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Caenogastropods and heterobranch gastropods from the Hettangian deposits of Luxembourg: palaeobiogeography and Early Jurassic faunal recovery in the western Tethys

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Abstract: We describe the Hettangian Caenogastropoda and Heterobranchia of the Luxembourg Sandstone Formation, a wedge of clastic sediments deposited along the eastern margin of Paris Basin during the Early Jurassic. Five new genera and 11 new species are erected: *Bourguetia bipartita* sp. nov., *Globularia delsatei* sp. nov., *Oonia feidtorum* sp. nov., *Oonia haasi* sp. nov., *Jurazyga* gen. nov., *Microschiza pauciornata* sp. nov., *Angulariopsis* gen. nov., *Tangarilda darestei* sp. nov., *Brouchilda laevigata* gen. et sp. nov., *Brouchilda mulleri* gen. et sp. nov., *Turritelloidea*? *bockfielsensis* sp. nov., *Gruendelifusus melusinae* gen. et sp. nov. and *Kaimella tenuilineata* gen. et sp. nov. Including the Patellogastropoda, Neritimorpha and Vetigastropoda recognized in a previous study, the fauna shows an overall high taxonomic diversity represented by 55 species belonging to 23 families. Multivariate and network analyses and parsimony analysis of endemicity were done to assess the palaeobiogeographic changes of the western Tethyan gastropod faunas during the Early Jurassic recovery. The results highlight the differentiation between the faunas of the European shelf and those of the intra-Tethyan carbonate platforms during the Hettangian to early Sinemurian interval, and the subsequent advent of a third faunal stock in the areas of pelagic deposition derived from the fragmentation and drowning of the carbonate platforms. Early in the Hettangian, areas of endemism with diversified faunas developed, which attests to a fast recovery after the Late Triassic biotic decline. Relationships between the degree of endemism and species richness within the main western Tethyan regions and within the major gastropod groups are discussed.

Key words: Gastropoda, systematics, Early Jurassic recovery, Hettangian, Luxembourg Sandstone Formation, palaeobiogeography.

ONCE considered a mass extinction of intermediate severity (Raup & Sepkoski 1982; Sepkoski 1996), the episode of biotic turnover at the Triassic–Jurassic transition has gained substantial attention over the last 20 years, and studies on the dynamics, magnitude, possible causes and aftermath of this event have flourished (Tanner 2018; Schoepfer *et al.* 2022 and references therein). As a result, the Late Triassic strong decline of biodiversity now emerges as one of the major crises of Phanerozoic life in both taxonomic loss and ecological severity (Alroy *et al.* 2008; Alroy 2010; Hautmann 2012; McGhee *et al.* 2013; Dunhill *et al.* 2018), and evidence is accumulating on its probable connection with the emplacement of the Central Atlantic Magmatic Province (CAMP) and associated environmental disturbances (Marzoli *et al.* 1999; Van de Schootbrugge & Wignall 2016; Larina *et al.* 2021; Capriolo *et al.* 2022). Of the marine invertebrates, ammonites, bivalves, brachiopods and corals were the groups most affected (Hallam 1981; Guex *et al.* 2004; Hautmann *et al.* 2008; Kiessling *et al.* 2009; Whiteside & Ward 2011; Stanley *et al.* 2018), even if uncertainties remain about the tempo and mode of their taxonomic decline (e.g. Hallam 2002; Tanner *et al.* 2004; Bambach 2006; Song *et al.* 2018; Lucas & Tanner 2018). The earliest Jurassic was also the time of an important global plate tectonic reorganization, marked by the initial rifting of the central Atlantic Ocean and the consequent break-up of Pangea (Scotese & Schettino 2017 and references therein).

Many studies have focused on reconstructing diversity trajectories of the major components of the marine biota during the Triassic–Jurassic crisis and the subsequent early Jurassic recovery (e.g. Allasinaz 1992; Kiessling *et al.* 2007; Ros *et al.* 2011; Guex *et al.* 2012; Pugh

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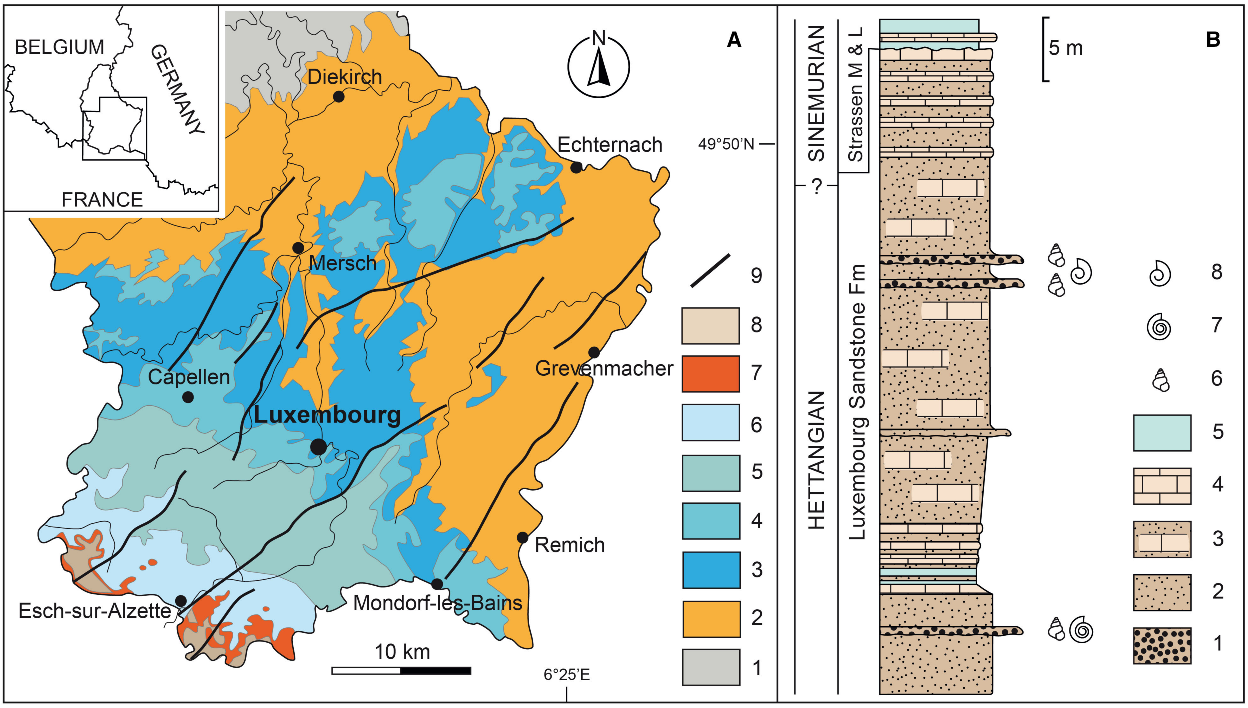

FIG. 1. A, simplified geological map of Gutland (central and southern Luxembourg). 1, Palaeozoic basement. 2, Triassic sediments. 3, Luxembourg Sandstone Formation including the marls of Elvange at its base (Hettangian – lowermost Sinemurian). 4, marls and limestones of Strassen (lower–upper Sinemurian). 5, marls and sandstones (upper Sinemurian – Pliensbachian). 6, 'bituminous shales' (uppermost Pliensbachian – Toarcian). 7, Minette ironstone (Toarcian–Aalenian). 8, Rumelange limestone and marl (lower Bajocian). 9, major fault lines. B, schematic stratigraphic column of section cropping out at the Feidt quarry near Brouch (Mersch, Grand-Duchy of Luxembourg). 1, rudstones. 2, sandstones. 3, calcite-cemented sandstones. 4, limestones. 5, marls. 6, gastropod-rich level. 7, *Caloceras* spp. 8, *Schlotheimia* spp. Map redrawn from Service géologique du Luxembourg (2007). Brouch section redrawn and modified from Van den Bril & Swennen (2008).

et al. 2014; Damborenea *et al.* 2017; Song *et al.* 2018; Atkinson & Wignall 2019), but gastropods have been relatively understudied in this regard (Batten 1973; Monari *et al.* 2011; Ferrari 2015; Pieroni *et al.* 2021). A comprehensive survey of the global taxonomic turnover of this class during the Norian–Pliensbachian interval has recently been carried out by Ferrari & Hautmann (2022), who reported a loss of 56% of gastropod genera at the Triassic–Jurassic boundary.

Being the first post-extinction stage, the Hettangian is a key interval to assess the extinction magnitude and pace of faunal recovery. It is therefore paramount to have the most complete and taxonomically updated picture of gastropod diversity during this stage. Gastropods from Hettangian outcrops of Europe have been the subject of numerous studies (Monari *et al.* 2011 and references therein) but most of them date back to the late 1800s and early 1900s and require a taxonomic revision. Moreover, newly collected material often awaits description in museums and research institutions. The collection of gastropods from the Hettangian Luxembourg Sandstone Formation housed at the Musée national d'histoire naturelle of Luxembourg is an example. This rich fauna was in part described by Meier & Meiers (1988) and Monari *et al.* (2011). These last authors dealt with the patellogastropod, neritimorph and vetigastropod groups and traced the evolutionary history of these clades in the early Jurassic. In the present paper we conclude the systematic study of this fauna with the description of the caenogastropods and heterobranch gastropods. We also propose an extensive analysis of the palaeobiogeographic relationships among the western Tethyan Early Jurassic faunas in order to assess the dynamics of the gastropod recovery in this region after the late Triassic loss of biodiversity.

GEOLOGICAL SETTING

The Luxembourg Sandstone Formation, or Grès de Luxembourg, is a wedge of clastic sediments deposited during the earliest Jurassic along the so-called Trier-Luxembourg Gulf, at the north-eastern margin of the Paris Basin (Berners 1983, 1985; Colbach 2005; Schäfer & Colbach 2021) (Fig. 1A). The sand body spread over a roughly E–Woriented belt encompassing westernmost Germany, the Gutland (central and southern Luxembourg) and Belgian and French Lorraine. It is mainly represented by a complex of prograding sand waves and bars deposited in a shallow marine, deltaic environment under tidal influence (Berners 1983, 1985; Van den Bril & Swennen 2008; Schäfer & Colbach 2021). The age of the Luxembourg Sandstone is diachronic, being lower Hettangian (*Psiloceras planorbis* Zone) to lower Sinemurian (*Arietites bucklandi* Zone) in Luxembourg, and Sinemurian in Belgium (Lucius 1948; Guérin-Franiatte & Muller 1986; Bock & Muller 1989, 2004; Guérin-Franiatte *et al.* 1991, 1995). In Luxembourg, the formation reaches a maximum thickness of *c.* 100 m and is limited at its base by the marls of Elvange and at its top by the marls and limestones of Strassen. It can be described lithologically as an alternation of yellowish ochre, poorly cemented sandstones and grey to whitish, cement-rich sandy limestones (Colbach 2005) (Figs 1B, 2A). The sedimentology and diagenetic history of the Luxembourg Sandstone have been studied in detail by Molenaar (1998) and Van den Bril & Swennen (2008), who interpreted the characteristic bimodal carbonate content of the sandstones and limestones as resulting from a first cementation phase, which occurred early in the oxic zone, close to the seawater–sediment interface and which was tightly controlled by sedimentary architecture, and a later cementation phase, acting after burial and under the influx of meteoric water.

Fossils are relatively rare in the unit and are mostly concentrated into coarse-grained levels, where they form coquina beds (Faber & Weis 2005; Guérin-Franiatte & Weis 2010) (Fig. 2B). Besides gastropods, ammonites of the genera *Caloceras* and *Schlotheimia* are very frequent, as well as bivalves, mainly cardiniids (*Cardinia* spp.), tancrediids, astartids and pteriomorphs (*Pinna*, *Pteria*, *Liostraea*) (MV pers. obs. 2024). Sponges, corals, bryozoans and rare nautilids are also present. Vertebrate remains include rare fishes (Delsate 1992; Duffin & Delsate 1993), marine reptiles (Delsate 2000), and theropod dinosaurs (Delsate & Ezcurra 2014). The coquina layers have been interpreted as forming in a shallow marine setting, either following reworking in tidal channels of previously deposited bioclasts or by winnowing during storm events. Upon burial, aragonite and high-magnesium calcite skeletal remains underwent neomorphic replacement with low-magnesium calcite (Van den Bril & Swennen 2008). Preservation of the fossils from the Luxembourg Sandstone Formation is generally good (Fig. 3), but the finest surface details of the shells, especially on the early whorls of gastropods, have been sometimes wiped out by abrasion and by strong recrystallization. In many cases, these processes were also responsible for the lack of preservation of the protoconch.

Institutional abbreviations. MNHNL, Musée national d'histoire naturelle, City of Luxembourg, Grand-Duchy of Luxembourg; UCBL, University Claude Bernard, Lyon 1, Villeurbanne, France (specimens belonging to the collections of the École Nationale Supérieure des Mines de Paris are indicated by the suffix -EM; specimens of the University collection are indicated by the suffix -FSL).

MATERIAL & METHOD

Most of the material described in this paper comes from two levels of the Luxembourg Sandstone Formation

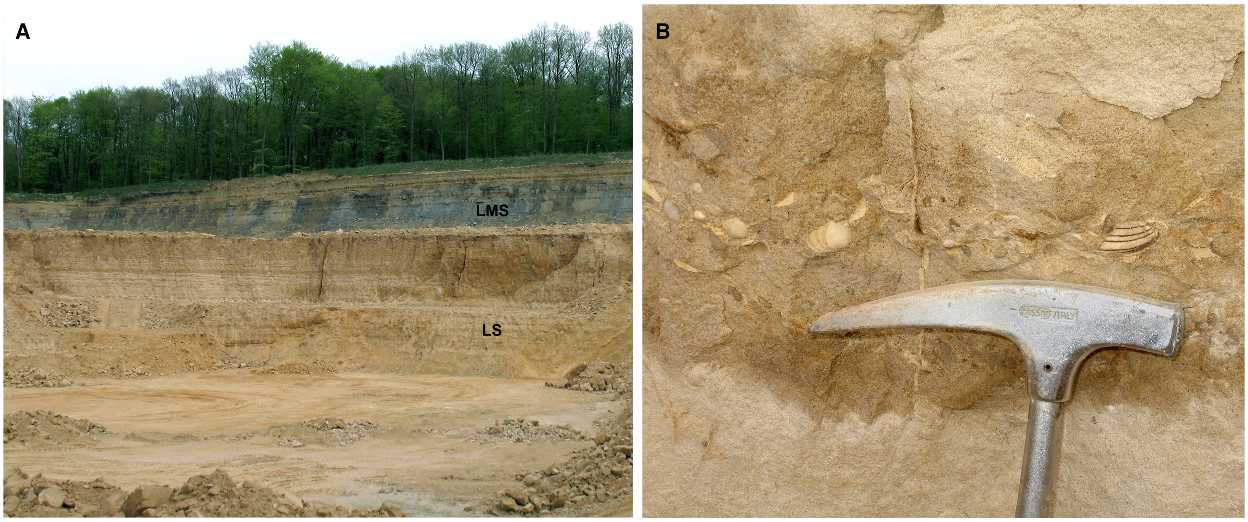

FIG. 2. Early Jurassic succession cropping out at the Feidt quarry, Brouch (Mersch, Grand-Duchy of Luxembourg). A, view of the of the upper part of the Luxembourg Sandstone Formation (LS) overlapped by the limestones and marls of Strassen (LMS). B, detail of the upper coquina bed.

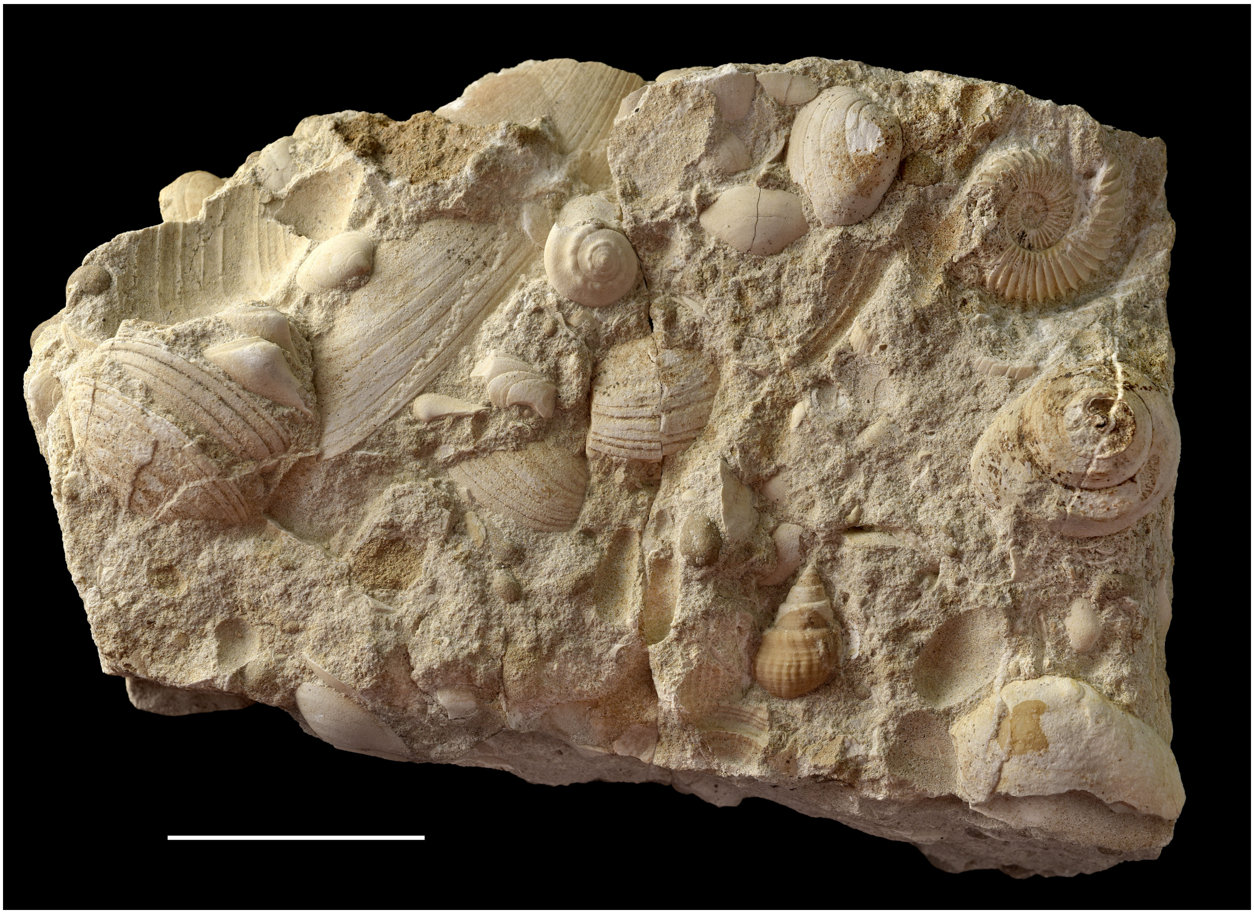

FIG. 3. Sample of Luxembourg Sandstone Formation from the *Schlotheimia angulata* Zone of Brouch (Mersch, Grand-Duchy of Luxembourg) showing the surface of the upper coquina bed. Scale bar represents 50 mm.

cropping out in the Feidt quarry at Reckinger Wald, near Brouch (Mersch), *c.* 20 km north of the city of Luxembourg (Figs 2, 4). These levels are dated to the lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone) and upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), respectively (details in Monari *et al.* 2011). The material described by Meier & Meiers (1988), which comes from the same quarry (upper level), has also been revised. A few other specimens from the Luxembourg Sandstone Formation have a less precise stratigraphical position and come from the following localities of the Grand-Duchy: Altwies (probably upper Hettangian, *Schlotheimia angulata* Zone), Bridel, Côte-d'Eich (city of Luxembourg), Hesperange and Itzig (Fig. 4). Some specimens also come from the Hettangian of Hettange-Grande (Moselle, north-eastern France). All of this material belongs to the collections of the MNHNL.

