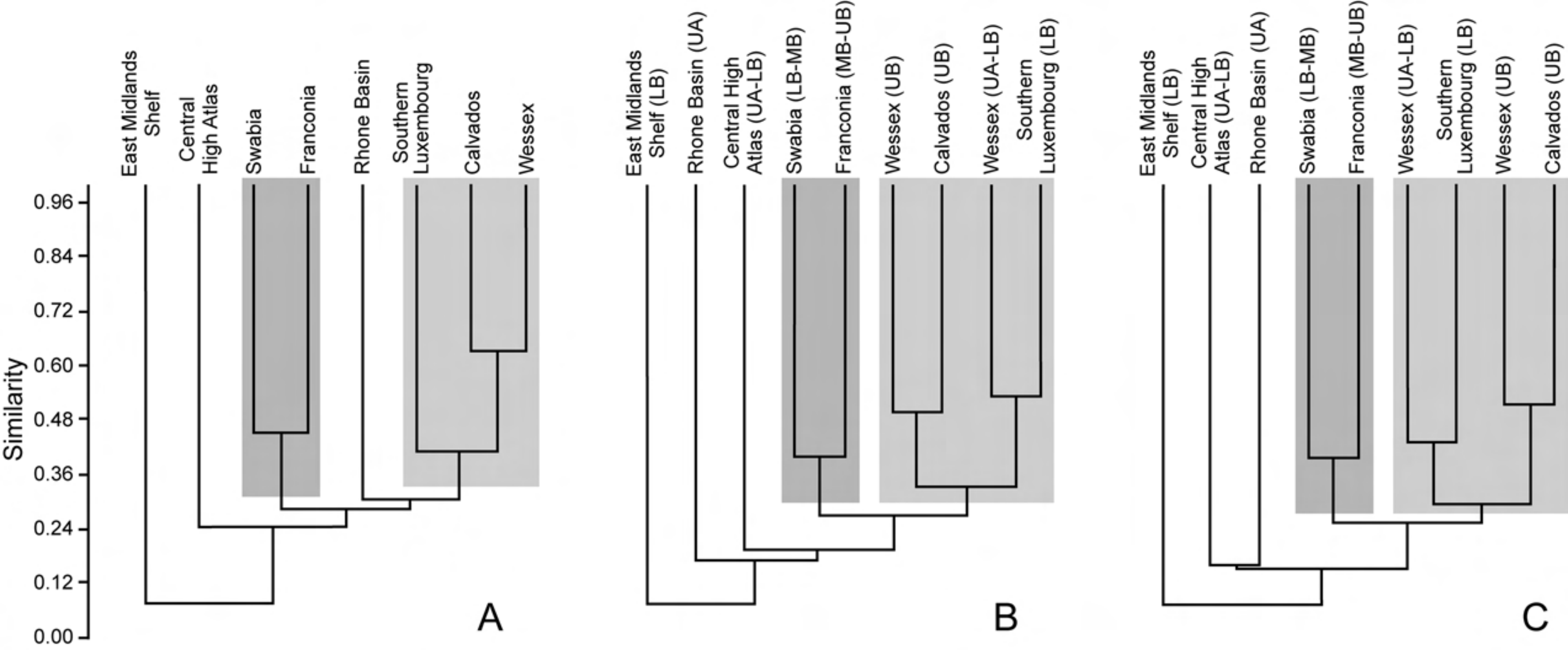
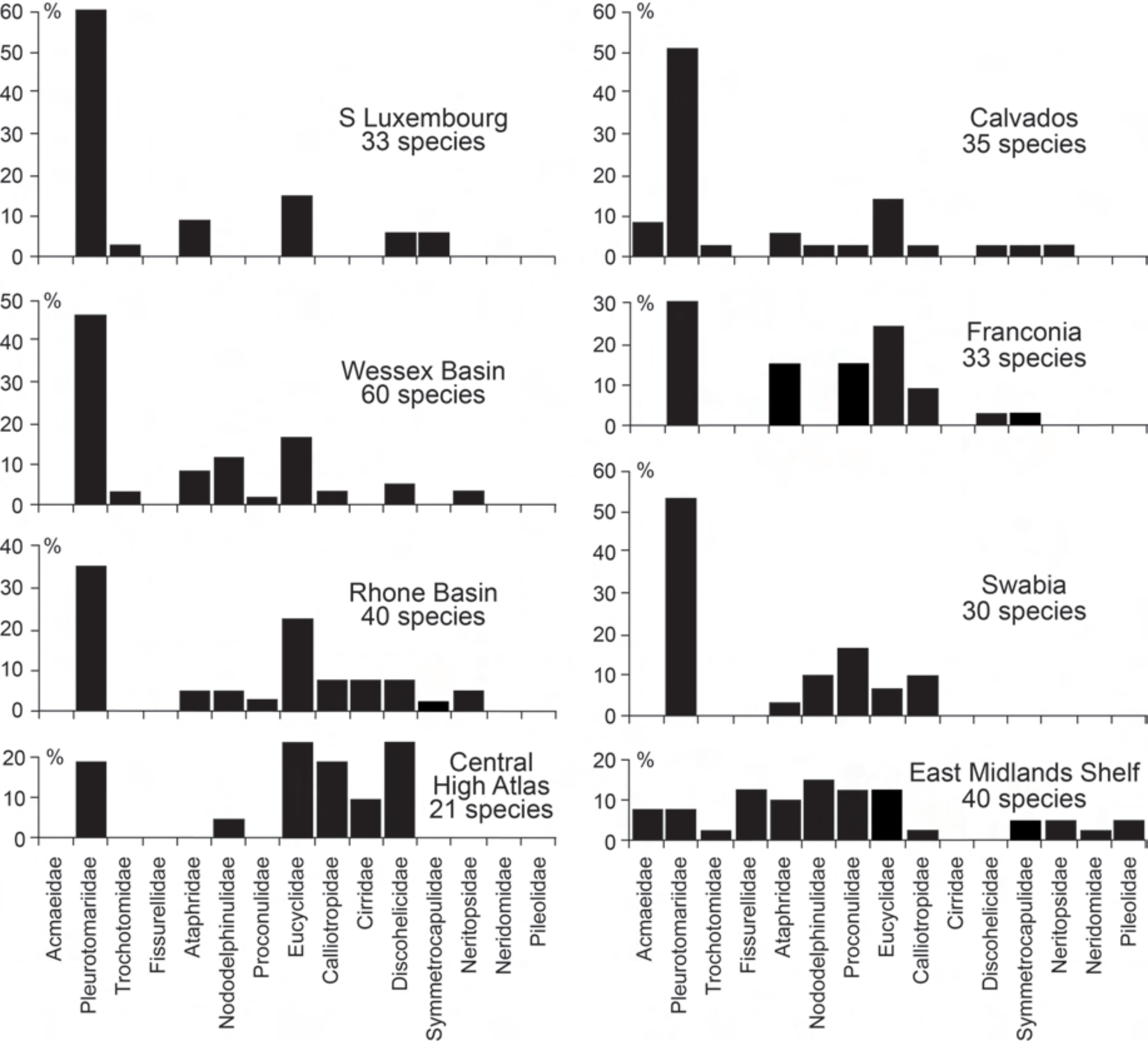