The material published by Deshayes (1850) and Terquem (1855) from the Hettangian of Hettange-Grande, by Piette (1856a) and Terquem & Piette (1865) from the Sinemurian of Ardennes department (north-eastern France), and by Dareste de la Chavanne (1912) from the upper Hettangian of Azy-le-Vif (Nièvre, central-eastern France), belonging to the collections stored at UCBL, has been studied for comparison purposes. When necessary, lectotypes have been designated for some taxa established by these authors. The online catalogues of type specimens of the Muséum national d'Histoire naturelle, Paris, France (https://science.mnhn.fr) and the British collections of the GB3D Type Fossils Online project (https://www.3d-fossils.ac.uk) have also been accessed.

The higher classification of the class Gastropoda Cuvier 1795 adopted here is basically that proposed by Bouchet *et al.* (2017). The descriptions are mainly focused on the ontogenetic changes of the shell characters, and most of the morphological terms used therein are defined in Cox (1960a). The specimens have been photographed using the focus stacking method after being coated with ammonium chloride. Images so obtained were processed with the Helicon Focus 8 software.

The basic approach of this palaeobiogeographic study was a comparison of the results obtained by applying different

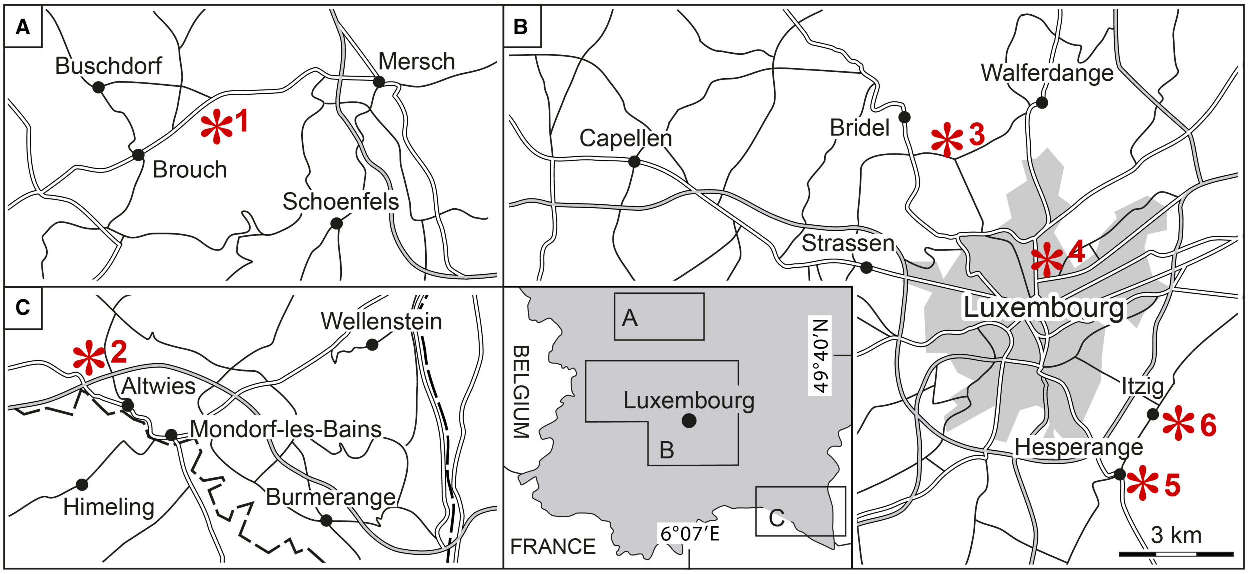

FIG. 4. Map of southern Luxembourg with the localities of the material studied. 1, Brouch. 2, Altwies. 3, Bridel. 4, Côte-d'Eich. 5, Hesperange. 6, Itzig.

quantitative methodologies and parameters to presence/absence matrices, in order to recognize shared traits and their changes in the palaeogeographic distribution of the western Tethyan gastropods during the early Jurassic recovery. This study is intended to be a preliminary step towards a more complete analysis. For this reason, we adopted the tools most commonly used in descriptive and explorative data analysis (Hammer & Harper 2024). Even the taxonomic level selected (i.e. the species) is significant. The genus is the taxonomic rank more frequently used in comparisons between assemblages at a wide geographic scale. However, the genus attribution of a species necessitates an in-depth study of shared characters, which are often difficult to identify without a revision of the original material, especially in the old literature. This would prevent the use of a wealth of information locked in many publications only because they are not taxonomically updated. In contrast, recognizing the taxonomic uniqueness of a species based on an accurate evaluation of the past literature can be more feasible than establishing the genus to which the species belongs. A similar, species-based approach was recently used by Friesenbichler *et al.* (2020) to study the dynamics of the recovery after the end-Permian mass extinction.

Our analysis is based on a very extensive database of the Hettangian to Pliensbachian gastropod species known for western Tethys (*c.* 1400 entries), compiled from published sources and direct examination of museum collections. Only species with suitable documentation (i.e. description, illustration and (sub)stage-defined stratigraphic occurrence) have been selected and critically evaluated to recognize synonyms and to provide a reliable taxonomy at species level.

Sample localities have been grouped according to geographic proximity, facies similarity and stratigraphic position in order to define wider areas treated as operational geographical units (OGUs). In most cases, these units correspond to sedimentary basins known to exist during the time intervals considered. Presence/absence matrices, with and without singletons, have been extracted from the database and analysed using multivariate methods of investigation (Q-mode cluster analysis and principal coordinates analysis), parsimony analysis of endemicity and network analysis.

Average linkage cluster analysis and principal coordinates analysis (PCoA) were performed with PAST v5.2 software (Hammer *et al.* 2001; Hammer & Harper 2024; Hammer 2025). PCoA was performed as a method of ordination analysis complementary to the cluster analysis, and the minimum spanning tree has been reported in the resulting plots. Matrices including singletons have been elaborated using Dice and Raup–Crick similarity coefficients (Dice 1945; Raup & Crick 1979). The latter coefficient has been used also to analyse matrices without singletons. In addition, the Ochiai similarity coefficient (Ochiai 1957) has been applied, resulting in dendrograms largely equivalent to those obtained with the Dice coefficient (Fig. S1). Dice and Ochiai coefficients essentially represent different types of ratio of the species in common among OGUs to the total number of species. Other similarity coefficients used in the palaeobiogeographic analysis of binary data, and based on the same principle, are the Jaccard (Jaccard 1901) and Simpson (Simpson 1943) coefficients (e.g. Dommergues *et al.* 2009; Angiolini *et al.* 2013; Vörös 2016; Huang *et al.* 2022). In the present case, the Jaccard dendrograms have a cophenetic correlation slightly higher than those obtained using the other indices. In spite of this, the Dice coefficient has been selected here simply because it stresses dissimilarities less and, consequently, the dendrograms produced, which have exactly the same topology as those obtained with the Jaccard coefficient, are less compressed towards the root and more easily readable. The Simpson index has been discarded because the cophenetic correlation is somewhat lower than those calculated with the other similarity indices. The Raup–Crick index is a probabilistic metric that takes into account, more than the other indices, the difference in the number of taxa between OGUs based on the frequency of the taxa in the whole dataset. Therefore, it provides more robust results when comparing samples with strong differences in the number of species (e.g. Hilton & Cleal 2007; Dera *et al.* 2011; Jin & Harper 2024), as in our case. In fact, as explained in the discussion of the results, the dendrograms obtained by the Dice and other similar coefficients seem in part more influenced by the asymmetric distribution of the data than those produced by the Raup–Crick coefficient. In any case, the results obtained with different indices show shared clusters that presumably reflect robust relationships between the OGUs involved.

Unlike the cluster analysis, which is a phenetic approach establishing areas of endemism by the overall similarity and species co-occurrence, the parsimony analysis of endemicity (Rosen & Smith 1988) promotes a historical view in which the disappearance of taxa also contributes to the definition of areas of endemism (Morrone 2014). Moreover, this analytical method assumes that the palaeogeographic distribution of the taxa is driven by parsimony. Thus, an area/species binary matrix is operationally treated in the same way as the cladistic taxonomy treats a species/characters matrix. Just as in cladistics the characters present in one single species are considered as autapomorphies, so the taxa present in one single OGU are not informative and should be removed from the matrix. Therefore, the matrices used in our analysis are derived from the dataset by removing singletons. The analysis has been performed using PAUP software, v4a, build 169 (Swofford 2003). Although it can be carried out under different criteria concerning rooting and character types (see Morrone 2014 for a synthesis), we have followed the original indication by Rosen & Smith (1988), who suggested the addition of a hypothetical outgroup area in which all species are missing in order to root the cladograms. All characters (species) were equally weighted and of ‘Dollo.up’ type. A heuristic search with starting tree(s) obtained via stepwise addition, random addition sequence and tree-bisection-reconnection branch-swapping was performed under ACCTRAN optimization.

Network analysis is being increasingly used in palaeobiogeography to study the relationship between localities and their evolution through time, based on the co-occurrence of taxa (e.g. Kiel 2017; Huang *et al.* 2018; Penn-Clarke & Harper 2021; Rong *et al.* 2020; Echevarría & Ros-Franch 2024; Jin & Harper 2024). In our case, the main output of this analysis is a bipartite network diagram in which both OGUs and taxa are represented by nodes connected by edges. A taxon (species) is connected to an OGU if it is present there, thus the network is based on presence/absence matrices. The datasets used are those without singletons, given that species known only from single OGUs do not contribute to network relationships. The network graphs have been realized with the Gephi software package (v0.10; Bastian *et al.* 2009) using the ForceAtlas2 algorithm (Jacomy *et al.* 2014), which spatializes the network simulating attraction/repulsion physical forces. OGU nodes are attracted to each other in proportion to the number of shared species, helping to visualize the level of connectedness and identify possible clusters (Hammer & Harper 2024). Further information on the datasets used is given in the results section of the analysis.

SYSTEMATIC PALAEONTOLOGY

Subclass CAENOGASTROPODA Cox 1960b
Superfamily uncertain
Family PSEUDOMELANIIDAE Hoernes 1884

Genus *Pseudomelania* Pictet & Campiche 1862

Type species. Pseudomelania gresslyi Pictet & Campiche 1862. Neocomian, Sainte-Croix (Switzerland).

Remarks. As noted in several studies (e.g. Stephenson 1952; Gründel 2001, 2012; Kaim 2004; Ferrari *et al.* 2016; Vitón *et al.* 2020), the holotype of *Pseudomelania gresslyi*, type species of the genus, is represented by an inner mould. This makes the status of the genus and its placement in the higher rank taxa uncertain.

Pseudomelania inornata (Terquem & Piette 1865)
comb. nov.
Figure 5

?	1850	*Chemnitzia phidias* d’Orbigny, p. 214.
?	1851	*Chemnitzia phidias* d’Orb.; d’Orbigny, p. 34, pl. 237, fig. 12.
* v	1865	*Turritella inornata* Terquem & Piette, p. 37, pl. 2, figs 14, 15.
?	1997	*Pseudomelania phidias* (d’Orbigny); Fischer & Weber, p. 13, pl. 3, fig. 2.

Material. 3 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR423, BR630, BR634.

Description. The shell is medium-sized (maximum height *c.* 30 mm), high-spired, slightly cyrtoconoidal, with pointed apex and composed of 8–10 whorls. The first teleoconch whorls are moderately and evenly convex with a height/width ratio of *c.* 0.5. The later whorls become slightly less convex and are pendent in outline. The periphery is angularly rounded and placed slightly above the suture. The height/width ratio of the penultimate whorl is 0.58. The suture is quite deeply impressed and oblique, inclined *c.* 78° on the spire axis. The base is low-conoidal, moderately convex, anomphalous. The aperture is oval, and angled at the sutural corner. The parietal lip is covered by a thin inductura extended to the columellar lip. The columellar lip is smooth, slightly arched and moderately robust. It is flanked by a weak, poorly defined axial spiral bulge and it passes smoothly into the parietal lip. The outer lip is simple.

The shell is smooth. The growth lines are opisthocline and widely opisthocyrt on the whorl surface, and prosocyrt on the peripheral region and on the base.

Remarks. Terquem & Piette (1865) established *Turritella inornata* on material from the Sinemurian of Ardennes. Two specimens are present in the UCBL Terquem collection (UCBL-EM 31521a and 31521b). One of them (UCBL-EM 31521a; Fig. 5A–C) is clearly the shell illustrated by the authors and is here selected as the lectotype, while the other is fragmentary. The lectotype slightly differs from the specimens described here in having lower whorls and a less incised suture. It also has a thick parietal inductura whereas in the only specimen from Luxembourg preserving the peristome the parietal inductura is thin. However, this specimen is much smaller and clearly represents a subadult shell. Most probably the inductura developed during the last growth. This is confirmed by the fact that the other specimen in the UCBL Terquem collection, which is broken in the axial direction, is also smaller than the lectotype; and the parietal region, visible in axial cross-section, is not thickened.

The material from Luxembourg is also comparable to *Pseudomelania phidias* (d'Orbigny 1850), a species from upper Hettangian – lower Sinemurian deposits of Côte d'Or (north-eastern France). However, the lectotype of this species, designated by Fischer & Weber (1997), is an inner mould and this prevents more detailed comparison. If *P. phidias* and *P. inornata* are synonyms, the name proposed by d'Orbigny should have priority. *Pseudomelania* sp. described by Gründel (2007a, p. 15, pl. 4, fig. 2a, b), from the upper Sinemurian of Baden-Württemberg (south-western Germany), differs from *P. inornata* in the much smaller size, lower and more numerous whorls and in the presence of a narrow subsutural shelf.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); Sinemurian, Rimogne (Ardennes, north-eastern France); ?upper Hettangian – lower Sinemurian, Côte d'Or (north-eastern France).

Genus *Bourguetia* Terquem & Jourdy 1869

Type species. Melania striata Sowerby 1814, *non* Perry 1811 (= *Phasianella saemanni* Oppel 1856). Bajocian, south-western England (Cox 1938).

Bourguetia deshayesea (Terquem 1855)

Figure 6

? 1854 *Chemnitzia turbinate* Chapuis & Dewalque, p. 77, pl. 11, fig. 3.
v 1855 *Turritella Zenkeni* [*sic*] Tqm (DKr. sp.); Terquem, p. 253, pl. 14, fig. 6, 6a.
v * 1855 *Turritella Deshayesea* Terquem, p. 253, pl. 14, fig. 7, 7a.
1855 *Melania cyclostoma* Terquem, p. 255, pl. 14, fig. 8.
? 1864 *Melania Zenkeni* [*sic*] (Dunker); Dumortier, p. 116, pl. 19, fig. 4.
? v 1865 *Cerithium breoni* Terquem & Piette, p. 65, pl. 6, figs 8, 9.
1907a *Bourguetia deshayesea* (Terquem); Cossmann, p. 27, pl. 4, fig. 11.
? 1909 *Turritella* (*Mesalia*) *zinkeni* Dunker sp.; Brösamlen, p. 274, pl. 20, figs 42, 43.
1909 *Turritella Deshayesea* Terq.; Cossmann, p. 71, pl. 2, fig. 3.
v 1912 *Bourguetia deshayesea* (Terquem); Dareste de la Chavanne, p. 578, pl. 16, fig. 10.
? 1934 *Mesalia zinkeni* Dunker; Kuhn, p. 42, pl. 2, fig. 20; pl. 3, fig. 21.
? 1997 *Promathilda* (*Turritelloidea*) *zinkeni* (Dunker); Hägele, p. 116, unnumb. text-fig.
2012 *Bourguetia zenkeni* [*sic*] (Dunker); Dejax *et al.*, p. 108, text-fig. 75.

Material. 6 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR216, BR405, BR424, BR695B, GL390A; Hesperange, Hettangian, exact stratigraphical level unknown: GL343.

Description. The shell is medium–large-sized (maximum height *c.* 75 mm), high-turbiniform, slightly cyrtoconoidal, composed of about eight whorls. The whorls are rather high, with a height/width ratio of 0.55. The height of the last whorl is slightly less than half of the shell height. The first teleoconch whorls are weakly convex on the whole, with periphery well below mid-whorl. They are flattish above the periphery and more rounded near the sutures. During growth the whorl surface becomes more convex, almost swollen and slightly pendent. The suture is oblique and impressed. The base is evenly rounded, constricted and elongated abapically. The aperture is broadly oval, with an acute sutural corner and extended abapically to form a lower spout. The parietal lip is covered by a thin inductura that passes smoothly to the columellar lip. The outer lip is simple and evenly convex.

The ornament is represented by 17–18 subequal spiral threads separated by narrow incisions. During growth, the threads

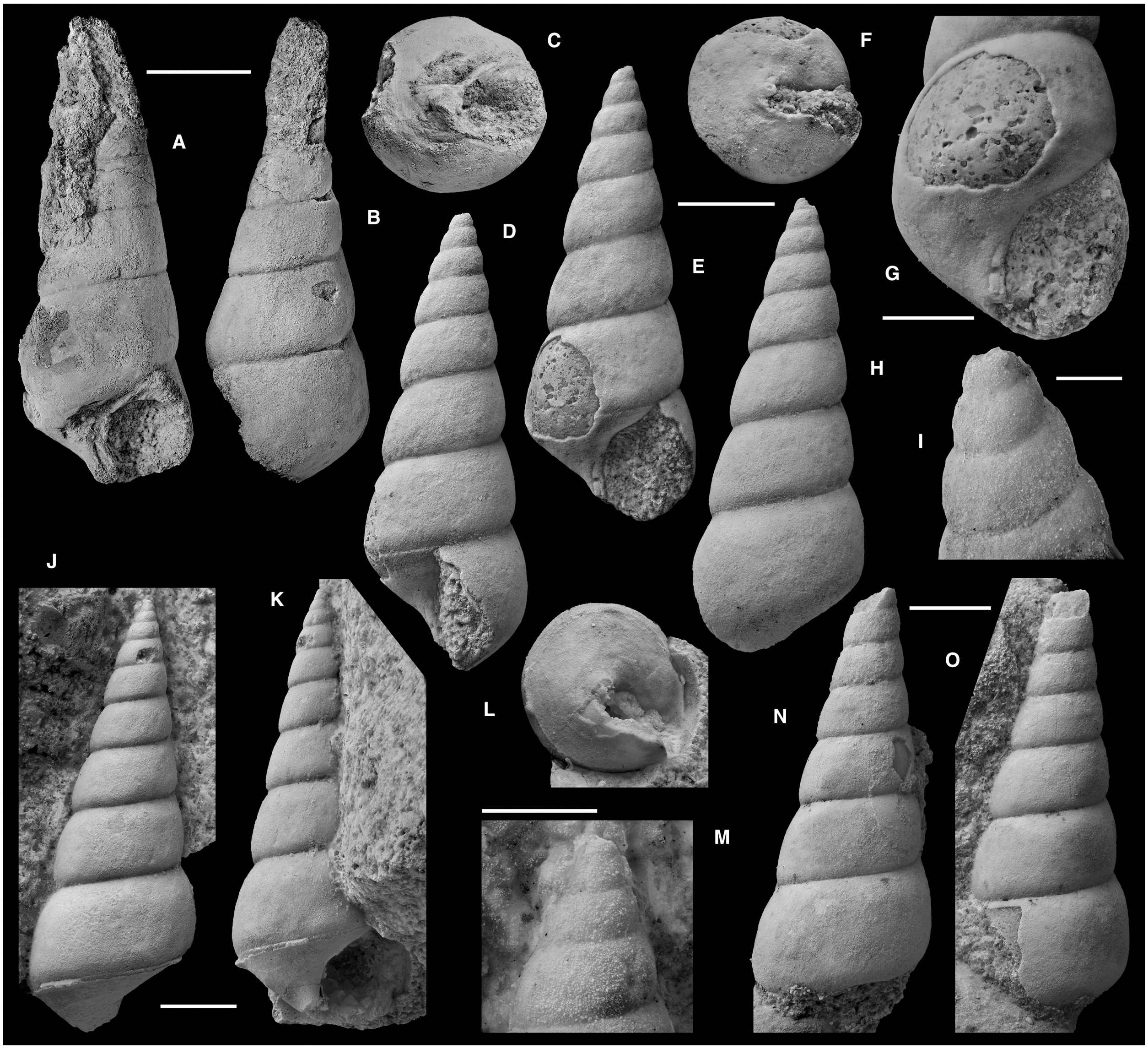

FIG. 5. *Pseudomelania inornata* (Terquem & Piette 1865). A–C, lectotype UCBL-EM 31521a in apertural, lateral and basal views. D–I, MNHNL BR630 in lateral, apertural and basal views, detail of the aperture, dorsal view and detail of the apical whorls. J–M, MNHNL BR634 in lateral, apertural and basal views, detail of the apical whorls. N–O, MNHNL BR423 in dorsal and lateral views. A–C, Rimogne, France, Sinemurian. D–O, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 10 mm (A–C); 4 mm (D, E, F, H); 2 mm (G, M); 1 mm (I); 5 mm (J–L, N, O).

become thicker and flatter, and on the last whorl some of them are bisected by new incisions. The base is sculptured by spiral threads that become progressively thicker and more distanced adaxially. The growth lines are strongly opisthocline and very slightly opisthocyrt or straight on the adapical region of the whorl surface. They are widely prosocyrt on the peripheral region and on the base.