Exposed land
Deltaic/shallow marine
Shallow marine
Deeper marine
Basins floored by oceanic crust
IrM
East Midlands Shelf
LBM
RM
BM
Wessex Basin
Calvados
AR
*
Franconia
Swabia
Rhone Basin
MC
MM
IM
Central High Atlas
SCM



Similarity
0.00
0.12
0.24
0.36
0.48
0.60
0.72
0.84
0.96
East Midlands Shelf
Central High Atlas
Swabia
Franconia
Rhone Basin
Southern Luxembourg
Calvados
Wessex
A
East Midlands Shelf (LB)
Rhone Basin (UA)
Central High Atlas (UA-LB)
Swabia (LB-MB)
Franconia (MB-UB)
Wessex (UB)
Calvados (UB)
Wessex (UA-LB)
Southern Luxembourg (LB)
B
East Midlands Shelf (LB)
Central High Atlas (UA-LB)
Rhone Basin (UA)
Swabia (LB-MB)
Franconia (MB-UB)
Wessex (UA-LB)
Southern Luxembourg (LB)
Wessex (UB)
Calvados (UB)
C



%
S Luxembourg
33 species
Wessex Basin
60 species
Rhone Basin
40 species
Central
High Atlas
21 species
Calvados
35 species
Franconia
33 species
Swabia
30 species
East Midlands Shelf
40 species
Acmaeidae
Pleurotomariidae
Trochotomidae
Fissurellidae
Ataphridae
Nododelphinulidae
Proconulidae
Eucyclidae
Calliotropidae
Cirridae
Discohelicidae
Symmetrocapulidae
Neritopsidae
Neridomidae
Pileolidae

Table 1

Species	HA	RB	SW	FR	SL	CA	WB	EM
ACMAEIDAE								
Scurriopsis sulcata (Eudes-Deslongchamps)						UB		
Scurriopsis disculus (Eudes-Deslongchamps)						UB		
Scurriopsis stansfordensis (Haber)								LB
Scurriopsis? *cuppula* (Eudes-Deslongchamps)						UB		
Pseudorhytidopilus hudlestoni (Rollier)								LB
Pseudorhytidopilus greppini (Haber)								LB
PLEUROTOMARIIDAE								
Pleurotomaria armata Münster	LB		LB		LB	UB	LB UB	
Pleurotomaria proteus Eudes-Deslongchamps			LB			LB UB	LB	
Pleurotomaria tuberculosa Defrance						UB	LB	
Pleurotomaria constricta Eudes-Deslongchamps				UB		UB		
Pleurotomaria ornata (Sowerby)					LB		LB	
Pleurotomaria actinomphala Eudes-Deslongchamps			LB MB		LB		UA	
Pleurotomaria actea in Hudleston (1895)							LB	
Pleurotomaria oxytera Hudleston					LB		LB	
Pleurotomaria ornatadepressa Hudleston					LB		UA	
Pleurotomaria baugieri d'Orbigny					LB			
Pleurotomaria faberi Monari & Gatto					LB			
Pleurotomaria undosa (Schübler)			LB					
Pleurotomaria subarenosa Hudleston							UA	
Pleurotomaria sp. = *P. ornatadepressa* in Roman (1935)		UB						
Leptomaria amoena (Eudes-Deslongchamnps)						UB		
Leptomaria agathis (Eudes-Deslongchamnps)						UB		
Leptomaria consobrina (Terquem & Jourdy)					UB			
Leptomaria fraga (Eudes-Deslongchamps)						UB	UB	
Leptomaria sulcata (Sowerby)		UA			LB			LB
Leptomaria obconica (Tawney)		mBJ			LB			
Leptomaria sulcatahumphriesiana (Hudleston)							LB	
Leptomaria alcyone (d'Orbigny)		UB			LB	UB	UB	
Leptomaria gibba Eudes-Deslongchamps		UA				LB		
Leptomaria nicsimoni Monari & Gatto					LB			LB
Laevitomaria amyntas (d'Orbigny)					LB		UA	
Laevitomaria fasciata (Sowerby)		mBj	LB MB		LB		LB	
Laevitomaria subplatyspira (d'Orbigny)							LB	
Laevitomaria cf. *subplatyspira* in Gatto *et al.* (2015)					LB			
Laevitomaria gyroplata (Eudes-Deslongchamps)			MB	UB		LB UB	LB UB	
Laevitomaria crossoliensis (Roman)		UA						
Laevitomaria auerbachensis (Kuhn, 1938)			LB MB	MB				
Laevitomaria? *fastigata* (Sieberer)			MB					
Bathrotomaria subreticulata (d'Orbigny)			LB MB	LB MB UB	LB	UB	LB UB	LB
Bathrotomaria amata (d'Orbigny)						UB	LB	
Bathrotomaria scrobinula (Eudes-Deslongchamps)						UB	LB UB	
Bathrotomaria? *trapezia* (Hudleston)							UB	
Szabotomaria ziqquratiformis sp. nov.					LB			
Szabotomaria sp. = P. subdecorata in Riche (1904)		UA						
Szabotomaria araris (Riche)		UA						
Szabotomaria depereti (Riche)		UA						
Szabotomaria vaffieri (Riche)		UA						
Szabotomaria? *friesensis* (Kuhn)				MB				
Obornella granulata (Sowerby)			MB		LB	UB	LB	
Obornella plicopunctata (Eudes-Deslongchamps)							UB	
Obornella lentiformis (Eudes-Deslongchamps)		mBJ UB	LB MB	MB UB		LB	UB	
Obornella phylax (Hudleston)							LB	
Obornella montreuilensis (Hébert & Eudes-Deslongchamps)			MB	MB UB				
Obornella yeovilensis (Tawney)	LB						UA LB	
Obornella cf. *suevica* in Gründel et alii (2012)			LB					
Obornella fallax (Eudes-Deslongchamps)						UB		
Pyrgotrochus punctatus (Sowerby)		UA			LB		UA LB UB	
Pyrgotrochus elongatus (Sowerby)	LB	UA mBJ	LB MB	UB	LB	UB	UA LB UB	
Pyrgotrochus bessina (Eudes-Deslongchamps)				MB UB		UB	UB	
Pyrgotrochus macrocephalus (Quenstedt)			MB	UB				
Pyrgotrochus cf. *macrocephalus* in Gründel *et al.* (2012)			LB					
Pleurotomariidae indet. in Conti & Monari (2001)	LB							
TROCHOTOMIDAE								
Trochotoma affinis Eudes-Deslongchamps					LB	LB	LB	
Trochotoma lindonensis (Hudleston)								LB
Trochotoma depressiuscula Lycett							UB	
FISSURELLIDAE								