Remarks. The specimens from Luxembourg match the syntypes of the species in the UCBL very well in shape and ornamentation (UCBL-EM 31482a and 31482b; Fig. 6A–D). *Bourguetia deshayesea* shares many shell characters with *Melania zinkeni* Dunker 1846 (p. 169; 1847, p. 108, pl. 13, figs 1–3; Gründel 2010, p. 14, pl. 2, figs 11–16 as *Turritelloidea*?) from the Hettangian beds of Halberstadt (Saxony-Anhalt, northern Germany) and some authors considered the two taxa synonyms (e.g. Bistram 1903; Cossmann 1907a; Dareste de la Chavanne 1912; Gaetani 1970). Gründel (2010) revised the type material of Dunker's taxon and concluded that most of the subsequent records of this species (e.g. Terquem 1855; Dumortier 1864; Brösamlen 1909; Khun 1934; Hägele 1997) cannot be confirmed with certainty, because they refer to specimens that differ from the type

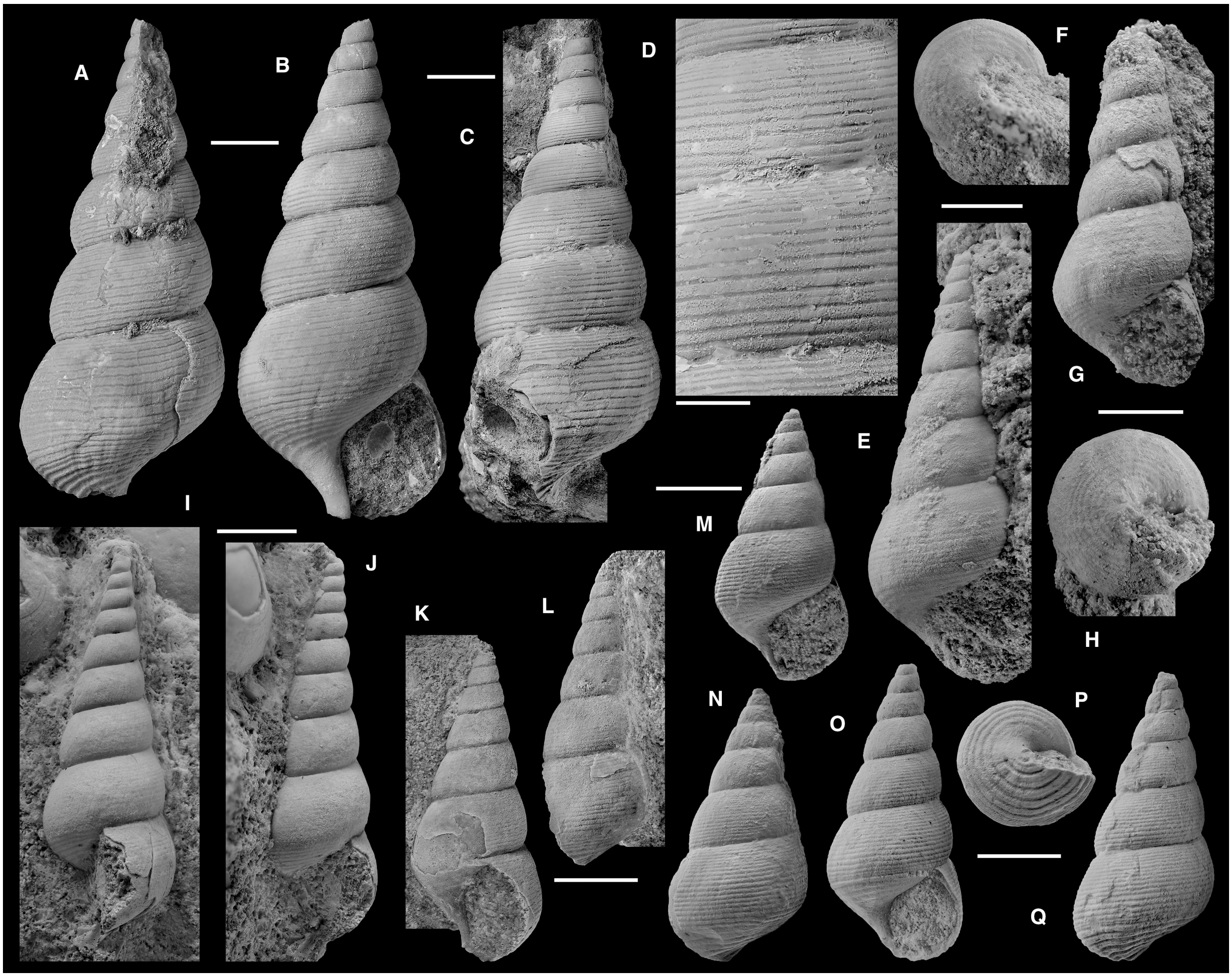

FIG. 6. *Bourguetia deshayesea* (Terquem 1855). A–B, syntype UCBL-EM 31482a in dorsal and apertural views. C–D, syntype UCBL-EM 31482b in lateral view; detail of the ornament. E–F, MNHNL BR405 in apertural and basal views. G–H, MNHNL BR424 in apertural and basal views. I–J, MNHNL BR216 in lateral and apertural views. K–L, UCBL-EM 33360 in apertural and lateral views; Hettange-Grande, France, upper Hettangian. M–N, MNHNL BR695B in apertural and dorsal views. O–Q, MNHNL GL390A in apertural, basal and dorsal views. A–D, K–L, Hettange-Grande, France, upper Hettangian. E–J, M–Q, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 10 mm (A–C); 5 mm (D–Q).

material in the significantly higher number of spiral threads (10–15 instead of 7–8). According to Gründel (2010), the low number of spirals is a character that distinguishes *T. zinkeni* from the very similar *T. deshayesea*. It is therefore possible that many records of *zinkeni* with a high number of spirals must be ascribed instead to *deshayesea*.

Chemnitzia turbinata Chapuis & Dewalque 1854, from the Hettangian – lower Sinemurian of southern Belgium, is probably a synonym of *B. deshayesea* but the original illustration does not enable this to be confirmed with certainty. Also, *Melania cyclostoma* Terquem 1855, a species from the upper Hettangian of Hettange-Grande, is very similar to *B. deshayesea*. Terquem (1855) described *M. cyclostoma* as smooth in the French text, but the Latin description says that its whorls are faintly spirally striated and the illustration shows a shell with a distinct spiral ornament. Unfortunately, the type material of this species has not been located in the UCBL. *Cerithium breoni* Terquem & Piette 1865, based on a single fragmentary shell from the Sinemurian of Ardennes, is strongly reminiscent of *B. deshayesea*. According to the original description, *C. breoni* has two columellar folds but these are not present in the holotype UCBL-EM 31535. The specimen ascribed by Terquem (1855) to *Turritella zenkeni* (UCBL-EM 33360; Fig. 6K, L) belongs to *B. deshayesea*.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France); upper Hettangian, Provenchères-sur-Meuse (Haute-Marne, north-eastern France); Hettangian, Hesperange (Grand-Duchy of Luxembourg).

Bourguetia bipartita sp. nov.
Figure 7

v 1988 *Bourguetia deshayesea* (Terquem); Meier & Meiers, p. 36, pl. 9, fig. 19a, b.
v 2012 *Bourguetia zenkeni* [*sic*] (Dunker); Guérin-Franiatte & Hanzo, p. 160, text fig. 109G.

LSID. https://zoobank.org/NomenclaturalActs/5417ccda-44d5-40c6-9090-b9c09d015f06

Derivation of name. From the Latin adjective *bipartitus*, meaning divided in two, referring to the two zones of whorl surface with different spiral ornamentation.

Type material. Holotype: MNHNL BR410 (Fig. 7A–E). Paratypes: MNHNL BR355, BR403, BR409, BR411, BR412, BR416, BR429, BR624, BR626, BR628, BR631, BR765, BR771, BR775, BR900, Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Type material and 60 specimens. Brouch, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone): MNHNL BR865, BR889; same locality, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR114, BR203, BR221-3, BR222-2, BR228, BR288, BR297, BR319, BR328, BR404, BR406, BR407, BR413–415, BR417, BR418-1, BR430, BR453, BR472-1, BR507, BR513, BR522, BR524, BR526, BR543, BR563, BR621–623, BR625, BR627, BR629, BR633, BR635, BR636, BR642, BR753, BR848A–B, BR855, BR858D, BR858G (5 specimens), BR947, BR961-2, BR965A–B, BR976-1, BR992-1, GL379-2, HE135, HE170-2, HE179; Hettangian, locality and exact stratigraphical level unknown: MNHNL GL211A–C.

Diagnosis. Shell medium–large-sized with high, acute, slightly coeloconoidal spire and impressed sutures. Spire whorls rather pendent, weakly concave adapically. Last whorl broad with convex base, constricted and elongate abapically. Aperture broadly oval, extended downwards in lower spout. Parietal lip passing into columellar lip through rounded angle. Columellar and parietal lips with thin callus. Ornament of numerous spiral threads, clearly thinner on adapical part of whorls.

Description. The shell is medium–large-sized (maximum height *c.* 75 mm, apex slightly broken), high-conoidal with an acute early spire, composed of *c.* 10 whorls. The shell outline is slightly coeloconoidal. The height of the last whorl is slightly less than half of the shell height. The first teleoconch whorls are weakly convex, with rounded periphery just below mid-whorl. They are rather high with a height/width ratio 0.59–0.67. Subsequently the whorls become more convex and their periphery shifts downward, making them distinctly pendent in outline. The height/width ratio of the whorls decreases progressively and that of the penultimate whorl is *c.* 0.46. On the mature whorls the adapical part of the surface becomes flat to slightly concave. The suture is somewhat oblique, impressed and distinctly incised. The last whorl is broad and its base is evenly convex, constricted and elongated abapically. A narrow umbilicus is present in the juvenile shell. During adult growth it is partly or fully hidden by the columellar callus. The aperture is broadly oval, with an acute sutural corner. The parietal lip is covered by a thin inductura that passes smoothly to the columellar lip. The columellar lip is moderately thick and almost straight or gently curved. It joins the parietal lip through a rounded, obtuse angle and extends downward where it forms a distinct lower spout featuring a furrow. The outer lip is simple and evenly convex.

The early whorls are ornamented by 12–15 fine spiral threads separated by furrows that are slightly narrower than the threads. During growth, the number of threads remains almost constant, but the threads on the periphery and abapical part of the whorl become thicker, flattish and more separated. The 6–8 threads on the adapical part of the whorl remain clearly thinner than the others, apart from the two spirals adjacent to the adapical suture, which sometimes are slightly more robust. The base is sculptured by spiral threads that become progressively thicker and more distanced adaxially. The growth lines are strongly opisthocline and very slightly opisthocyrt or straight on the adapical region of the whorl surface. They are widely prosocyrt on the peripheral region and on the base.

Remarks. All of the studied specimens lack the protoconch. The peristome is variably incomplete but the observable characters clearly indicate the presence of a distinct lower spout. Two juvenile specimens (MNHNL BR407 and BR222-2) show an umbilical chink, whereas in the other specimens the columellar callus extends over the umbilical area. The abundant material studied is moderately variable in shell shape and ornament. Some specimens are more clearly coeloconoidal in outline, due to the later whorls being more inflated. The adapical band of thinner spirals varies in overall width, and the threads on it also vary slightly in strength. The new species is clearly similar to the above described *Bourguetia deshayesea* (Terquem 1855) but it is readily distinguishable by the different pattern of spiral ornamentation: in Terquem's species the spiral threads are flattish, subequal in thickness and separated by a narrow incision, whereas in the new species only the thicker threads on the periphery are flattish and those on the abapical part of the whorls are clearly thinner than the others and all of the threads are separated by furrows, not by narrow incisions. Moreover, *T. deshayesea* has a slightly cyrtoconoidal shape and the whorls are less pendent and not concave subsuturally.

Melania zinkeni Dunker 1846 differs from *Bourguetia bipartita* mainly in having fewer spiral threads. Moreover, these are subequal in strength.

Stratigraphic & geographic range. Lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone) and upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

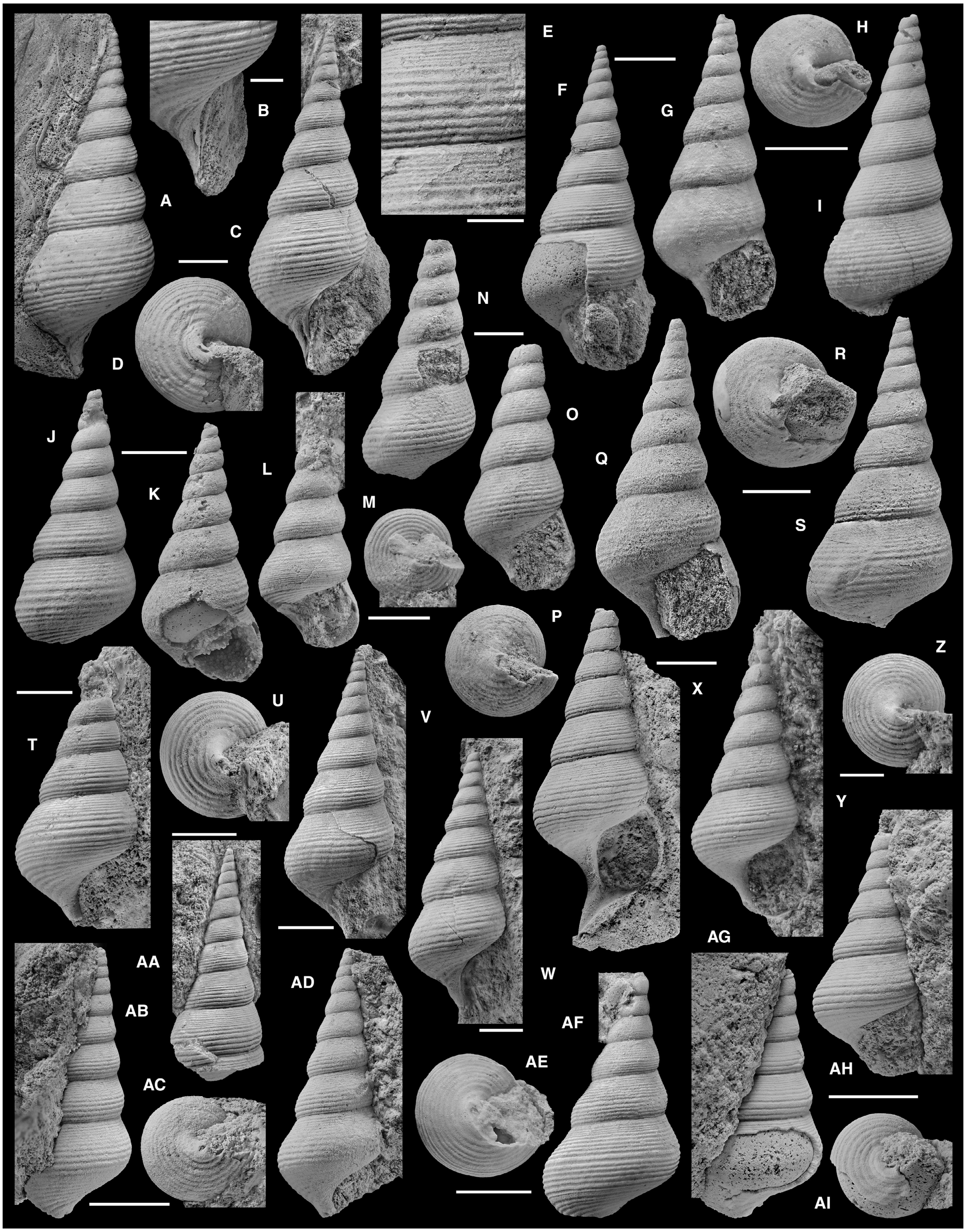

FIG. 7. *Bourguetia bipartita* sp. nov. A–E, holotype MNHNL BR410 in dorsal view; detail of the inner lip, apertural and basal views, detail of the ornament. F, paratype MNHNL BR411 in apertural view. G–I, paratype MNHNL BR355 in apertural, basal and dorsal views. J–K, paratype MNHNL BR775 in dorsal and apertural views. L–M, paratype MNHNL BR412 in apertural and basal views. N–P, paratype MNHNL BR429 in dorsal, apertural and basal views. Q–S, paratype MNHNL BR628 in apertural, basal and dorsal views. T–U, paratype MNHNL BR900 in apertural and basal views. V, paratype MNHNL BR626 in apertural view. W, paratype MNHNL BR624 in apertural view. X, paratype MNHNL BR631 in apertural view. Y–Z, paratype MNHNL BR409 in apertural and basal views. AA, paratype MNHNL BR403in lateral view. AB–AD, paratype MNHNL BR771 in dorsal, basal and apertural views. AE–AF, paratype MNHNL BR416 in basal and dorsal views. AG–AI, paratype MNHNL BR765 in dorsal, apertural and basal views. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 10 mm (A, C, D, F–K, Q–X, AA–AI); 5 mm (B, E, L–P, Y, Z).

Bourguetia? *dubia* (Terquem 1855) comb. nov.
Figure 8A–I

* v 1855 *Pterocera dubia* Terquem, p. 275, pl. 17, fig. 5, 5a; pl. 26, fig. 8a, b.
v 1865 *Pterocera dubia* Terq.; Terquem & Piette, p. 61.

Material. 2 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR637, BR638.