Emarginula scalaris Sowerby								LB
Emarginula lindonensis Hudleston								LB
Emarginula hudlestoni Haber								LB
Rimulopsis clathrata (Sowerby)								LB
Rimulopsis rugosa (Hudleston)								LB
ATAPHRIDAE								
Ataphrus acis (d'Orbigny, 1850)						UB	UB	
Ataphrus acmon (d'Orbigny)		UA	LB MB	LB MB UB	LB	UB	UA UB	
Ataphrus obtortus (Hudleston)					LB		LB UB	
Ataphrus laevigatus (Sowerby)		UA UB		MB	LB		UA	LB
Ataphrus sp. 1 in Gründel (2003)				UB				
Ataphrus sp. 2 in Gründel (2003)				UnBj				
Chartronella dimidiata (Sowerby)							UA UB	
Chartronella sp. = *T. spiratus* in Hudleston (1894)								LB
Trochopsidea? *lindecolina* (Hudleston, 1894)								LB
Trochopsidea? sp. = ?*T. laevigatus* in Hudleston (1894)								LB
Crossostoma? cf. *pratti* in Kuhn (1938)				MB				
NODODELPHINULIDAE								
Amphitrochus duplicatus (Sowerby)						UB	UB	
Amphitrochus? *attochus* (Hudleston)							UA	
Amphitrochus? *spaticus* (Hudleston)								LB
Nododelphinula kahlenbergensis (Gründel *et al.*, 2012)			UA					
Nododelphinula shaleri (Tawney)							UA	
Nododelphinula santonis (Hudleston)								LB
Nododelphinula altabicarinata (Hudleston)								LB
Falsamotrochus abbas (Hudleston)	UA LB						UA	
Falsamotrochus winwoodi (Tawney)							UA	
Falsamotrochus duryanus (d'Orbigny)		UA					UB	
Falsamotrochus? *substrigosus* (Hudleston)							UB	
Etalotrochus latus Gründel *et al.*, 2012			LB					
Etalotrochus sp. in Gründel *et al.* (2012)			LB					
Metriomphalus lyelli (Hudleston)								LB
Metriomphalus depressiusculus (Hudleston)								LB
Metriomphalus fourneti (Riche)		UA						
Metriomphalus? *altaacanthicus* (Hudleston)								LB
PROCONULIDAE								
Proconulus costatonodosus Gründel *et al.*, 2012			LB					
Proconulus guisei (Lycett)			LB					
Proconulus acanthus (d'Orbigny)						UB		
Proconulus? *subimbricatus* (Hudleston)								LB
Procunulus sp. = *T.* cf. *bixa* in Hudleston (1894)								LB
Muricotrochus squamosior (Hudleston)								LB
Muricotrochus aff. *substrigosus* in Kuhn (1938)				MB				
Ueckerconulus monilitectus (Phillips)		UA	LB	LB				
Ueckerconulus brutus (d'Orbigny)			MB					
Uerckeconulus bijugatus (Quenstedt)			UB	unBj				
Ueckerconulus vicinus (Hudleston)								LB
Ueckerconulus dunkeri (Morris & Lycett)								LB
Ueckerconulus sp. 1 in Gründel (2003)				UB				
Ueckerconulus? *marga* (Hudleston)				UB			UB	
EUCYCLIDAE								
Ambercyclus orbignyanus (Hudleston)				MB	LB	UB	LB UB	
Ambercyclus murchisoni (Münster)	LB	mBJ	LB	MB			LB	
Ambercyclus goniatus (Eudes-Deslongchamps)						UB	UB	
Ambercyclus ornatus (Sowerby)	UA LB	UA UB		MB	LB	unBj	UA	
Ambercyclus densinodosus (Hudleston)		UA					UA	
Ambercyclus praetor (Goldfuss)			LB MB	MB UB	LB			
Ambercyclus belia (d'Orbigny)						UB		
Ambercyclus centurio (Münster in Goldfuss)				UB				
Ambercyclus cygneus (Hudleston)								LB
Ambercyclus gemmatus (Lycett)								LB
Ambercyclus? *subelongatus (*Riche)		UA						
Gerasimovcyclus aedilis (Münster)				MB				
Eucycloidea bianor (d'Orbigny)						UB		
Eucycloidea tenuistria (Münster)	LB							
Eucycloidea schlosseri (Kuhn)				MB UB				
Eucycloidea carinocrenata (Lycett)		UB						
Eucycloidea cf. *etheridgii* in Conti & Monari (2001)	UA LB							
Eucycloidea sp. = *Purpurina* sp. in Marzloff *et al.* (1936)		UB						
Eucyclus? *turbinoides* (Hudleston)							UA	
Eucyclus? *elongatus* Hudleston	LB	UA						
Eucyclus? cf. *elongatus* in Kuhn (1938)				MB				

Ooliticia phillipsii (Morris & Lycett)							LB	LB
Ooliticia polytimeta (Hudleston)		UA			LB		UA	
Ooliticia cf. *polytimeta* (Hudleston)								LB
Ooliticia recteplanata (Tawney)		UA			LB			
Ooliticia weldonis (Hudleston)							UB	LB
Marloffsteinia? *milleri* (Hudleston)							UA	
CALLIOTROPIDAE								
Tuberotropis tuberosus Gründel *et al.*, 2012			UA					
Tuberotropis staffelbergensis (Kuhn)				MB				
Biarmatoidella biarmata (Münster)	LB		MB	MB UB		UB	UB	
Biarmatoidella lorioli (Greppin)	LB	UB	LB MB	MB UB				
Riselloidea dorsetensis (Hudleston)		mBJ					UA	LB
Riselloidea couzonensis (Riche)		UA						
Riselloidea? sp. in Conti & Monari (2001)	UA LB							
Sadkia richensis Conti & Monari	UA LB							
CIRRIDAE								
Cirrus fourneti (Dumortier)		UA						
Cirrus sp. A in Conti & Monari (2001)	LB							
Cirrus sp. B in Conti & Monari (2001)	LB							
Hamusina hudlestoni (Roman)		UA						
Hamusina subbertheloti (Roman)		UA						
DISCOHELICIDAE								
Discohelix subequalis (d'Orbigny)	UA					UnBj		
Costatohelix guembeli (Ammon)	UA							
Costatohelix albinatiensis (Dumortier)	LB	UA						
Costatohelix spinosus (Hudleston)							UA	
Costatohelix tuberculosusdexter (Hudleston)							UB	
Costatohelix cf. *costata* in Conti & Monari (2001)	LB							
Costatohelix? sp. = *Discohelix* sp. in Conti & Monari (2001)	LB							
Asterohelix bidentata (Kästle)				UB				
Colpomphalus crussoliensis (Roman)		UA						
Colpomphalus bathmis (Roman)		UA						
Colpomphalus thuyi sp. nov.					LB			
Colpomphalus tigratus sp. nov.					LB			
Nummocalcar polygonoides (Hudleston)							UB	
NERITOPSIDAE								
Neritopsis abbas (Hudleston) (*fide* Rollier, 1919)							UA	
Hayamia bajocensis (d'Orbigny)		UB				UB	LB UB	
Hayamiella aff. *decussata* (Münster)								LB
Hayamiella *incisa* (Hudleston)								LB
Bandelopsis? *dumortieri* (Rollier)		UA						
NERIDOMIDAE								
Neridomus tumidula (Phillips)								LB
PILEOLIDAE								
Pileolus plicatus in Hudleston (1894)								LB
Pileolus laevis Sowerby								LB
SYMMETROCAPULIDAE								
Symmetrocapulus tessoni (Eudes-Deslongchamps)		UB		UnBj	LB	UB		LB
Symmetrocapulus? ancyloides (Sowerby)								LB
Fabercapulus semisculptus sp. nov.					LB			
Number of species	**21**	**40**	**30**	**33**	**33**	**35**	**60**	**40**