Description. The shell is large-sized (maximum height 98.4 mm) and high-spired. The whorls are poorly convex with a noticeably rounded upper third. The suture is impressed and moderately inclined. The last whorl is quite globose and its height is almost half of the reconstructed height of the shell. The base is slightly downward elongated and constricted in its axial region. It passes smoothly to the whorl flank.

The ornament consists of *c.* 10 faint and thin spiral threads on the axial region of the base, which fade progressively in the abaxial direction. The growth lines are strongly opisthocline and opisthocyrt above the periphery, becoming distinctly prosocyrt on the base.

Remarks. In the description of the species, Terquem (1855) reported the presence of weak angulations of the whorl surface. According to him, these angulations might indicate the presence of digitations, hence the attribution of the species to the genus *Pterocera* Lamarck 1799 (= *Lambis* Röding 1798, superfamily Stromboidea Rafinesque 1815). However, none of the three syntypes in UCBL-EM (UCBL-EM 31505a, 31505b and 31505c; Fig. 8A–G) shows these angulations nor any trace of a pronounced siphonal canal, therefore the strombid affinity of the species is untenable, as already suggested by Gründel *et al.* (2009). The best preserved syntype, although fragmentary, is here selected as lectotype (UCBL-EM 31505a; Fig. 8A–D) because it agrees well with the specimen figured in Terquem (1855) pl. 26, fig. 8, which was probably heavily reconstructed. The two specimens from Luxembourg here described are not well preserved: one lacks the apical spire and the other is partially decorticated with a broken base. However, they agree rather well with the original material of Terquem (1855) in general shape, ornamentation and shape of growth lines.

The species is here ascribed dubitatively to the genus *Bourguetia* Terquem & Jourdy 1869 on the basis of its general form and shape of the growth lines, but it differs from the most typical species of this genus in lacking a spiral ornamentation on the spire whorls.

Rostellaria costae Sharpe 1850 (p. 193, pl. 20, fig. 1; as *Pseudomelania* in Mouterde & Rocha 1981, p. 59, pl. 2, fig. 4 and in Vitón *et al.* 2020, p. 155, figs 8, 12.5–12.7) from the upper Sinemurian of the Lusitanian Basin (western Portugal) is very similar in general shape to *B.*? *dubia*, but differs in having fewer and much thicker spiral threads on the neck.

Stratigraphic & geographic range. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Genus *Torusanina* Gründel 2012

Type species. Melania heddingtonensis Sowerby 1813. Oxfordian, England.

Torusanina sp.
Figure 8J–K

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR891.

Description. The shell is medium-sized (height 28.6 mm), turriculated, composed of *c.* 10 whorls. The whorls are rather high, with a height/width ratio of *c.* 0.75. The adult whorls have a weak subsutural bulge that becomes more distinct and seemingly slightly angulated on the last whorl. The adapical part of the whorl below the bulge is slightly concave, whereas the abapical part is convex and slightly swollen at the periphery. The suture is somewhat oblique and runs in a wide furrow between the peripheral convexity of the previous whorl and the subsutural bulge. The base is relatively low, subconoidal and seems to be slightly downward elongated.

Remarks. The specimen is poorly preserved and partly embedded in matrix. The characters of the aperture are unknown and the ornament is not evident. The general characters of the shell approach closely those of the genus *Torusanina* Gründel 2012, but the poor preservation prevents a comparison at species rank. According to the list of species originally included by Gründel (2012), the stratigraphic distribution of *Torusanina* spans the Toarcian to Oxfordian. The present finding would move the first occurrence of the genus back to the upper Hettangian.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Family COELOSTYLINIDAE Cossmann, 1908
Genus *Coelostylina* Kittl 1894

Type species. Melania conica Münster 1841. Carnian, Southern Alps (north-eastern Italy).

Coelostylina paludinare (Terquem 1855)
Figure 9A–I

* 1855 *Cerithium paludinare* Terquem, p. 278, pl. 16, fig. 17a–c.
1913 *Cerithium paludinare* Terq.; Cossmann, p. 253.
v 1988 *Coelostylina paludinare* (Terquem); Meier & Meiers, p. 38, pl. 10, fig. 22a, b.

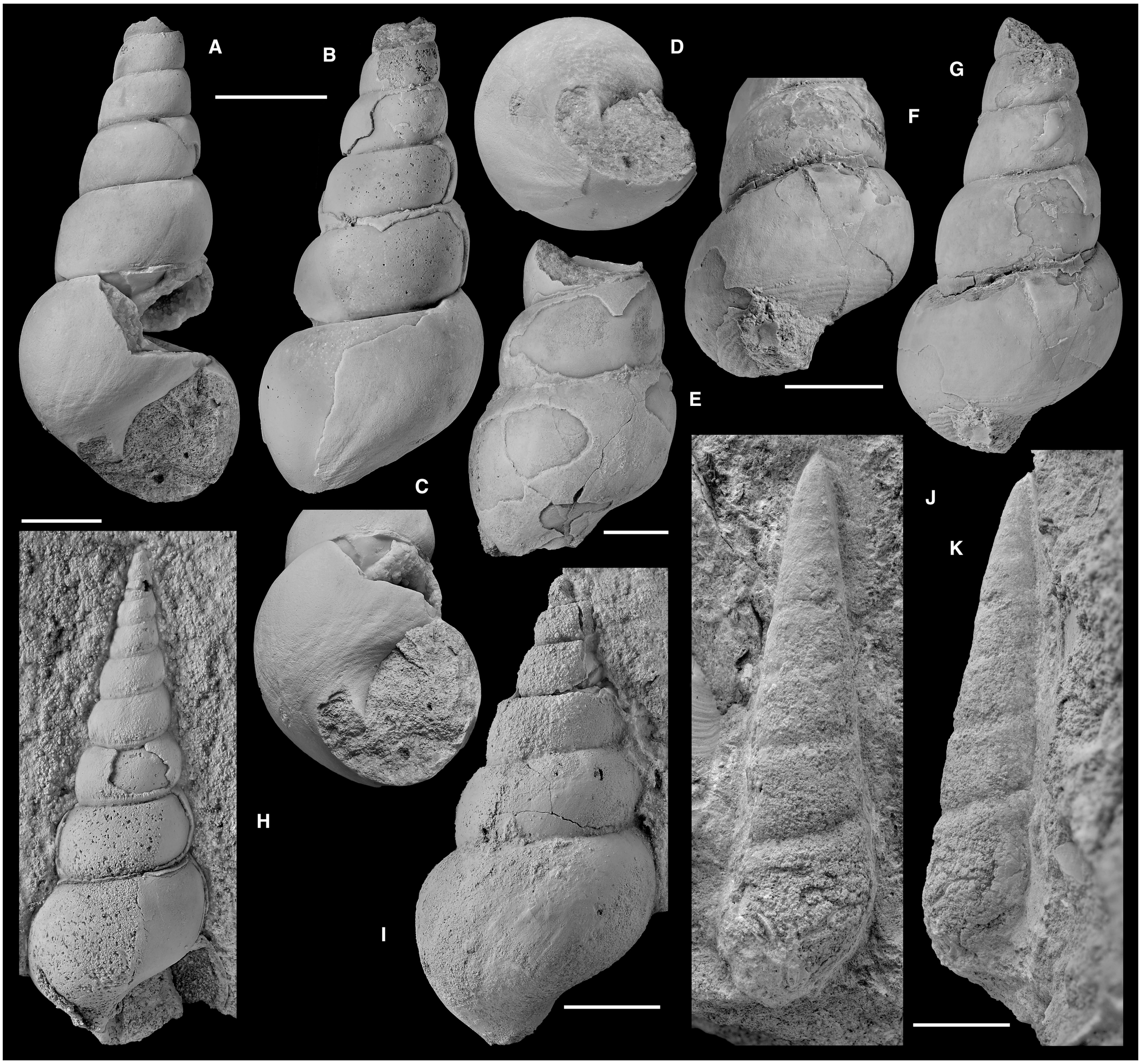

FIG. 8. Family Pseudomelaniidae Hoernes 1884. A–I, *Bourguetia*? *dubia* (Terquem 1855): A–D, lectotype UCBL-EM 31505a in apertural, dorsal, oblique basal and basal views; E, paralectotype UCBL-EM 31505b in dorsal view; F–G, paralectotype UCBL-EM 31505c in oblique basal and dorsal views; H, MNHNL BR637 in apertural view; I, MNHNL BR638 in dorsal view. J–K, *Torusanina* sp., MNHNL BR891 in dorsal and lateral views. A–G, Hettange-Grande, France, upper Hettangian. H–K, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 20 mm (A–D, I); 10 mm (E–H); 5 mm (J, K).

Material. 4 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR449C, BR562-2, BR583, GL665 (Fig. 9A–I).

Description. The shell is medium-sized (maximum height *c.* 15 mm), high-turbiniform, slightly cyrtoconoidal and composed of 5–6 moderately convex whorls. The early teleoconch whorls are slightly pendent in outline due to the position of the periphery, which is slightly above the suture. Their height/width ratio is *c.* 0.6. On later whorls, the periphery shifts upward, the whorl surface becomes regularly convex and the height/width ratio decreases to almost 0.5. On the penultimate whorl the periphery is slightly below the middle. The suture is moderately impressed, linear and weakly oblique. The base is convex and low, with a narrow umbilical chink. The aperture is oval and pointed at the sutural corner. The peristome is discontinuous on the parietal lip. The inner lip is thin and slightly detached from the base. It is straight and slightly leftward diverging from the spire axis in abaxial direction.

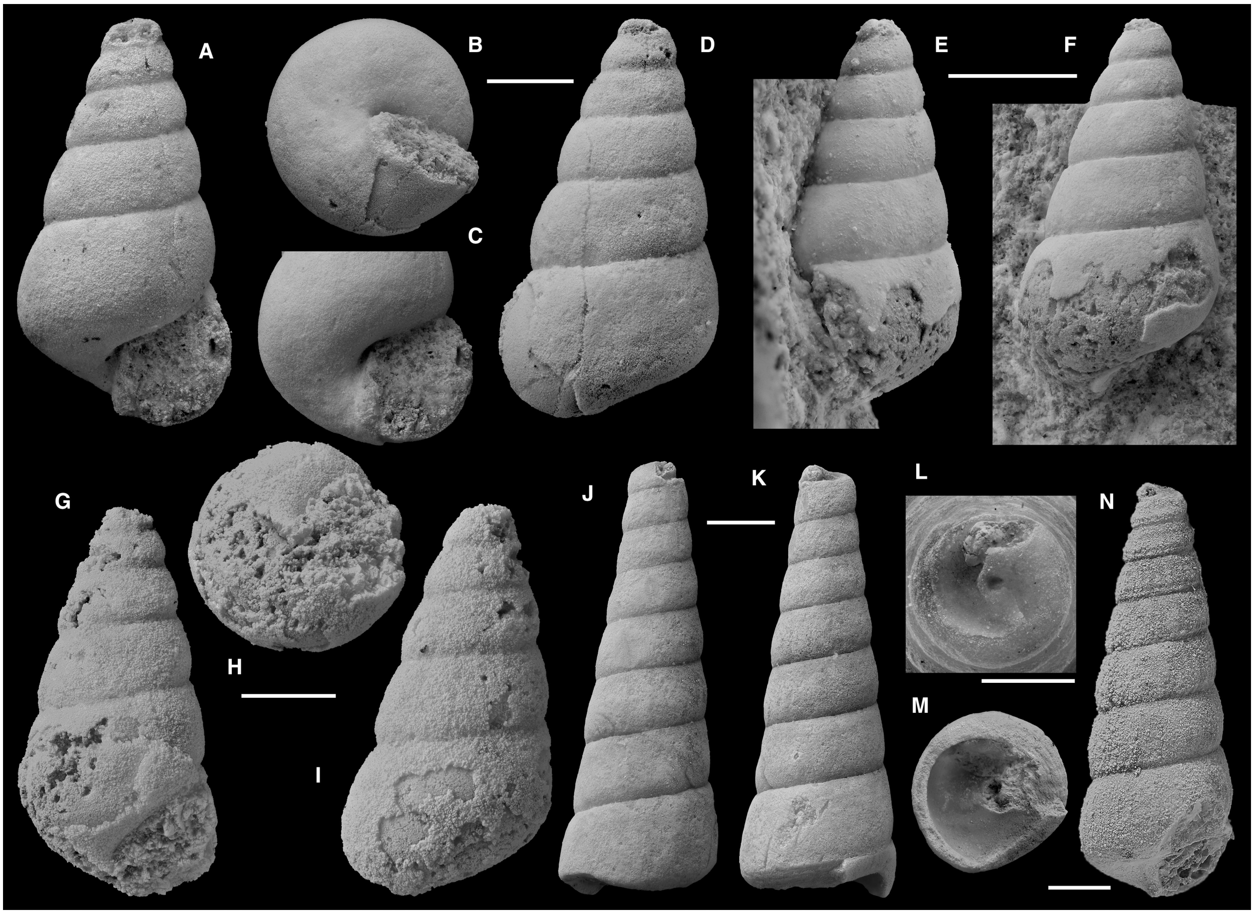

FIG. 9. Coelostylinid gastropods and *Cerithium rotundatum* Terquem 1855. A–I, *Coelostylina paludinare* (Terquem 1855): A–D, MNHNL BR583 in apertural, basal, oblique basal and dorsal views; E–F, MNHNL BR449C in lateral and apertural views; G–I, MNHNL GL665 in apertural, basal and dorsal views. J–M, *Trypanostylus*? sp., MNHNL BR301A in lateral, apertural and basal views, detail of the broken apical region showing the narrow umbilical cavity. N, *Cerithium rotundatum* Terquem 1855, holotype UCBL-EM 31498 in apertural view. A–M, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). N, Hettange-Grande, France, upper Hettangian. Scale bars represent: 3 mm (A–D, G–I); 5 mm (E, F); 2 mm (J, K, M); 1 mm (L, N).

The shell is smooth. The growth lines are very thin and scarcely visible. They are slightly opisthocline and gently opisthocyrt on the spire whorls and prosocyrt on the base.

Remarks. The specimens are strongly recrystallized and lack the protoconch but match well the specimen figured by Terquem (1855, pl. 16, fig. 17) in both shell shape and whorl height/width ratio. Unfortunately, the type material of the species has not been found in the UCBL-EM collection. Gründel (2010) considered *C. paludinare* a junior synonym of *Coelostylina krausseana* (Dunker 1846) (p. 168; Dunker 1847, p. 107, pl. 13, fig. 10a, b as *Paludina*; Huckriede 1967, p. 156, pl. 20, figs 26–29; Gründel 2010, p. 7, pl. 2, figs 6, 7) from the Hettangian beds of Halberstadt (Saxony-Anhalt, northern Germany). However, the last whorl of this species is proportionally higher and its base is more elongate abapically. Moreover, the early teleoconch whorls are proportionally lower and regularly convex, while in *C. paludinare* they are pendent.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Hettange-Grande (Moselle, north-eastern France).

Genus *Trypanostylus* Cossmann 1896

Type species. Eustylus zitteli Kittl 1894. Carnian, Southern Alps (north-eastern Italy).

Remarks. Cossmann (1896) proposed *Trypanostylus* as a replacement name for *Eustylus* Kittl 1894 (*non* Schoenherr 1843, Coleoptera) in the first issue of volume 43 of the *Journal de Conchyliologie* (p. 63) dated 1 January 1895. Cossmann (1909, p. 59) and Neave (1940, p. 585) reported 1895 as the year of publication of the genus. However, some authors (Winckworth 1936; Fischer-Piette 1937; Breure & Fontaine 2019) demonstrated that the dates printed on the frontispiece of the *Journal* were only nominal and that the publication of the issues was often later than that date. According to these sources, the year of publication of Cossmann's note is 1896 (see also Kabat 1990, p. 254).

Kittl (1894) did not fix a type species for *Eustylus*. Cossmann (1896) designated *Eustylus zitteli* Kittl 1894 as the type species but he later (Cossmann 1909) used *Eustylus militaris* Kittl 1894 instead. This last designation is invalid (ICZN 1999, art. 69.1).

Trypanostylus? sp.

Figure 9J–M

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR301A.

Description. The shell is medium-sized (height *c.* 13 mm), slender, turritelliform and preserves seven, slightly convex whorls. The suture is weakly impressed and moderately incised. The periphery runs on the lower half of the whorl making the whorl outline weakly pendent. The base is seemingly quite low, slightly conoidal, and narrowly umbilicated. It is very slightly convex and passes into the whorl flank through a rounded angulation.

Remarks. The specimen lacks the apical spire and the final part of the last whorl. The shell appears smooth. It also lacks growth lines, probably due to strong recrystallization. A narrow, subcircular umbilicus is visible both on the damaged base and on the broken apical region, showing a narrow umbilical cavity along the whole axis of the shell. This feature and the general shape of the shell are reminiscent of the genus *Trypanostylus* Cossmann 1896. However, this genus has axial ribs on the early teleoconch, a character that cannot be verified in the specimen here described due to the lack of apical spire.

Cerithium rotundatum Terquem 1855 (p. 278, pl. 17, fig. 8, 8a, b) from the Grès d'Hettange is similar to the specimen described here but is much smaller and has lower and slightly more convex whorls. Terquem (1855) described the species as smooth. However, Cossmann (1913, p. 196, pl. 6, fig. 103) recognized traces of a collabral ornament and ascribed the species to *Anoptychia* Koken 1892. On examination of the holotype of *C. rotundatum* (UCBL-EM 31498; Fig. 9N), the early whorls are seen to be ornamented by a pair of abapical spiral cord-like threads and a much weaker adapical thread crossed by closely spaced, thin collabral riblets. Therefore, the species probably belongs to *Proacirsa* Cossmann 1912. Also, the specimen from Rhaetian – lower Hettangian beds of Liguria (north-western Italy) assigned by Capellini (1866, p. 444, pl. 2, fig. 5) to *C. rotundatum* was originally described as smooth, but the scarce information and the poor illustration prevent detailed comparison. The shell from the Hettangian deposits of Provenchères-sur-Meuse (Haute-Marne, north-eastern France) classified by Cossmann (1907a, p. 25, pl. 4, fig. 12) as *Trypanostylus* cf. *nudus* (Münster *in* Goldfuss 1844) is also similar to the specimen here described but has more convex and higher whorls.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Superfamily CAMPANILOIDEA Douvillé 1904

Family AMPULLINIDAE Cossmann *in* Cossmann & Peyrot 1919

Genus *Globularia* Swainson 1840

Type species. Ampullaria sigaretina Lamarck 1804. Lutetian, Grignon (Île-de-France, northern France).

Globularia obtusa (Deshayes 1850) comb. nov.

Figure 10

* 1850 *Ampullaria obtusa* Deshayes, p. 45, pl. 72, fig. 24.
v 1855 *Ampullaria obtusa* Desh.; Terquem, p. 247, pl. 13, fig. 3, 3a.
v 1865 *Ampullaria obtusa* Desh.; Terquem & Piette, p. 32.
v 1913 *Tretospira obtusa* (Desl.) [*sic*]; Cossmann, pl. 10, fig. 34.

Material. 2 specimens. Hesperange, Hettangian, exact stratigraphic level unknown: MNHNL GL120, GL260.

Description. The shell is medium-sized (maximum height *c.* 50 mm), globose and composed of about four convex whorls. The apex is obtuse, dome-like and the spire is moderately elevated. The early preserved whorls are regularly convex. Subsequently, the adapical part of the whorl becomes flat. On the last two whorls, this part of the shell becomes a slightly inclined ramp that rapidly increases in width and is delimited by a rounded to angularly rounded outer edge. The sutures are impressed and sub-horizontal. The periphery is evenly convex. Whorls embrace at periphery. The last whorl is inflated, with no clear demarcation between the lateral face and the base. The base is high and evenly convex. The aperture is broad, ovate, with a strongly convex outer lip. The peristome is very slightly prosocline. The parietal lip has a thin inductura that extends onto the columellar lip. The outer lip is simple.

One of the specimens has very faint and irregular spiral cords. One of them is about at the midline of the lateral face of the penultimate and last whorls. Another cord marks the periphery, and three, perhaps four widely and subregularly spaced cords run on the base. The growth lines are somewhat strong and form very shallow and irregular growth folds. They are nearly orthocline to weakly prosocline and prosocyrt on the whorl surface and very gently sinuous on the base, that is, slightly opisthocyrt on the peripheral and adaxial part of the base and more markedly prosocyrt on the abaxial half of the base.

Remarks. One of the specimens is an internal mould, the other (Fig. 10G–L) lacks the earliest spire and the basal part of the peristome. Specimens from the UCBL Terquem collection supplement

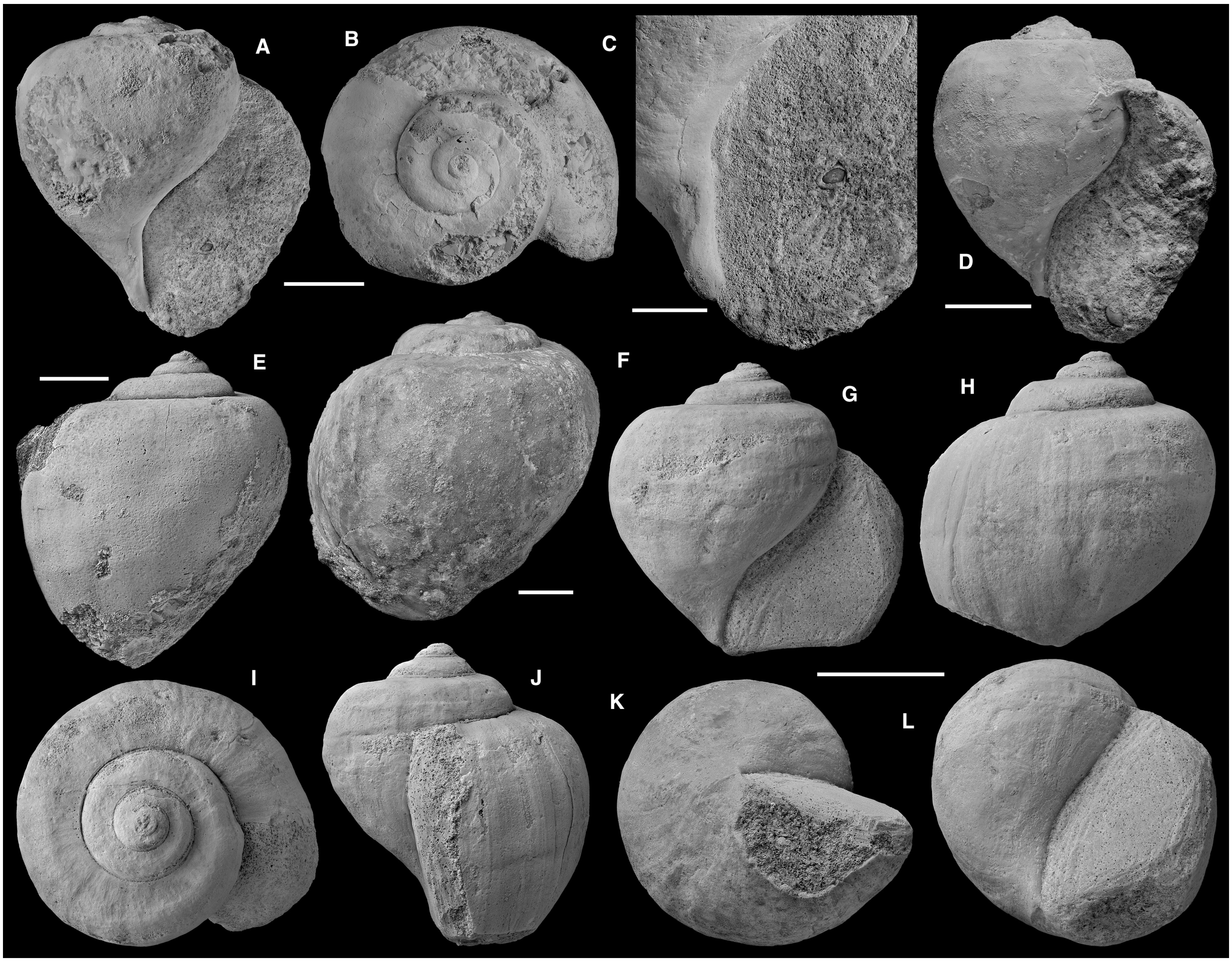

FIG. 10. *Globularia obtusa* (Deshayes 1850). A–C, UCBL-EM 31474 in apertural and apical views, detail of the aperture; D, UCBL-EM 33408 in apertural view; E, UCBL-EM 33409 in dorsal view; F, UCBL-EM 33410 in dorsal view; G–L, MNHNL GL120 in apertural, dorsal, apical, lateral, basal and oblique basal views. A–F, Hettange-Grande, France, upper Hettangian. G–L, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 20 mm (A, B, D, G–L); 10 mm (C, E, F).

the description of the species: the apertural characters can be fully examined in the type specimen UCBL-EM 31474 (Fig. 10A–C) figured by Terquem (1855, pl. 13, fig. 3, 3a) and in another specimen from the Gres d'Hettange (UCBL-EM 33408; Fig. 10D). The parietal and columellar lips are joined by an obtuse, rounded angulation. Both are covered by a moderately thick and rather expanded inductura. The inductura folds over the axial region of the columella, covering a narrow opening, presumably an umbilical chink. The columellar lip stops abruptly at the junction with the basal lip, which is thin and rounded, similar to a shallow and wide lower outlet. The spiral ornamentation described above in the specimen from Luxembourg is present in two specimens of the Terquem collection (UCBL-EM 33408 and 33409; Fig. 10D, E). However, the specimen figured by Terquem (1855) and another one from the Deshayes collection (UCBL-EM 33410; Fig. 10F) are completely smooth. Similar faint spiral cords have been occasionally observed also in *Tretospira subangulata* (d'Orbigny 1850) (see below).

Deshayes (1850) figured *A. obtusa* without providing description and locality information. However, he later implicitly but unequivocally stated that the species was found in the Grès d'Hettange (note in Terquem 1855, p. 231). This is also confirmed by the label of the specimen from the Deshayes collection cited above.

Terquem (1855) distinguished two morphs of the species: a low-spired morph with the angulation of the last whorl slightly less rounded than in Deshayes's form, and another morph with higher whorls and, consequently, a more prominent spire. The specimen figured by him would best match the first of these two morphs. The specimen from Luxembourg would best match the second morph.

Cossmann (1913) considered *Ampullaria planulata* Terquem 1855 (p. 247, pl. 13, fig. 4, pl. 14, fig. 3; Cossmann 1913, p. 174, pl. 10, figs 29, 30 as *Tretospira*) a possible synonym of *G. obtusa*. However, *A. planulata* is considerably smaller than *A. obtusa* and has an only slightly prominent spire. The outer lip is more expanded.

It is worth mentioning that Caze *et al.* (2011) found that some Cenozoic *Globularia* species show a residual colour pattern of zigzagging axial stripes. Instead, Terquem (1855) described a colour pattern of parallel, regularly spaced brownish axial stripes. This pattern is still visible in two specimens from the UCBL-EM collection.

Stratigraphic & geographic range. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France); Hettangian, Hesperange (Grand-Duchy of Luxembourg).

Globularia delsatei sp. nov.

Figure 11A–F

? 1966 *Ampullospira pisolina* (Terquem & Piette); Bourrouilh, p. 47, text-fig. 22.

v 1988 *Tretospira obtusa* (Deshayes); Meier & Meiers, p. 44, pl. 14, fig. 31.

LSID. https://zoobank.org/NomenclaturalActs/732d9d60-5c33-4087-9a36-2dc8d9969904

Derivation of name. Species dedicated to Dominique Delsate, scientific collaborator of the MNHNL and vertebrate specialist.

Holotype. MNHNL BR349 (Fig. 11A–F).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Holotype only.

Diagnosis. Shell medium-sized, smooth. Spire prominent, gradate with rounded shoulder. Teleoconch whorls strongly convex. Last whorl with flat and subhorizontal ramp edged by rounded shoulder. Base with narrow umbilical chink. Peristome discontinuous on parietal lip. Umbilical lip thin, sharp and gently arched, and continuous with parietal lip. Shallow but distinct lower outlet at junction of inner lip with basal lip.

Description. The shell is medium-sized (height 18.4 mm), globose and composed of five, strongly convex whorls. The spire is prominent, gradate with rounded shoulder, and slightly coeloconoidal. The surface of early teleoconch whorls is quite strongly and regularly convex. On the penultimate whorl the subsutural region becomes gradually flat, forming a subhorizontal ramp that widens during growth. The outer edge of the ramp is rounded. The last whorl is rather broad and expanded, with an evenly rounded periphery. The base is evenly convex, downward elongated and with a very narrow umbilical chink. The aperture is broad and subelliptical. The peristome is very slightly prosocline and discontinuous on the parietal lip. The inner lip appears as a sharp, gently arched lamina bordering the umbilical chink and smoothly joining the parietal lip. The basal lip forms a shallow but distinct lower outlet at the junction with the inner lip. The outer lip is strongly convex and simple.

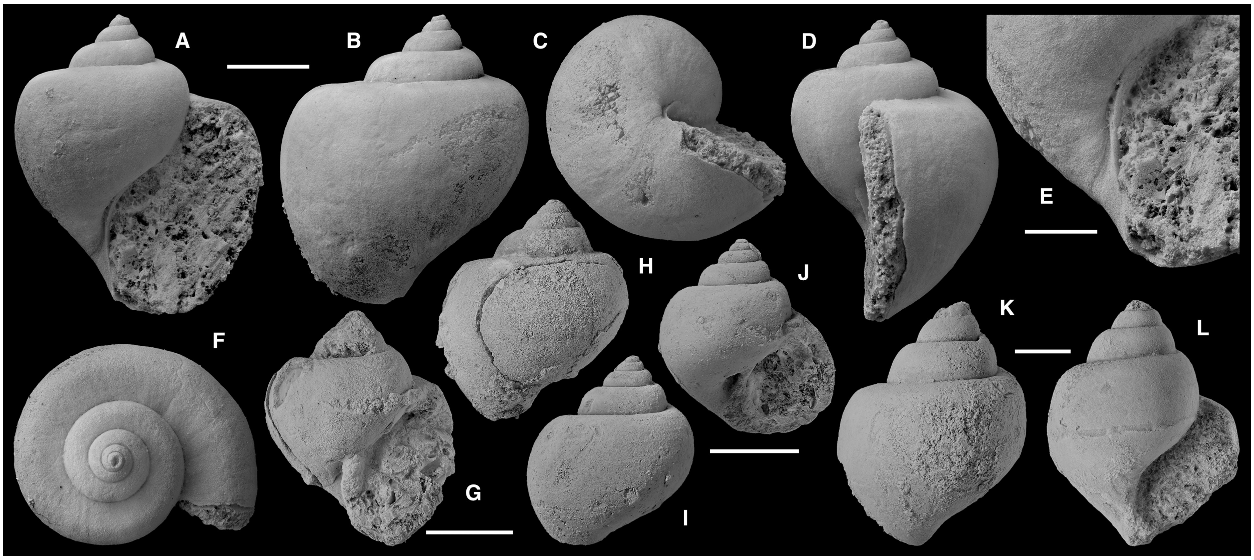

FIG. 11. Family Ampullinidae Cossmann *in* Cossmann & Peyrot 1919. A–F, *Globularia delsatei* sp. nov., holotype MNHNL BR349, apertural, dorsal, basal, lateral, oblique basal and apical views. G–J, *Natica pisolina* Terquem & Piette 1865: G–H, lectotype UCBL-EM 33411, apertural and dorsal views; I–J, paralectotype UCBL-EM 33412, dorsal and apertural views. K–L, *Ampullaria gracilis* Terquem 1855, holotype UCBL-EM 33413, dorsal and apertural views. A–F, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). G–J, Ardennes, France, Sinemurian. K–L, Hettange-Grande, France, upper Hettangian. Scale bars represent: 5 mm (A–D, F); 3 mm (E, G, H, K, L); 2 mm (I, J).

The shell is smooth. The growth lines are thin, almost orthocline and slightly prosocyrt on the ramp and slightly opisthocyrt on the whorl flank. They are opisthocyrt on the abaxial region of the base and prosocyrt on its adaxial part.

Remarks. The single available specimen is in a good state of preservation but lacks the protoconch. The shape of the shell of *Globularia delsatei* is very close to that of *Natica pisolina* Terquem & Piette 1865 (p. 31, pl. 1, figs 17–19) from the Sinemurian of the Ardennes. Two syntypes are present in the UCBL-EM collection and it appears that the original illustration of the taxon is a combination of both. The most complete specimen, UCBL-EM 33411 (Fig. 11G, H), is here selected as lectotype. The other specimen, UCBL-EM 33412 (Fig. 11I, J), is a juvenile. On direct examination of the type material of *N. pisolina*, its shell has a distinctly open umbilicus and its inner lip is slightly thickened. In contrast, *G. delsatei* has a very narrow umbilical chink bordered by a thin inner lip. Moreover, in *N. pisolina* the periphery of the last whorl is placed lower, the spire whorls are less convex and the shell is considerably smaller than that of *G. delsatei*. The shell described by Bourrouilh (1966) as *Ampullospira pisolina* (Terquem & Piette 1865), from the lower Sinemurian of the eastern High Atlas (Morocco) (Dresnay 1966), is very similar to *G. delsatei*. Even if it is slightly smaller it could belong to the same species. *Ampullaria gracilis* Terquem 1855 (p. 249, pl. 13, fig. 7; Terquem & Piette 1865, p. 32) from the Hettangian beds of Hettange-Grande is also similar in general shape to *G. delsatei*. The only specimen of *A. gracilis* that was available to Terquem (1855) when he erected the taxon is still preserved in the UCBL Terquem collection (UCBL-EM 33413, Fig. 11K, L), and is the holotype of the species by monotypy. The shell seems anomphalous but the axial region of its base is not well preserved. It differs from *G. delsatei* in having higher and less convex spire whorls, a less distinct ramp and less inflated last whorl.

Globularia obtusa (Deshayes 1850) is more than three times bigger than *G. delsatei*. The spire is less prominent and less coeloconoidal. *Globularia planulata* (Terquem 1855) from the Hettangian beds of Hettange-Grande is similar to *G. delsatei* in the shape of the last whorl but has a much lower spire.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); ?lower Sinemurian, eastern High Atlas (Morocco).

Genus *Oonia* Gemmellaro 1878

Type species. *Melania abbreviata* Terquem 1855, *non* Roemer 1836 (= *Pseudomelania hettangiensis* Cossmann 1909). Upper Hettangian, Hettange-Grande (Moselle, north-eastern France).

Oonia feidtorum sp. nov.

Figure 12A–I

v 1988 *Melania abbreviata* Terquem; Meier & Meiers, p. 40, pl. 12, fig. 26a, b.

LSID. https://zoobank.org/NomenclaturalActs/af668fa5-6263-4c85-8a44-7415ef1f36c8

Derivation of name. Species dedicated to the Feidt family, owners of the Brouch quarry, passionate about geology, who always allow free access to the quarry for scientific studies.

Type material. Holotype: MNHNL BR353 (Fig. 12A–E). Paratype: MNHNL BR687, Brouch (Mersch, Grand-Duchy of Luxembourg), upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Type material only.

Diagnosis. Shell medium-sized, smooth, coeloconoidal and narrowly phaneromphalous. Spire whorls moderately convex. Last whorl broad, inflated and nearly two-thirds of shell height. Parietal lip with strong inductura forming robust and wide callus on umbilical lip. Surface of callus arched, slightly concave and extended towards inner side of aperture. Basal lip slightly reflected outward limiting a wide and shallow lower outlet.

Description. The shell is medium-sized (maximum height 30 mm), broadly coeloconoidal, moderately high-spired and composed of about five whorls. The spire whorls are moderately convex and the suture is slightly impressed and weakly oblique. The convexity of the whorls increases slowly during growth and the subsutural part of the whorl becomes flatter. The last whorl is broad and inflated, and is nearly two-thirds of the height of the shell. Its subsutural part becomes slightly concave near the aperture. The periphery is evenly rounded. The base is broadly conical and narrowly phaneromphalous. The periumbilical rim is rounded but the umbilical wall is steep. The aperture is relatively wide, teardrop shaped and distinctly pointed at the sutural corner. A strong, non-adhering inductura reinforces the whole inner lip and extends towards the inner side of the aperture. It expands and covers part of the umbilicus, forming a slightly concave surface edged by a sharp outer rim on the umbilical lip. The basal lip is evenly convex and in continuity with the abapical part of the outer lip. It is very slightly reflected outward and forms a wide and shallow lower outlet.

The shell is smooth. The growth lines are weakly sinuous, and make low and weak growth folds on the last whorl. They are slightly prosocline–prosocyrt on the whorl surface, widely and gently opisthocyrt on the peripheral area and abaxial part of the base, and prosocyrt on the adaxial part of the base.

Remarks. The specimens lack the apical part. The surface of the shell seems slightly abraded and this makes the growth lines difficult to see. The shell shape of *Oonia feidtorum* is very similar to that of *Tylostoma sellae* Gemmellaro 1878 (p. 196, pl. 7, figs 28, 29, 53, 54; Fucini 1913, p. 16, pl. 1, figs 66, 67 as

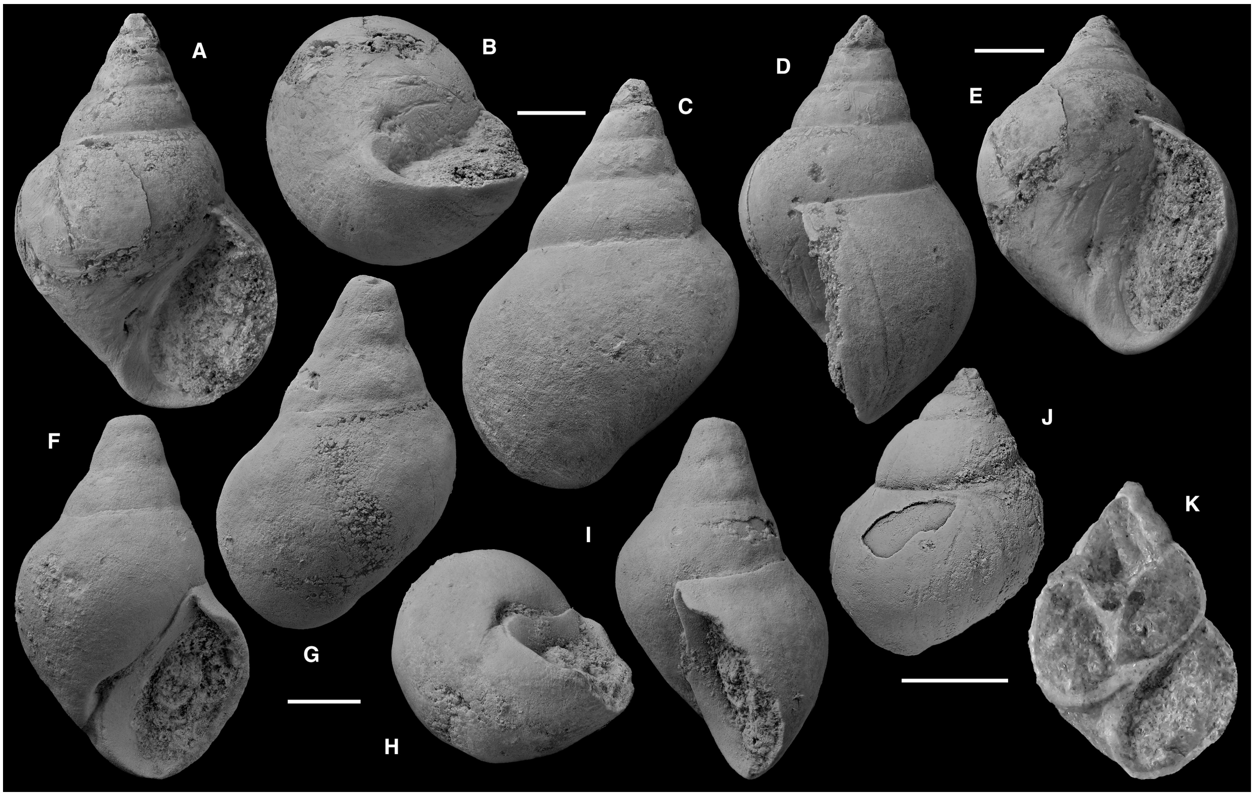

FIG. 12. *Oonia* Gemmellaro 1878. A–I, *Oonia feidtorum* sp. nov.: A–E, holotype MNHNL BR353 in apertural, basal, dorsal, lateral and oblique basal views; F–I, paratype MNHNL BR687 in apertural, dorsal, basal, and lateral views. J–K, *Oonia hettangiensis* Cossmann 1909, holotype UCBL-EM 31484 in dorsal and apertural views. A–I, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). J–K, Hettange-Grande, France, upper Hettangian. Scale bars represent 5 mm.