TABLE S1. Measurements of the most representative specimens of the family Pleurotomariidae. Linear measurements are in millimetres. The asterisk (*) indicates measurements made on incomplete specimens. See text for the institutional abbreviations and Figure 2 for the abbreviations of the dimensions.

specimen	H	HL	HA	W	WA	α_{ap}	α_{pl}	α_{m}
Bathrotomaria subreticulata (d'Orbigny, 1850)								
MNHNL BU103	24.2	15.7	9.6	22.2	10.3	91°	57°	64°
MNHNL BU111	33.4	18.9	10.0	26.7	13.7	91°	47°	57°
MNHNL BU131	25.9	17.4	11.6	24.1	-	88°	59°	68°
MNHNL BU137A1	17.6*	11.5*	6.8*	16.6	8.3	102°	66°	67°
MNHNL RB034A	32.7*	20.0*	12.3	35.7	-	-	65°	65°
MNHNL RB038	21.0	12.9	7.1	18.6	-	95°	56°	62°
MNHNL RB049	13.7	10.1	7.1	17.1	-	98°	73°	75°
MNHNL RB105A	18.5	12.2	7.6	18.8	-	92°	70°	74°
MNHNL RB305B	26.5	16.2	9.3	25.4	11.9	91°	53°	67°
MNHNL RB312A	25.4	15.9	10.3	27.1	-	91°	61°	70°
MNHNL RB312B	24.4	15.5	9.7	23.0	11.9	93°	-	66°
MNHNL RB313A1	19.2	12.4	10.4	20.8	-	89°	72°	71°
MNHNL RB376I	20.9	13.6	8.0	20.2	10.0	106°	59°	68°
MNHNL ZS154	18.2	12.1	7.8	15.0	-	92°	65°	69°
MNHNL ZS167B	31.4	19.4	12.6	31.4	-	83°	59°	62°
MNHNL ZS175A	30,9	-	-	20,9	-	97°	39°	57°
MNHNL ZS312	22.1	14.5	8.3	21.4	-	89°	63°	67°
MNHNL ZS313	23.3	15.8	9.5	24.0	11.9	93°	64°	71°
MNHNL ZS368B	35.4	20.4	11.8	31.4	15.2	-	68°	63°
MNHNL ZS525	24.7	16.2	10.8	26.9	-	86°	66°	69°
MNHNL ZS531	30.4	18.8	10.9	27.6	13.0	86°	62°	64°
Szabotomaria ziqquratiformis sp. nov.								
MNHNL BU122	25.2	16.8	10.0	27.7	13.9	105°	67°	77°
MNHNL MDB161	18.1	12.5	7.8	26.3*	-	104°	82°	84°
MNHNL MDB230	23.0	15.7	9.8	28.0	13.7	103°	69°	80°
MNHNL MDB255	23.2	15.0	8.9	30.0	15.0	107°	69°	79°
MNHNL MDB347	28.5	17.8	10.0	31.6	-	105°	60°	74°
MNHNL RB033A	25.2	15.6	9.0	24.1*	-	105°	-	77°
MNHNL RB171A	17.8*	13.5	9.6	26.5	-	-	-	82°
MNHNL RB171B	19.0	13.9	10.0	25.6	-	109°	85°	83°
MNHNL RB245B	29.3	19.6	11.4	33.6	15.0	108°	68°	78°
MNHNL RB255	26.4	17.6	11.1	31.6	14.5	111°	82°	81°
MNHNL ZS367	24.3*	16.5*	10.1*	27.8	-	103°	66°	75°
MNHNL ZS494S2	24.6	16.1	9.3	30.9	15.6	109°	65°	79°
Obornella granulata (Sowerby, 1818)								
MNHNL BU229	24.8	19.5	15.8	35.5	-	96°	107°	110°
Pyrgotrochus punctatus (Sowerby, 1818)								
MNHNL BU120A	22.7	9.2	5.0	16.1	7.6	62°	42°	41°
MNHNL BU120B	25.6	10.8	5.8	19.5	9.4	64°	45°	44°
MNHNL MDB305C	27.5	13.1	8	24.2	-	-	56°	48°
MNHNL RB168	39.5	16.8	9.2	28.4	-	-	48°	45°
MNHNL RB226B	65.7	23.9	13.5	53.3	-	-	53°	51°
MNHNL RB298	56.2	16.4	8.8	47.8	20.6	66°	48°	52°
MNHNL RB353	77.1*	28.6	13.9	55.0	-	-	46°	47°
MNHNL RB421A	33.0	14.3	8.7	26.0	-	66°	53°	51°
MNHNL ZS163	32.2*	8.9*	6.1*	25.8*	-	66°	56°	53°
MNHNL ZS168A	49.5*	22.0	13.0	42.8	-	-	54°	52°
MNHNL ZS174	60.9	25.6	13.5	48.2	-	-	45°	48°
MNHNL ZS179	23.6	10.1	6.2	18.0	-	65°	46°	42°
MNHNL ZS204	27.3	12.8	7.8	24.0	-	-	52°	48°
MNHNL ZS233A	34.9	15.3	9.8	29.1	14.2	61°	48°	45°
MNHNL ZS258	61.8*	26.8	15.7	58.6	-	-	52°	51°
MNHNL ZS259	56.1*	22.8*	12.5*	46.7*	-	70°	57°	50°
MNHNL ZS321C	35.4	13.9	7.5	28.5	13.1	-	50°	47°
MNHNL ZS380	47.5*	21.0*	12.0*	40.2*	-	-	47°	47°
MNHNL ZS510	22.7*	11.1	6.5	22.7	11.6	-	55°	50°
Pyrgotrochus elongatus (Sowerby, 1818)								
MNHNL BU101A	33.5	16.2	7.7	28.9	13.7	72°	52°	53°
MNHNL BU172	40.8	18.7	10.4	35.4	-	-	53°	55°
MNHNL RB034B	37.6	19.5	12.1	35.7	-	-	53°	54°
MNHNL RB036	45.0	22.8	14.4	39.4	-	-	39°	50°
MNHNL RB040	21.9	19.4	7.4	20.6	-	79°	58°	51°
MNHNL RB048	34.3	14.5	7.9	30.4	-	81°	54°	53°
MNHNL RB055A	46.1	21.3	11.5	41.0	-	70°	53°	55°
MNHNL RB055B	25.9	17.3	9.1	22.0*	-	77°	55°	55°
MNHNL RB127	32.1	14.2	8.3	31.7	-	-	52°	56°
MNHNL RB139	26.9	13.8	8.8	23.8	-	74°	52°	51°
MNHNL RB244	43.7	22.1	12.5	35.4	-	74°	54°	56°
MNHNL RB354	50.6	25.0	14.4	38.3	-	75°	48°	50°
MNHNL ZS151	37.3	16.7	7.6	31.3	7.5	-	53°	54°
MNHNL ZS172A	33.2	14.8	8.2	28.7	13.7	-	49°	54°
MNHNL ZS173A	29.2	14.6	8.8	29.2	-	-	54°	56°
MNHNL ZS187A	37.5*	18.5	10.0	38.3	18.2	-	67°	60°
MNHNL ZS187B	45.8	22.1	11.6	47.4	20.8	68°	75°	62°
MNHNL ZS219	40.2	20.0	12.1	36.7	-	-	48°	52°
MNHNL ZS230	34.7	16.6	9.5	30.0	13.2	-	59°	56°
MNHNL ZS233B	33.2	14.4	7.8	28.8	-	-	54°	50°
MNHNL ZS240	38.3	16.5	9.2	35.4	16.2	-	53°	55°
MNHNL ZS320	31.8	14.5	8.4	29.3	14.3	69°	74°	56°
MNHNL ZS321A	31.7	13.8	6.1	27.3	13.0	-	53°	52°
MNHNL ZS321B	35.7	16.8	7.0	32.7	-	73°	56°	55°
MNHNL ZS322	47.7	18.0	10.0	34.5	16.3	77°	40°	45°
MNHNL ZS333A	20.3	10.9	5.9	18.4	-	-	51°	52°
MNHNL ZS385	43.3	23.0	11.0	39.8	-	-	55°	57°
MNHNL ZS494E	26.5	12.1	6.1	24.0	12.0	82°	55°	54°
MNHNL ZS522A	34.3	14.0	7.5	31.6	15.0	76°	56°	58°
MNHNL ZS529	46.4	22.4	12.9	41.4	-	-	50°	53°

TABLE S2. Measurements of the most representative specimens of the families Trochotomidae, Ataphridae, Eucyclidae and Discohelicidae. Linear measurements are in millimetres. The asterisk (*) indicates measurements made on incomplete specimens. See text for the institutional abbreviations and Figure 2 for the abbreviations of the dimensions.