Omphaloptycha) from the Sinemurian of north-eastern Sicily. In *O. feidtorum* the spire is slightly less elevated, the spire whorls are higher, the last whorl is more inflated and the parietal inductura is thicker. The type species of the genus *Oonia*, namely *Oonia hettangiensis* Cossmann 1909 (= *Melania abbreviata* Terquem 1855, p. 255, pl. 14, fig. 12, 12a, b, *non* Roemer 1836; Cossmann 1909, p. 86) from the upper Hettangian beds of Hettange-Grande, is also similar to *O. feidtorum*. The holotype of *O. hettangensis* (UCBL-EM 31484; Fig. 12J, K) housed in the Terquem collection is a shell partially cut in axial section, as illustrated also by Terquem (1855). It differs from *O. feidtorum* in having a conoidal–cyrtoconoidal shell outline, whereas in the new species from Luxembourg the shell is broadly coeloconoidal. Moreover, in *O. hettangiensis* the spire whorls are higher and more convex and the spire is lower and less acute. *Phasianella nana* Terquem 1855 (p. 267, pl. 16, fig. 3, 3a, b) also shares a similar general shape with the new species. However, the specimen on which the taxon is based, which seems to be missing from the UCBL-EM collection, is considerably smaller than *O. feidtorum* (height 7 mm, *fide* Terquem 1855, p. 267), is anomphalous and has more inflated spire whorls.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Oonia haasi sp. nov.
Figure 13

v 1988 *Melania* sp.; Meier & Meiers, p. 41, pl. 12, fig. 26a, b.

LSID. https://zoobank.org/NomenclaturalActs/192e9345-43d6-43c2-93e1-90fe9327e257

Derivation of name. Species dedicated to Robert Haas, long-time collaborator of the MNHNL and discoverer of the first dinosaur remains in the Luxembourg Sandstone of Brouch.

Type material. Holotype: MNHNL BR982 (Fig. 13A–G). Paratypes: MNHNL BR354, BR639, BR849, Brouch (Mersch, Grand-Duchy of Luxembourg), upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

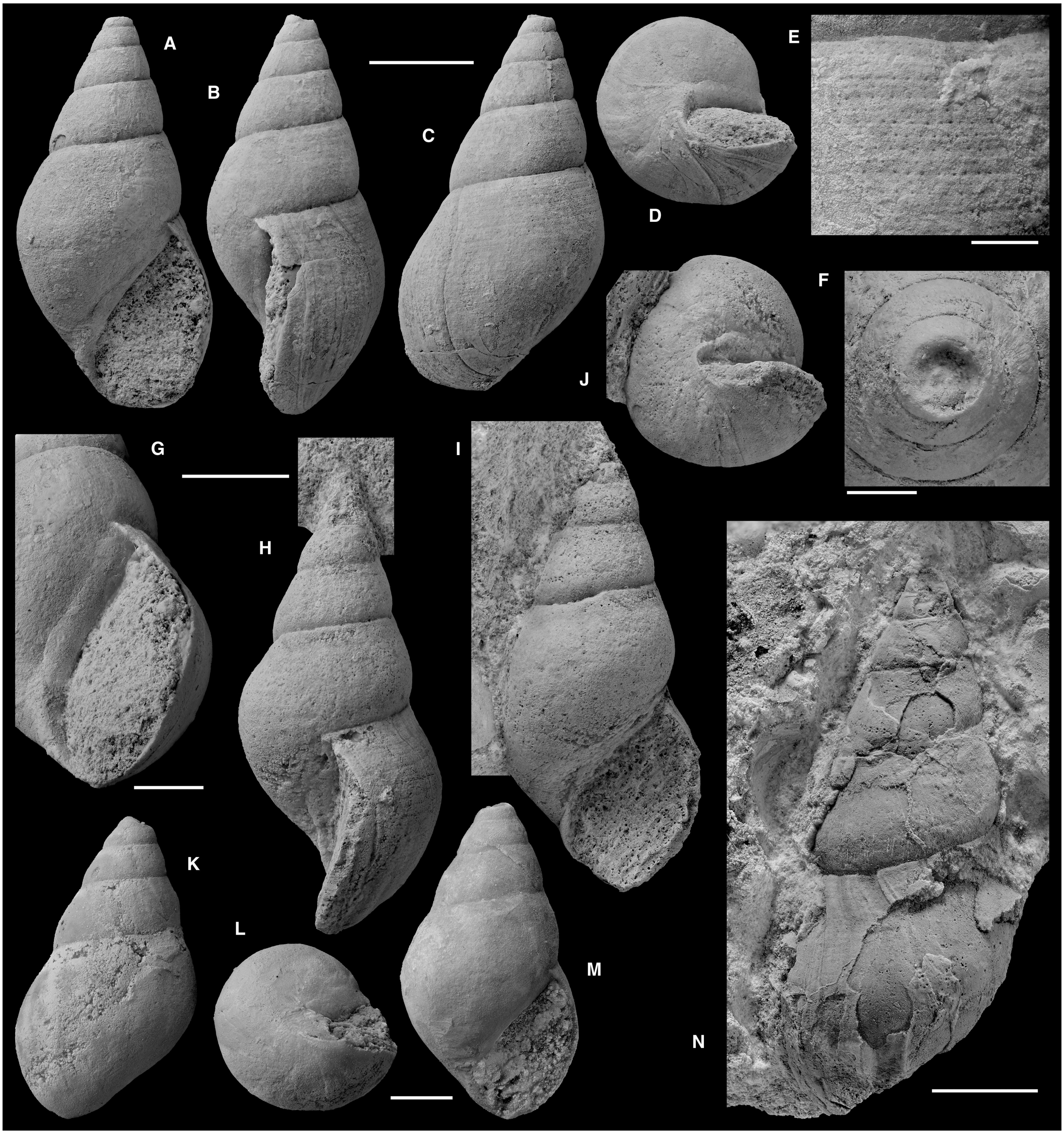

FIG. 13. *Oonia haasi* sp. nov. A–G, holotype MNHNL BR982 in apertural, lateral, dorsal and basal views, detail of the micro-ornament, detail of the apical part and oblique basal view; H–J, paratype MNHNL BR639 in lateral, apertural and basal views; K–M, paratype MNHNL BR354 in dorsal, basal and apertural views; N, paratype MNHNL BR849, dorsal view. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 10 mm (A–D, H–J, N); 2 mm (E, F); 5 mm (G, K–M).

Material. Type material only.

Diagnosis. Shell medium–large-sized, fusiform. Spire slightly cyrtoconoidal composed of moderately convex and pendent whorls. Last whorl high about two-thirds of shell height. Base conoidal and anomphalous. Thick inductura on parietal lip extended over whole inner lip. Sharp and evenly arched outer rim edging columellar lip and smoothly joining the basal lip. Wide and shallow outlet on basal lip. Ornament of thin, closely spaced and evenly distributed spiral lines punctuated by minute pits.

Description. The shell is medium–large-sized (maximum height *c.* 55 mm), fusiform and composed of at least six whorls. The spire is slightly cyrtoconoidal. The teleoconch whorls are moderately convex and separated by oblique, slightly impressed sutures. The convexity of the whorls increases slightly during growth and the surface of the whorl above the periphery becomes flat, then very slightly concave on the last whorl. The periphery is rounded and runs distinctly below mid-whorl, making the whorl pendent. The last whorl is high, about two-thirds of the height of the shell. The base is conoidal, moderately convex and downwards elongated. The aperture is teardrop shaped and distinctly pointed at the sutural corner. The parietal lip has a rather thick inductura that extends downwards on the columellar lip and covers the axial region of the base. The outer rim of the columellar lip is evenly arched and passes smoothly to the basal lip where it forms a wide and poorly defined lower outlet. The outer lip is simple and sharp.

The ornament consists of closely spaced, thin spiral striae, quite evenly distributed all over the shell and punctuated by very small pits. The growth lines are slightly prosocline and gently sinuous on the whorl surface, that is, prosocyrt adapically and opisthocyrt abapically, including on the peripheral region of the base. They are distinctly prosocyrt on the median part of the base and become opisthocyrt towards the axial region of the shell.

Remarks. The available specimens are generally well preserved, but all lack the apical part. The punctuated micro-ornament is not able to be seen in slightly abraded shells. The holotype MNHNL BR982 seems to have a septum closing the apical end of the spire (Fig. 13F). If this is the case, the lack of the apical part in all of the available specimens could be due to a decollated apex rather than to poor preservation.

Oonia globosa (d'Orbigny 1850) (p. 213; d'Orbigny 1851, p. 33, pl. 237, figs 8–11; Fischer & Weber 1997, p. 13, pl. 1, fig. 21; *non* Bourrouilh 1966, p. 45, fig. 19) from the Sinemurian (?) of French Jura (south-eastern France) is considerably smaller than *Oonia haasi* and differs in having a proportionally smaller last whorl and non-pendent whorls. Moreover, it lacks a punctuated micro-ornament. *Chemnitzia* (*Pseudomelania*) *marii* Gemmellaro 1878 (p. 148, pl. 6, figs 24–26) from the Sinemurian of north-eastern Sicily differs from *O. haasi* in being more slender and in having a narrow subsutural shoulder, which make the spire slightly gradate. It also lacks a punctuated micro-ornament. *Actaeonina pompilia* Gemmellaro 1878 (p. 121, pl. 7, figs 8, 9) from the same locality of the preceding species is close to *O. haasi* in the shape of the shell and in the ornament of punctuated spiral striae. It differs in being smaller, almost half of the size of *O. haasi*, and in having evenly convex, non-pendent spire whorls. In *O. haasi* the callus of the inner lip is rather thick, whereas, according to Gemmellaro (1878), in *A. pompilia* it is thin. *Phasianella liasina* Terquem 1855 (p. 267, pl. 16, fig. 4, 4a) shares with *O. haasi* the similar general form. The specimen from Hettange-Grande figured by Terquem (1855) is lacking from the UCBL-EM collection. Instead, there are two badly preserved specimens from the Sinemurian beds of the Ardennes, which are probably those cited by Terquem & Piette (1865, p. 54). *Phasianella liasina* differs from *O. haasi* in being much smaller (height 15 mm) and smooth, and in having non-pendent whorls and a thin callus. *Oonia feidtorum* differs from *O. haasi* in having a smaller shell with a broad last whorl. Moreover, the base is umbilicated and the shell is smooth. *Melania acuta* Moore 1867a (p. 546, pl. 14, figs 20, 21), from the lower Sinemurian of Brocastle (Glamorgan, Wales, UK), is very similar to *O. haasi* in the shape of whorls and apertural characters. However, it differs in having an ornamentation of smoothened spiral cords, of which the peripheral and subsutural ones are more prominent. *Coelostylina algarvensis* Böhm 1901 (p. 220, pl. 8, figs 11, 12; 1903, p. 11, pl. 1, figs 10–12; Fischer & Palain 1971, p. 118, pl. 1, figs 8, 9) from the Hettangian of the Algarve (southern Portugal) differs in having a slightly gradate spire. Moreover, the spiral striae are not punctuated. *Pseudomelania amurensis* Kiparisova 1952 (p. 27, pl. 7, figs 1, 3, 4, 9) from the Hettangian–Sinemurian of the Amur region (eastern Russia) has a proportionally higher spire and differs also in having a subsutural spiral groove and bulge.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Superfamily PSEUDOZYGOPLEUROIDEA Knight 1930
Family ZYGOPLEURIDAE Wenz 1938

Genus *Jurazyga* nov.

LSID. https://zoobank.org/NomenclaturalActs/e02a8841-ee71-492e-b8a7-7056a7d0bc1f

Derivation of name. From the geologic period 'Jurassic' and the suffix *-zyga*, referring to the stratigraphic distribution and zygopleurid affinity of the new genus.

Type species. Melania theodori Terquem 1855. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France).

Diagnosis. Shell medium–large-sized, slender. Whorls pendent in outline, flattish to slightly concave along subsutural region and separated by linear, moderately impressed and somewhat inclined suture. Base convex and conoidal. Aperture elliptical to teardrop shaped. Ornament of slightly sinuous collabral ribs, variably swollen on peripheral region, attenuating or vanishing before reaching adapical suture. Spiral ornament absent or weak.

Remarks. The new genus *Jurazyga* is introduced here for a group of morphologically homogeneous Early Jurassic gastropods that until now have been unsatisfactorily referred to *Zygopleura* Koken 1892 (discussion in Cossmann 1907b, 1909). Pieroni *et al.* (2021) already noted that these species differ from the type species of the genus, *Zygopleura hybridissima* Nützel 1998 (Carnian, Southern Alps, north-eastern Italy), and from the typical Triassic members of *Zygopleura* in the much larger size, the pendent outline of the whorls and in the ornament of strong, opisthocline collabral ribs that are swollen or subnodose at periphery and do not extend from suture to suture. Moreover, they have higher whorls edged by less impressed sutures (see Pieroni *et al.* 2021 for further details).

Ederazyga Pieroni *et al.* 2021 from the Upper Triassic of the Southern Alps and central Iran differs from *Jurazyga* in having a marked spiral ornament and sharp growth lines, making the shell surface rough. In shape, size and general ornament *Jurazyga* is also comparable to *Pseudokatosira* Nützel & Gründel, 2007. However, in *Pseudokatosira* the early teleoconch is ornamented by closely spaced axial riblets that attenuate or vanish after several whorls, and the strong axial ribs reappear only on the fully adult part of the shell. *Jurazyga* does not show this particular ontogenetic change of ornament pattern.

Included species & distribution. The genus occurs in the Hettangian and Pliensbachian beds of the western European shelf and in the Sinemurian carbonate platform deposits of the Mediterranean region. Besides the type species, the following species belong to *Jurazyga*:

Zygopleura subnodosa (d'Orbigny 1850), nom. nov. pro *Melania nodosa* Eudes-Deslongchamps 1842a (p. 219, pl. 12, fig.1) *non* Münster (1841) (d'Orbigny 1851, p. 37, pl. 237 bis, fig. 6; Fischer & Weber 1997, p. 15, pl. 1, fig. 8), Upper Pliensbachian, Calvados (northern France);

Zygopleura subnodosa (d'Orbigny) *sensu* Dareste de la Chavanne (1912, p. 571, pl. 16, fig. 2), upper Hettangian, Nièvre (central-eastern France);

Zygopleura vinosimonensis Fischer & Weber 1997 (p. 16; described as *Loxonema* (*Z.*) *subnodosa* in Cossmann 1902, p. 189, pl. 4, figs 2, 4; described as *Zygopleura subnodosa* in Cossmann 1913, p. 186, pl. 10, figs 4, 5), Hettangian, Vendée (western France);

Chemnitzia polyplecta Gemmellaro 1878 (p. 137, pl. 6, figs 7, 8; Fucini 1895, p. 316, pl. 12, fig. 5, 5a; Di Stefano 1887, p. 432, pl. 2, figs 11, 12), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy), Taormina (eastern Sicily, southern Italy) and Monte Pisano (Tuscany, central Italy);

Chemnitzia moorei Gemmellaro 1878 (p. 136, pl. 6, figs 4, 5), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy);

Chemnitzia appenninica Gemmellaro 1878 (p. 138, pl. 6, fig.10, pl. 9, figs 1, 2), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy);

Chemnitzia veturia Gemmellaro 1878 (p. 139, pl. 6, fig. 6; Fucini 1895, p. 319, pl. 12, fig. 12, 12a), Sinemurian, Rocca Busambra (north-western Sicily, southern Italy) and Monte Pisano (Tuscany, central Italy).

Jurazyga theodori (Terquem 1855) comb. nov.
Figure 14A–E

* v 1855 *Melania theodori* Terquem, p. 257, pl. 14, fig. 6, 6a.
1865 *Melania theodori* Terq.; Terquem & Piette, p. 38.
v 1988 *Zygopleura etalensis* (Piette); Meier & Meiers, p. 40, pl. 11, fig. 25a, b.

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR352.

Description. The shell is medium-sized (height *c.* 33 mm), slender, high-spired, with an almost conoidal outline and composed of 7–8 whorls. The height/width ratio of the whorls is *c.* 0.60. The height of the last whorl is almost half of the reconstructed height of the shell. The early teleoconch whorls are weakly convex and their periphery runs slightly below mid-whorl. During growth, the peripheral region becomes progressively more inflated and shifts downwards. The surface above the periphery becomes flat to weakly concave and the outline of the whorls becomes more distinctly pendent. The suture is rather oblique, very slightly impressed, almost linear or slightly wavy due to the collabral ornament. The base is somewhat convex on the whole, subconoidal, constricted in its lower part and anomphalous. The aperture is teardrop shaped, pointed at the sutural corner where the peristome is slightly thickened. The parietal lip has a thin inductura that extends over the whole columellar lip. The columellar lip is almost straight and passes through a wide arch into the parietal lip. The basal lip seems slightly reflected outward.

The ornament consists of opisthocline, weakly opisthocyrt, broad and round-topped collabral ribs. These are slightly swollen on the peripheral region and gradually fade before reaching the adapical suture. Their number per whorl increases slightly during growth: the juvenile whorls bear 9 ribs whereas the last whorl has 12 ribs. The rib interspaces are slightly wider than the ribs. On the base, the ribs extend slightly below the periphery, then fade rapidly. The remaining part of the base seems smooth. The growth lines are opisthocline and opisthocyrt above the periphery, and seemingly prosocyrt on the peripheral region. They are not visible on the base.