specimen	H	HL	HA	W	WA	α_{ap}	α_{pl}	α_{m}
Trochotoma affinis **Eudes-Deslongchamps, 1842**								
MNHNL RB236	30.0	23.1	-	48.4	-	-	110°	-
MNHNL RB237	29.1*	25	18.8	48.3	-	-	108°	-
MNHNL RB342	19.0	12.9	8.8	22.5	-	86°	107°	78°
MNHNL ZS106	32.3	19.8	9.1	44.8	20.9	90°	97°	82°
MNHNL ZS168B	32.4*	26.8	19.5	47.8	-	-	107°	-
MNHNL ZS369	30.6	20.6	7.4	44.6	-	-	96°	85°
MNHNL ZS373	33.5	22.9	13.8	42.7	-	-	98°	78°
MNHNL ZS488B	-	20.4	9.8	41.1	19.6	-	88°	-
MNHNL ZS511	29.2*	20.0*	13.1*	37.0*	-	-	107°	-
Ataphrus acmon **(d'Orbigny, 1853)**								
MNHNL BU137B2	10.2	8.2	4.3	9.0	4.1	-	50°	67°
MNHNL BU137B3	6.5	5.6	3.5	6.4	3.3	140°	67°	75°
MNHNL BU137B4	8.3	6.8	3.7	7.6	3.4	139°	55°	73°
MNHNL MDB249F	7.7	6.4	3.3	7.5	3.7	142°	58°	76°
MNHNL RB101	8.0	6.5	3.8	7.4	3.4	-	57°	73°
MNHNL RB376C1	9.6	7.2	3.6	7.8	4.2	144°	41°	65°
MNHNL RB376C2	9.3	7.4	4.3	7.9	3.5	138°	46°	68°
MNHNL RB381	9.1	7.9	-	9.7	-	-	65°	74°
MNHNL ZS589B1	12.2	10.7	-	12.9	-	-	72°	80°
Ataphrus obtortus **Hudleston, 1894**								
MNHNL BU137B6	6,6	6,1	4,9	7.3	4.0	178°	90°	86°
Ataphrus laevigatus **(Sowerby, 1818)**								
MNHNL RB041C	7.9*	6.8*	4.6*	9.5	-	-	99°	89°
MNHNL RB055C	3.9	3.6	2.7	4.5*	-	156°	102°	91°
Ambercyclus orbignyanus **(Hudleston, 1892)**								
MNHNL BM382	48.9*	32.2*	-	39.2	-	-	73°	64°
Ambercyclus ornatus **(Sowerby, 1819)**								
MNHNL MDB239	31.8	23.8	17.5	23.8	-	-	54°	62°
MNHNL MDB249B	25.6	16.6	10.9	16.0	8.5	49°	45°	51°
MNHNL MDB324	26.8	19.9	14.2	20.1	-	-	53°	57°
MNHNL RB061	31.5	23.4	17.2	24.3	-	-	61°	59°

specimen	H	HL	HA	W	WA	α_{ap}	α_{pl}	α_{m}
MNHNL RB144	20.9	15.4	10.0	16.5	8.9	-	70°	68°
MNHNL RB304B	27.4*	19.0	11.8	22.0	12.6	-	63°	63°
MNHNL RB311J	35.4	26.1	19.0	23.6	12.7	57°	67°	62°
MNHNL RB376A1	26.0	17.9	11.6	16.0	8.5	49°	45°	52°
MNHNL RB376A2	19.4	13.1	8.9	12.2*	5.9*	47°	60°	56°
MNHNL ZS160B1	29.5	21.1	13.6	23.6	13.2	-	62°	63°
MNHNL ZS245B	30.4*	20.6	13.2	22.0	11.9	-	51°	57°
MNHNL ZS292	27.2	19.0	12.8	19.8	11.0	49°	63°	59°
MNHNL ZS425	30.5	20.7	13.4	20.4	10.7	-	56°	59°
Ambercyclus praetor **(Goldfuss, 1844)**								
MNHNL RB376E	17.3*	12.2*	6.9*	12.8*	7.1*	-	59°	64°
Oolitícia polytimeta **(Hudleston, 1892)**								
MNHNL BU137C2	9.9*	6.7*	-	8.6*	-	90°	74°	68°
MNHNL MDB395	17.8	13.5	-	13.8	-	-	60°	62°
MNHNL RB311H1	19.8	14.4	9.2	15.2	7.3	70°	60°	64°
MNHNL ZS384	21.4	16.7	-	17.5	-	-	60°	65°
Oolitícia recteplanata **(Tawney, 1873)**								
MNHNL BU137C1	17.5	11.7	8.0	13.6	6.8	66°	58°	59°
MNHNL MDB277	14.9	9.7	6.8	10.2	5.2	82°	53°	54°
MNHNL RB311H2	16.2	11.4	6.4	11.5	5.9	-	50°	63°
MNHNL RB311H3	13.6*	9.8*	-	8.3*	-	73°	-	-
MNHNL ZS260A	20	13.6	9.3	11.1	-	-	45°	55°
Colpomphalus thuyi **sp. nov.**								
MNHNL ZS124B	7.2	6.5	6.0	11.2*	2.0*	-	154°	131°
Colpomphalus trigatus **sp. nov.**								
MNHNL ZS124A	8.8	7.5	6.4	14.4	3.8	-	134°	153°

CAP-SHAPED SHELLS

specimen	L	Lp	H	Hap	W
Symmetrocapulus tessoni **(Eudes-Deslongchamps, 1843)**					
MNHNL BM358	45.0*	35.9	19.0	-	32.2
Fabercapulus semisculptus **sp. nov.**					
MNHNL ZS101D	35.0	28.3	11.4	10,3	27.1

TABLE S3. Systematic list and number of specimens of vetigastropod and neritimorph species from the Lower Bajocian deposits of southern Luxembourg and adjacent French territory. Lo, Longwy; Di, Differdange; Ru, Rumelange.

species	Lo	Di	OR	stratigraphical position
Superfamily **PLEUROTOMARIOIDEA** Swainson, 1840 Family **Pleurotomariidae** Swainson, 1840				
Pleurotomaria armata Münster in Goldfuss, 1844	-	21	-	Discites-Laeviuscula Zones
Pleurotomaria ornata (Sowerby, 1818b)	-	37	-	Discites-Laeviuscula Zones
Pleurotomaria actinomphala Eudes-Deslongchamps, 1849	-	17	-	Discites-Laeviuscula Zones
Pleurotomaria oxytera Hudleston, 1895	-	3	-	Discites-Laeviuscula Zones
Pleurotomaria ornatadepressa Hudleston, 1895	-	3	-	Discites-Laeviuscula Zones
Pleurotomaria baugieri d'Orbigny, 1850	-	10	-	Discites-Laeviuscula Zones
Pleurotomaria faberi Monari & Gatto, 2013	-	2	-	Discites-Laeviuscula Zones
Leptomaria sulcata (Sowerby, 1818)	-	6	-	Discites-Laeviuscula Zones
Leptomaria obconica (Tawney, 1873)	-	1	-	Discites-Laeviuscula Zones
Leptomaria alcyone (d'Orbigny, 1850)	1	-	-	undiff. lower Bajocian
Leptomaria nicsimoni Monari & Gatto, 2014	-	1	-	Discites-Laeviuscula Zones
Laevitomaria amyntas (d'Orbigny, 1850)	-	5	-	Discites-Laeviuscula Zones
Laevitomaria fasciata (Sowerby, 1818)	1	-	-	undiff. lower Bajocian
Laevitomaria cf. *subplatyspira* (d'Orbigny, 1850)	1	-	-	undiff. lower Bajocian
Bathrotomaria subreticulata (d'Orbigny, 1850)	-	106	-	Discites-Laeviuscula Zones
Szabotomaria ziqquratiformis gen. et sp. nov.	-	26	-	Discites-Laeviuscula Zones
Obornella granulata (Sowerby, 1818)	1	-	-	undiff. lower Bajocian
Pyrgotrochus punctatus (Sowerby, 1818)	-	35	-	Discites-Laeviuscula Zones
Pyrgotrochus elongatus (Sowerby, 1818)	-	122	-	Discites-Laeviuscula Zones
Family **Trochotomidae** Cox, 1960				
Trochotoma affinis Eudes-Deslongchamps, 1843	-	17	-	Discites-Laeviuscula Zones
Superfamily **TURBINOIDEA** Rafinesque, 1815 Family **Ataphridae** Cossmann, 1915				
Ataphrus acmon (d'Orbigny, 1850)	-	21	-	Discites-Laeviuscula Zones
Ataphrus obtortus (Hudleston, 1894)	-	1	-	Discites-Laeviuscula Zones
Ataphrus laevigatus (Sowerby, 1818)	-	2	-	Discites-Laeviuscula Zones
Superfamily **EUCYCLOIDEA** Koken, 1896 Family **Eucyclidae** Koken, 1896				
Ambercyclus orbignyanus (Hudleston, 1892)	-	-	1	Humphriesianum Zone
Ambercyclus ornatus (Sowerby, 1819)	- 1	78 -	- -	Discites-Laeviuscula Zones undiff. lower Bajocian
Ambercyclus praetor (Goldfuss, 1844)	-	1	-	Discites-Laeviuscula Zones
Oolitícia polytimeta (Hudleston, 1892)	-	10	-	Discites-Laeviuscula Zones
Oolitícia recteplanata (Tawney, 1873)	-	23	-	Discites-Laeviuscula Zones
Superfamily **DISCOHELICOIDEA** Schröder, 1995 Family **Discohelicidae** Schröder, 1995				
Colpomphalus thuyi sp. nov.	-	1	-	Discites-Laeviuscula Zones
Colpomphalus tigratus sp. nov.	-	1	-	Discites-Laeviuscula Zones
Superfamily **SYMMETROCAPULOIDEA** Wenz, 1938 Family **Symmetrocapulidae** Wenz, 1938				
Symmetrocapulus tessoni (Eudes-Deslongchamps, 1843)	-	-	1	Humphriesianum Zone
Fabercapulus semisculptus gen. et sp. nov.	-	1	-	Discites-Laeviuscula Zones