Remarks. The specimen is slightly abraded and lacks the apical spire and the lower part of the peristome. The internal mould shows that the basal lip is slightly reflected outward, which indicates possibly the presence of a short lower outlet. The holotype (by monotypy) of *Jurazyga theodori* (Terquem 1855) is a fragmentary and badly preserved specimen (UCBL-EM 31483; Fig. 14A, B), but it agrees well with the specimen from Luxembourg. Terquem (1855) described two obscure spiral cords on the whorls, but these are not detectable on the holotype examined. The basal spiral cord visible in the original illustration provided by Terquem is actually the remnant of a subsequent, non-preserved whorl.

Chemnitzia subnodosa d'Orbigny 1850 differs from *J. theodori* in being bigger (almost twice the size) and in having lower whorls and a less conoidal base. Moreover, the collabral ribs are sharper and more spaced. The specimen UCBL-FSL 27071 (Fig. 14F, G) from the upper Hettangian of Azy-le-Vif ascribed by Dareste de la Chavanne (1912, p. 571, pl. 16, fig. 3) to *Zygopleura subnodosa* is very similar to *J. theodori* in the shape of the shell and ornament pattern. It differs in having lower whorls, with the periphery slightly higher on the whorl. The collabral ribs are more prominent and more swollen on the peripheral region. *Zygopleura vinosimonensis* Fischer & Weber 1997 has a less acute spire angle, higher and more convex whorls, and more

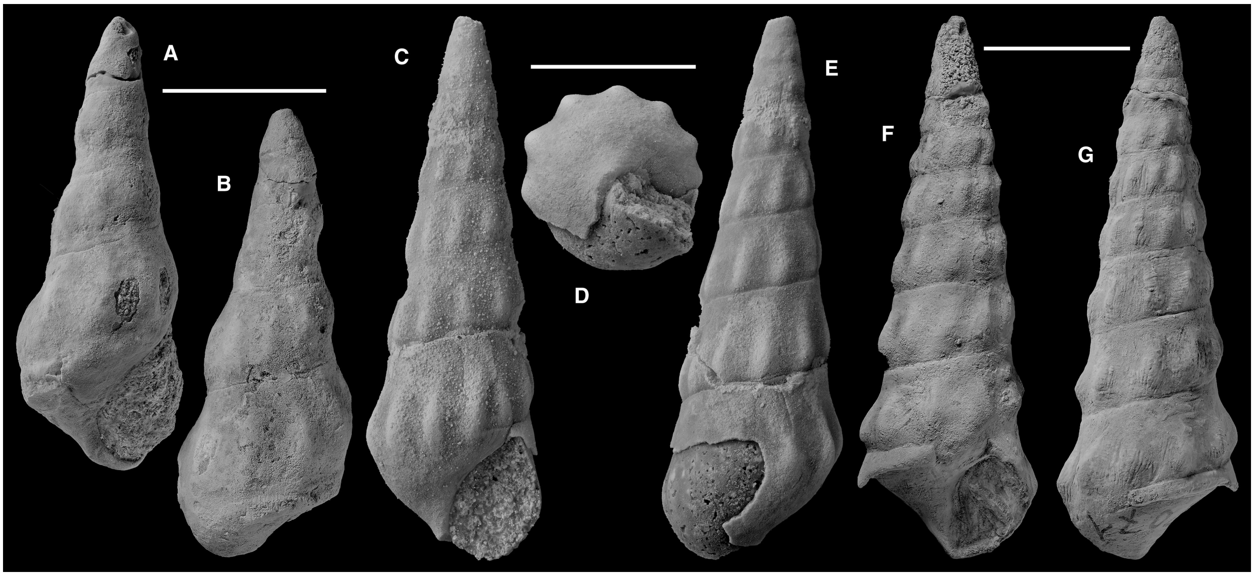

FIG. 14. *Jurazyga* gen. nov. A–E, *Jurazyga theodori* (Terquem 1855): A–B, holotype UCBL-EM 31483 in apertural and dorsal views; C–E, MNHNL BR352 in apertural, basal and dorsal views. F–G, *Zygopleura subnodosa* (d'Orbigny 1850) *sensu* Dareste de la Chavanne (1912), UCBL-FSL 27071 in apertural and dorsal views. A–B, Hettange-Grande, France, upper Hettangian. C–E, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). F–G, Azy-le-Vif, France, upper Hettangian. Scale bars represent 10 mm.

prominent collabral ribs. Its collabral ribs are stronger and swollen in the central part of the whorl, making the outline of the whorl less pendent.

Among the numerous early Jurassic *Zygopleura*-like species known from the carbonate platforms of the central part of western Tethys listed by Pieroni *et al.* (2021, tab. 1), *Chemnitzia polyplecta* Gemmellaro 1878, especially the specimen figured by Fucini (1895, p. 316, pl. 12, fig. 5, 5a, named as *Zygopleura*), is the most similar to *J. theodori*. However, it has lower whorls and fewer collabral ribs. Moreover, the shell is almost twice the size of *J. theodori*.

Stratigraphic & geographic range. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Family PROTORCULIDAE Bandel 1991

Genus *Anulifera* Zapfe 1962

Type species. Zygopleura (*Anulifera*) *variabilis* Zapfe 1962. Rhaetian, Northern Calcareous Alps (Austria).

Remarks. Zapfe (1962) described in great detail *Anulifera* Zapfe 1962 and its type species *Anulifera variabilis* (Zapfe 1962) (p. 60, text-figs 2–4, pl. 2, figs 1–9). Nützel *et al.* (2010, p. 222, figs 6.9–11) emended the diagnosis of the genus and added further information on the type species. The genus is characterized by relatively large, high-spired and spirally striated shells with a wide, steep, concave or flat supraperipheral part of the whorl and a bulging periphery placed slightly above the suture of the adult whorls. The periphery bears one or two rows of nodes that may be very slightly elongated in the opisthocline direction. The pattern of nodes and spiral threads seems to be present in the juveniles of the type species (Nützel *et al.* 2010, fig. 6.10), but not in those of other species, as for example *Stephanozyga binodosa* Fallahi *et al.* 1983 (p. 63, pl. 1, fig. 4), a species from the Norian–Rhaetian of Iran referred to *Anulifera* by Nützel & Senowbari-Daryan (1999, p. 118, pl. 5, figs 3–8) and Nützel *et al.* (2010, p. 222, fig. 6.1–6). Unfortunately, the protoconch of the genus is unknown and the details of the aperture are uncertain. Zapfe (1962) stated that in the type species there is no anterior canal and that the peristome is continuous, but in all of the specimens figured by him the base of the shell is incomplete and the sharp angulation of the lower part of whorl visible in cross-section (Zapfe 1962, fig. 2) could reflect at least a short spout. A shallow anterior canal was assumed also by Fallahi *et al.* (1983) for *A. binodosa*. In contrast, both *Anulifera chubutensis* Ferrari 2013 (p. 585, figs 3F–G; Ferrari 2017, p. 9, fig. 2.40), from the lower Pliensbachian – lower Toarcian of Chubut Province and from the Pliensbachian of Nequén Province (Argentina), and *Anulifera sigmoidea* Ferrari & Damborenea 2015 (p. 636, figs 2.23–2.31), from the middle Toarcian of Chile and lower Bajocian of Nequén Province (Argentina), have holostomatous apertures. A spiral keel below the peripheral row of nodes, exposed on the spire or just covered by the suture, is present in the type species, in *A. binodosa* and in *Moerkeia*? *burmensis* Healey 1908 (p. 81, pl. 9, figs 50–52), a species from the Raethian beds of Myanmar ascribed to *Anulifera* by Nützel & Senowbari-Daryan (1999) and Nützel *et al.* (2010).

In the general shape of teleoconch *Anulifera* has a strong similarity to *Pseudokatosira* Nützel & Gründel 2007. However, *Pseudokatosira* has a characteristic change of ornament pattern during ontogeny that is not present in *Anulifera*. Moreover, in *Pseudokatosira* the adult whorls bear quite strong collabral ribs that are swollen or subnodose at the periphery, whereas in the mature whorls of *Anulifera* the peripheral nodes are not associated with distinct ribs.

Anulifera verrucosa (Terquem 1855) comb. nov.

Figure 15A–R

? 1854 *Cerithium Dumonti* Chapuis & Dewalque, p. 106, pl. 14, fig. 4.
? 1854 *Cerithium conforme* Chapuis & Dewalque, p. 106, pl. 14, fig. 5.
v 1855 *Cerithium porulosum* Terquem, p. 276, pl. 17, fig. 10.
* v 1855 *Cerithium verrucosum* Terquem, p. 277, pl. 17, figs 9, 9a.
1864 *Cerithium verrucosum* (Terquem); Dumortier, p. 138, pl. 18, fig. 11; pl. 25, fig. 3.
1867a *Cerithium verrucosum* Terq.; Moore, p. 532, pl. 16, fig. 23.
? 1867a *Cerithium nodulosum* Moore, p. 543, pl. 14, fig. 9.
v 1912 *Zygopleura verrucosa* Terquem; Dareste de la Chavanne, p. 573, pl. 16, fig. 5.
v 1912 *Zygopleura morencyana* Terquem et Piette; Dareste de la Chavanne, p. 574, pl. 16, fig. 6.
1913 *Zygopleura verrucosa* (Terquem); Cossmann, p. 185, pl. 9, figs 76, 77; pl. 10, fig. 6; pl. 11, fig. 6.
v 1988 *Zygopleura porulosa* (Terquem); Meier & Meiers, p. 39, pl. 10, fig. 23a, b.
v 1988 *Zygopleura verrucosa* (Terquem); Meier & Meiers, p. 39, pl. 11, fig. 24a, b.
non 1997 *Katosira porulosa* (Terquem 1855); Hägele, p. 81, unnumb. text-fig. (= *Kosmopleura hoelderi* Gründel 2003).

Material. 26 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR118-1, BR174, BR251, BR289, BR351, BR402, BR421-1, BR422, BR425, BR426, BR452-1, BR516, BR572, BR584-1, BR643, BR644, BR646–649, BR763, BR858E, BR974, BR981, BR989, GL390D.

Description. The shell is medium–large-sized (maximum height *c.* 100 mm, probably up to 110–120 mm), high-spired, campaniliform, composed of at least 10 whorls. The height/width ratio of the teleoconch whorls is *c.* 0.50. The first preserved teleoconch whorls are rounded and seem to lack ribs or nodes. The subsequent whorls become first slightly convex to almost flat, then distinctly pendent, due to the development of a bulging periphery placed at the lower half of the whorl. The whorl surface above the periphery is wide, steep and slightly concave. The suture is oblique and poorly impressed. The base is anomphalous, conoidal, with a convex surface and constricted in its lower part to form a moderately long neck. On the juvenile shell, the base bears an obtuse angulation below the periphery just covered by the suture. This angulation tends to vanish during growth. The aperture is elliptical–ovate, sharply angulated at the sutural corner and in the lower part. The peristome is transversely rhomboidal, higher than wide and seemingly with a very short anterior canal. The columellar lip is thickened and passes through a continuous curve to the parietal lip. A moderately thick inductura covers both the columellar and parietal lips, forming a thickening at the sutural corner. The outer lip is simple, with a rounded but distinct angulation at the periphery and a weak angulation on its basal part.

The collabral ornament of the early teleoconch consists of low and thick, opisthocline ribs that are slightly inflated above the suture. On the subsequent whorls, the ribs become rapidly more swollen in the abapical half of the whorl and fade on the sutural ramp. They change into strong, collabrally elongate nodes that extend below the periphery but disappear just before reaching the suture. The nodes strengthen during growth, but their number per whorl remains constant in the range 14–16. The spiral ornament consists of 10–20 closely spaced, slightly flattened threads separated by thin furrows on the supraperipheral part of the whorl. The basal angulation is marked by a seemingly sharp spiral cord on the early shell. On the later whorls this spiral cord disappears or becomes very low. The surface of the base below the basal subangulation is ornamented with 6–7 spiral threads and furrows that are more marked and more spaced than those of the whorl flank. The growth lines are distinctly opisthocline and opisthocyrt above the periphery, strongly prosocline on the peripheral nodes and on most of the base, seemingly opisthocyrt on the axial region of the base.

Remarks. Most of the specimens are fragmentary, lacking the apex and part of the peristome. They are also often abraded and recrystallized, which makes the spiral ornaments and the growth lines difficult to detect. The material described here has a certain degree of variation in shape and ornament. The shape of shell is slightly coeloconoidal to slightly cyrtoconoidal and also the spire angle is slightly variable. The surface of the whorls above the periphery varies from fairly concave to almost flat. The peripheral nodes can be variably prominent and numerous, and also more or less elongate in the collabral direction. The number of spiral threads is also variable.

Cossmann (1913) included *Cerithium porulosum* Terquem 1855 in the synonymy list of *Cerithium verrucosum* Terquem 1855. The species variability described above and the examination of the type material of both *C. porulosum* (UCBL-EM 31499; Fig. 15C) and *C. verrucosum* (UCBL-EM 31506; Fig. 15A, B) support his opinion. Given that Cossmann (1913) was the first person to establish this relationship, *verrucosum* is the valid name for the species (ICZN 1999, art. 24.2). Cossmann (1913) noted also that *Cerithium dumonti* Chapuis & Dewalque 1854, from the Luxembourg Sandstone Formation of Belgian Lorraine, seems to be indistinguishable from *C. verrucosum*. *Cerithium conforme* Chapius & Dewalque 1854, from the same locality and stratigraphical interval, is another

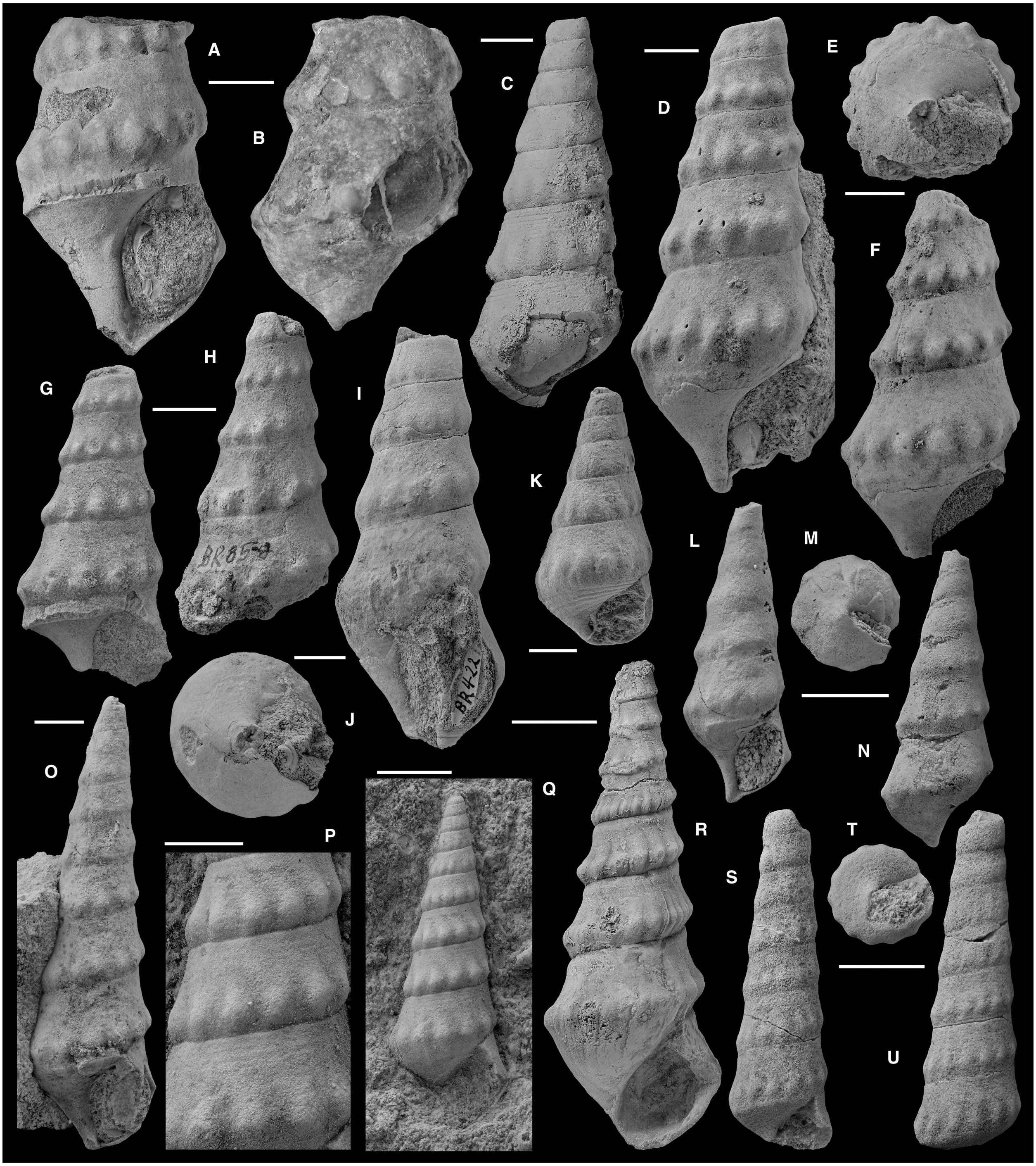

FIG. 15. *Anulifera* Zapfe 1962. A–R, *Anulifera verrucosa* (Terquem 1855): A–B, syntype UCBL-EM 31506 in apertural and dorsal views; C, UCBL-EM 31499 syntype of *C. porulosum* Terquem 1855 in dorsal view; D, MNHNL BR421-1 in apertural view; E–F, MNHNL BR425 in basal and apertural views; G–H, MNHNL BR858E in apertural and dorsal views; I–J, MNHNL BR422 in apertural and basal views; K, MNHNL BR648 in apertural view; L–N, MNHNL BR426 in apertural, basal and dorsal views; O, MNHNL BR351 in apertural view; P–Q, MNHNL BR452-1, detail of the ornament and apertural view; R, UCBL-FSL 27067 in apertural view. S–U, *Anulifera* sp., MNHNL BR645 in apertural, basal and dorsal views. A–C, Hettange-Grande, France, upper Hettangian. D–Q, S–U, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). R, Azy-le-Vif, France, upper Hettangian. Scale bars represent: 10 mm (A, B, D–J, L–N, Q–U); 5 mm (C, K, O, P).

species very close to *A. verrucosa*. However, on the basis of the original illustration, *C. dumonti* has more nodes per whorl and both it and *C. conforme* have been described by Chapuis & Dewalque (1854) as lacking spiral ornamentation.

A number of Hettangian–Sinemurian species show a close similarity to *A. verrucosa*. *Cerithium morencyacum* Terquem & Piette 1865 (p. 64, pl. 6, fig. 7), from the Sinemurian beds of the Ardennes, has higher whorls, a bulged subsutural region and a sharper and less prominent periphery bearing smaller and more numerous nodes. The specimens from the upper Hettangian of Azy-le-Vif ascribed by Dareste de la Chavanne (1912, p. 574, pl. 16, fig. 6, 6a–d) to that species (named as *Zygopleura morencyana* [*sic*]) are fairly similar to *A. verrucosa*. In these specimens the peripheral nodes are more closely spaced and more elongate in the collabral direction but this is considered here to be in the range of intraspecies variation of *verrucosa*. According to Dareste de la Chavanne (1912), in *Z. morencyana* the spiral sculpture is absent, but on direct examination of his material (specimens UCBL-FSL 27067-27070; Fig. 15R) the presence of thin and closely spaced spiral lines was noted. *Stephanocosmia* (*Goniospira*) *nodulosa* Dareste de la Chavanne 1912 (p. 575, pl. 16, fig. 7) has a more slender shell with higher whorls. The suture is more oblique and the peripheral keel is higher on the whorl surface. *Zygopleura carinifera* Dareste de la Chavanne 1912 (p. 572, pl. 16, fig. 4, 4a–c) differs from *A. verrucosa* in lacking spiral ornament and in the smooth peripheral keel. *Cerithium nodulosum* Moore 1867a (p. 543, pl. 14, fig. 9; *non* Bruguière 1792), from the upper Hettangian – lower Sinemurian of Somerset (south-western England), might be a junior synonym of *A. verrucosa*. The type specimen illustrated by Moore (1867a) shows a few differences from *A. verrucosa*: it has slightly less numerous and more spaced peripheral nodes, a weakly convex sutural ramp and it apparently lacks spiral ornamentation.

Anulifera verrucosa is close to *Pseudokatosira*? *seminodosa* (Nützel & Senowbari-Daryan 1999) (p. 113, pl. 4, figs 4, 5; Fallahi *et al.* 1983, p. 61, pl. 1, figs 2–3 named as *Stephanozyga jenningsi* (Douglas); Nützel *et al.* 2010, p. 218, figs 5.1–5.5) from the Rhaetian beds of Nayband Basin (Iran). Nützel *et al.* (2010) argued that *A. verrucosa* differs from *P.*? *seminodosa* only in the more marked spiral ornament and in the more adapical position of nodes. However, in the Triassic species the spiral ornament is represented by a multitude of extremely thin striae that cover the whorl surface, including the row of nodes (Nützel *et al.* 2010, figs 5.2 and 5.4), whereas in *A. verrucosa* there are 10–20 flattish threads separated by thin furrows only on the sutural ramp above the nodes. Moreover, *A. verrucosa* has proportionally higher whorls, and its base is ornamented by spiral threads, whereas in *P.*? *seminodosa* the base is smooth.

Stratigraphic & geographic range. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Rhône Basin (southern France) and Azy-le-Vif (Nièvre, central-eastern France); upper Hettangian – lower Sinemurian of Somerset (England).

Anulifera sp.
Figure 15S–U

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR645.

Remarks. The specimen, which lacks the apical whorls and the lower part of the base, is 39 mm high. Its surface is quite smoothened by abrasion. Given that the sutural angle of the parietal lip is strongly thickened, the specimen probably represents an adult shell. It differs from *Anulifera verrucosa* (Terquem 1855) in having a more turriculate and acute shell, and lower base. The periphery bears smaller and less prominent nodes. Although *A. verrucosa* is a rather variable species, none of the available specimens is clearly transitional. *Anulifera* sp. is reminiscent of *Cerithium morencyacum* Terquem & Piette 1865 (p. 64, pl. 6, fig. 7). It differs in the more acute shell, less concave whorls and less prominent nodes. *Anulifera chubutensis* Ferrari 2013 differs from *Anulifera* sp. in having slightly convex whorls with sharper and smaller nodes. These are in contact with the abapical suture, whereas in the specimen MNHNL BR645 from Luxembourg they are not.

Superfamily LITTORINOIDEA Children 1834
Family PURPUROIDEIDAE Guzhov 2004

Genus *Microschiza* Gemmellaro 1878

Type species. Turbo philenor d'Orbigny 1850 (= *Turbo semiornatus* Münster *in* Goldfuss 1844). Hettangian, Hettange-Grande (Moselle, north-eastern France).

Remarks. The genus *Microschiza* Gemmellaro 1878 has been assigned to the family Purpurinidae Zittel 1895 by Fischer & Weber (1997), Ferrari (2017) and Nützel *et al.* (2022). Here the genus is placed into the family Purpuroideidae Guzhov 2004, for which the type and only genus included so far is *Purpuroidea* Lycett 1848 (type species *Murex nodulosus* Young & Bird 1828). Some species ascribed to *Purpuroidea* (e.g. *Purpuroidea bicincta* (Piette 1856b), *Purpuroidea perstriata* Cossmann *in* Douvillé 1925 and *Purpuroidea subgracilis* Péron 1900) have a less gradate spire and less prominent nodes than the type species and seem to be transitional towards *Microschiza*. This would indicate a close relationship between this genus and *Purpuroidea*.

Microschiza semiornata (Münster *in* Goldfuss 1844)
Figure 16

* 1844 *Turbo semiornatus* Münster *in* Goldfuss, p. 94, pl. 193, fig. 8a, b.
1850 *Turbo Philenor* d'Orbigny, p. 214.
1852 *Turbo angulati* Quenstedt, p. 420, pl. 33, fig. 32.
1853 *Turbo Philenor* d'Orb.; d'Orbigny, p. 326, pl. 326, fig. 1.

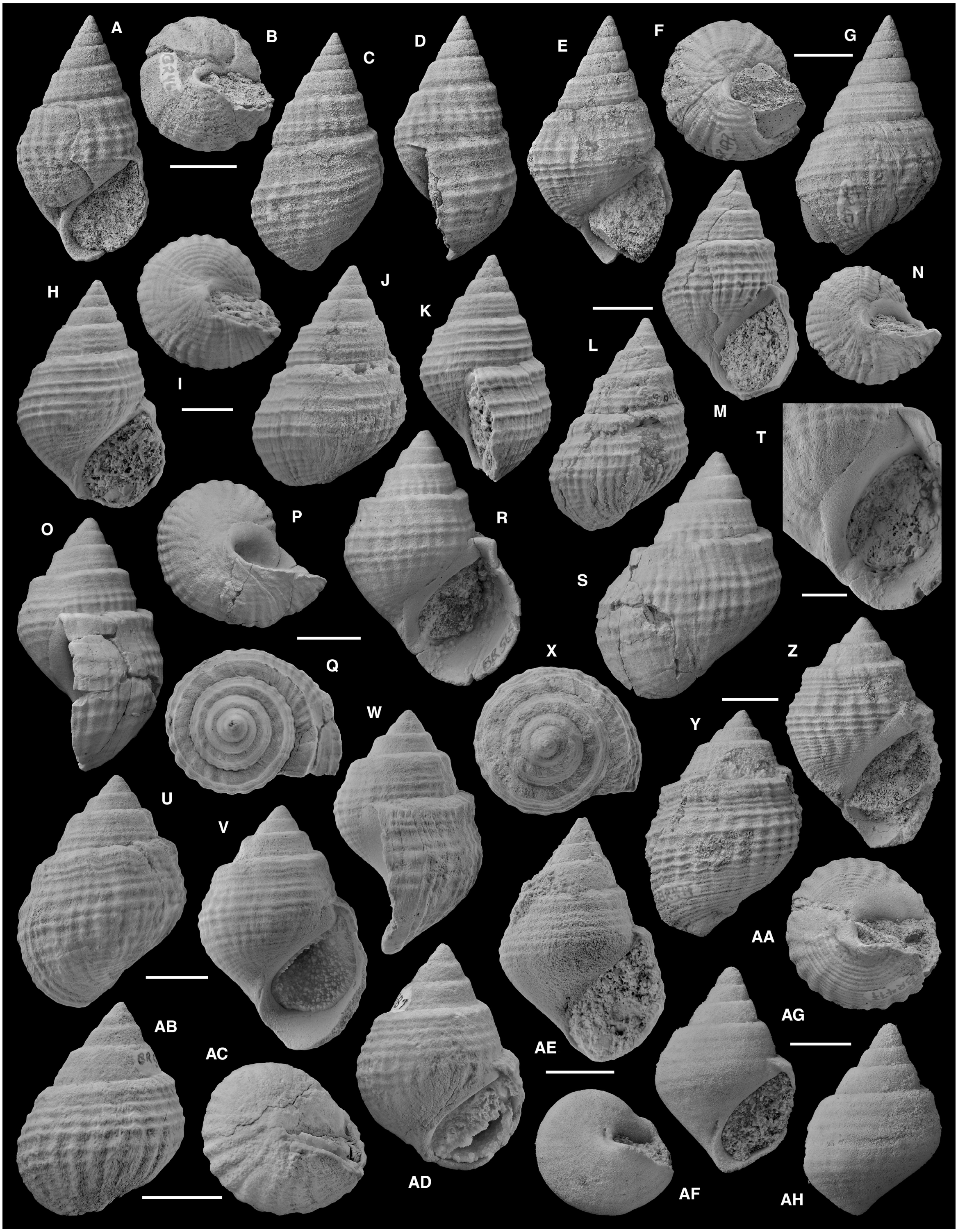

FIG. 16. *Microschiza semiornata* (Münster *in* Goldfuss 1844). A–D, MNHNL BR468 in apertural, basal, dorsal and lateral views. E–G, MNHNL BR477A in apertural, basal and dorsal views. H–K, MNHNL BR581C in apertural, basal, dorsal and lateral views. L–N, MNHNL BR581D in dorsal, apertural and basal views. O–T, MNHNL BR565A in lateral, basal, apical, apertural, dorsal views, detail of the aperture. U–X, MNHNL BR565E in dorsal, apertural, lateral and apical views. Y–AA, MNHNL BR477B in dorsal, apertural and basal views. AB–AD, MNHNL BR581A in dorsal, basal and apertural views. AE, MNHNL BR695A in apertural view. AF–AH, MNHNL BR858C in basal, apertural and dorsal views. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 10 mm (A–G, L–S, U–AD); 5 mm (H–K, T, AE); 3 mm (AF–AH).

1854 *Natica koninckana* Chapius & Dewalque, p. 81, pl. 11, fig. 7.
1854 *Chemnitzia aliena* Chapius & Dewalque, p. 78, pl. 11, fig. 4.
v 1855 *Littorina clathrata* Desh.; Terquem, p. 250, pl. 14, fig. 4, 4a, b (wrongly reported as fig. 2 in text and plates explanation).
1866 *Turbo angulati*; Quenstedt, p. 504, pl. 42, fig. 32.
1882 *Littorina clathrata* Desh.; Quenstedt, p. 272, 416, pl. 194, figs 57, 58; pl. 201, fig. 59.
1885 *Turbo angulati*; Quenstedt, p. 645, pl. 50, fig. 31.
1909 *Littorina semiornata* Münster sp.; Brösamlen, p. 252, pl. 19, figs 47, 48.
1909 *Pseudomelania* (*Microschiza*) *clathrata* (Desh.); Cossmann, p. 92, pl. 1, figs 20, 21.
v 1988 *Microschiza clathrata* (Deshayes); Meier & Meiers, p. 42, 47, text-fig. 7; pl. 13, fig. 28a, b.
1997 *Microschiza semiornata* (Muenster); Hägele, p. 79, unnumb. text-fig.
1997 *Microschiza philenor* (d'Orbigny); Fischer & Weber, p. 128, pl. 23, figs 22, 23.
2003 *Microschiza semiornata* (v. Münster); Gründel, p. 28, pl. 7, figs 2, 3.
2012 *Microschiza philenor* (d'Orbigny); Hanzo, p. 72, text-fig. 46A.
2012 *Microschiza philenor* (d'Orbigny); Dejax *et al*., p. 109, text-fig. 76A–C.
2012 *Microschiza semiornata* (Münster *in* Goldfuss); Guérin-Franiatte & Hanzo, p. 160, text-fig. 109H.
2012 *Microschiza philenor* (d'Orbigny); Guérin-Franiatte & Hanzo, p. 192, text-fig. 141E.

Material. 220 specimens. Brouch, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone): MNHNL BR866C, BR866D; Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR101, BR104, BR110, BR113, BR116, BR124, BR126, BR129, BR139-1, BR139-2, BR141-1, BR141-2, BR142, BR145, BR155, BR170, BR172, BR175, BR177-1, BR177-2, BR177-3, BR208–210, BR212–214, BR227, BR230, BR231, BR232-1, BR236–238, BR240, BR246, BR250-1, BR250-2, BR252, BR253, BR255, BR256, BR262, BR265, BR274-1, BR274-2, BR276-2, BR277-1, BR277-2, BR277-3, BR277-4, BR278, BR312, BR316, BR321-2, BR322–326, BR330-1, BR330-2, BR335-1, BR335-2, BR340–B, BR346, BR372A–B, BR421-2, BR434-2, BR449A–B, BR451, BR468, BR473-2, BR474–476, BR477A–F, BR478A–D, BR479-1, BR479-2, BR480A–C, BR482, BR483–485, BR492A, BR514, BR540, BR553, BR554, BR557–559, BR560-1, BR560-2, BR562-1, BR565A–E, BR576, BR579A–F, BR581A–G, BR582, BR584-2, BR614-2, BR674-2, BR681, BR683, BR684, BR689, BR695A, BR699, BR707, BR709, BR711, BR712, BR715, BR718, BR734, BR741, BR742, BR755, BR766, BR858A–C, BR887, BR888, BR892, BR897, BR909, BR910, BR914-2, BR918, BR944, BR951, BR961-1, BR968, BR976-2, BR984-1, BR988-2, BR990-1, BR990-2, HE124-1, HE124-2, HE134, HE145, HE148, HE155, HE157, HE158, HE170-1, HE171, GL312, GL313, GL389; Brouch, Hettangian, exact stratigraphical level unknown: MNHNL GL150; Hesperange, Hettangian, exact stratigraphical level unknown: GL139A–B; Bridel, Hettangian, exact stratigraphical level unknown: MNHNL GL148, GL212 (24 specimens); Itzig, Hettangian, exact stratigraphical level unknown: MNHNL GL119A–B; Altwies, Hettangian, exact stratigraphical level unknown: MNHNL GL149; Hettangian, locality and exact stratigraphical level unknown: MNHNL GL144A–C, GL199A–B.

Description. The shell is medium-sized (maximum height *c.* 50 mm), from moderately acute to rather globose, ovate in outline. The teleoconch is composed of about six whorls. The earliest teleoconch whorls are weakly convex with a narrow and rounded sutural shelf. During growth the sutural shelf becomes progressively wider and step-like, giving the spire a subgradate outline. The outer edge of the sutural shelf becomes sharp. On the adult part of the shell the flank of the whorl is flattened and slightly oblique. It is concave below the shoulder, making the sutural shelf slightly bulging. The suture is subhorizontal and runs at or slightly below the periphery of the preceding whorl. The last whorl is broad, with strongly rounded to slightly angular periphery. The base is subconoidal–globose and anomphalous. The aperture is wide, teardrop shaped, with a markedly acute, almost channelled sutural angle and a rounded, slightly downward elongate abapical part. The peristome is almost orthocline. The parietal lip is provided by an inductura that is thin on the juvenile shell and becomes rather thick on the fully adult shell. The parietal inductura thickens the sutural corner and passes smoothly into the columellar lip. It is slightly expanded on the base and covers its axial region. The outer rim of the inductura is sharp. The basal lip is slightly concave and gently reflected outward, forming a shallow and wide lower outlet.

The sculpture consists of a network of spiral cords and collabral ribs. The spiral elements are commonly thinner than the axial ornament. The sutural shelf lacks spiral ornament or bears 2–3, obscure to distinct spiral threads. The shoulder is marked by a sharp spiral cord, or a cord-like thread coupled with another spiral cord/thread below it. The concave spiral band of the whorl below the shoulder is smooth or ornamented by 1–2, occasionally three spiral elements that commonly are more spaced and thinner than the others. The abapical half of the whorl bears two strong spiral cords. The lower one is slightly more marked than the other and corresponds to the periphery. A third lowermost spiral cord is exposed on the spire or just covered by the suture. The collabral ornament consists of rounded, prominent and evenly distributed collabral ribs on the sutural shelf and whorl flank. These ribs are commonly less distinct on the concave band of the whorl flank. They make a coarse network with the spiral sculpture forming rounded nodes at the intersection points. The collabral ribs extend to the base where they are rather strong. The spiral ornament of the base consists of 10–20 variably strong and spaced threads/cords. They are commonly stronger and more widely spaced on the peripheral abaxial region of the base and become thinner and more closely spaced towards the axial region. The growth lines and collabral ribs are prosocline and almost straight on the sutural shelf, orthocline to very slightly prosocline and widely opisthocyrt on the whorl flank and on the peripheral region of the base, and prosocyrt on the remaining part of the base.

Remarks. *Microschiza semiornata* (Münster *in* Goldfuss 1844) is the most abundant gastropod species of the Luxembourg Sandstone Formation cropping out at Brouch. The species is highly variable in shell shape, whorl height and ornament strength. Commonly, specimens with a narrower spire angle have higher spire whorls and a proportionally lower last whorl. In these specimens the spiral cords are less marked and the axial sculpture is weaker. Consequently, the nodes are less prominent.

Fischer & Weber (1997) considered *Turbo philenor* d'Orbigny 1850 distinct from *M. semiornata*. In contrast, Gründel (2003) maintained that *M. semiornata* has a high intraspecies variability that encompasses, other than *T. philenor*, also *Turbo angulati* Quenstedt 1866 and *Littorina clathrata* Terquem 1855. The study of the very rich material described here confirms Gründel's (2003) opinion.

Stratigraphic & geographic range. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Vic-de-Chassenay (Côte d'Or, north-eastern France); upper Hettangian, Baden-Württemberg (south-western Germany); lower Sinemurian, Jamoigne (Belgian Luxembourg, Belgium); Hettangian, Hesperange, Bridel, Itzig, Altwies (Grand-Duchy of Luxembourg); Hettangian, Robiac (Gard, southern France).

Microschiza pauciornata sp. nov.
Figure 17A–N

LSID. https://zoobank.org/NomenclaturalActs/fc5e9004-5ce4-4b67-9a7a-393be6d4e53f

Derivation of name. From the Latin adjectives *paucus*, meaning 'poor/scant' and *ornatus*, meaning 'ornamented', referring to the weak spiral sculpture.

Type material. Holotype: MNHNL BR866B (Fig. 17G–J). Paratypes: MNHNL BR813, BR866A, Brouch, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone); MNHNL BR933A, BR933B, same locality, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone).

Material. Type material only.

Diagnosis. Shell medium-sized, conoidal, with broad last whorl and rounded angular periphery. Spire whorls flattish with narrow subsutural shelf. Aperture transversely oval. Last whorl about two-thirds of height. Inner lip with moderately thick inductura covering axial cavity. Ornament of faint, closely spaced spiral lines and threads.

Description. The shell is medium-sized (maximum height *c.* 19 mm), composed of 6–7 whorls and has a conoidal spire. The earliest teleoconch whorls are very slightly convex and limited by almost flush sutures. A narrow subsutural shelf appears gradually on the subsequent whorls, making the spire very slightly gradate. The outer edge of the subsutural shelf is angular to angularly rounded. The flank of the whorls below the shelf is slightly convex and oblique but tends to become flatter on the last whorl. The periphery is rounded angular, almost overlapped by the suture on the spire whorls and placed slightly below the middle on the last whorl. The last whorl is broad and becomes gently concave below the edge of the subsutural shelf. Its height is about two-thirds of the shell height. The base is low conoidal, with a moderately convex surface slightly constricted abapically. The aperture is transversely oval, higher than wide, acutely angulated at the sutural corner. The parietal lip passes smoothly into the columellar lip and the whole area of the inner lip is reinforced by a somewhat thick inductura. This inductura expands slightly on the axial region of the base to cover an axial cavity. The lower part of the basal lip is extended downward and slightly reflected outward to form a lower outlet. The outer lip is simple and pendent in outline.

The shell is ornamented by very faint, closely spaced spiral lines and, occasionally, some thin spiral threads. The growth lines are distinctly sinuous on the body whorl, orthocline to slightly prosocline and gently opisthocyrt on the whorl surface and on the abaxial part of the base, and prosocyrt on the adaxial part of the base. They can form subevenly distributed, very shallow folds on the last whorl.

Remarks. The specimens lack the protoconch, and the peristome is variably incomplete. The spiral ornament is very faint and hardly visible in those shells that are strongly affected by recrystallization. The above described *Microschiza semiornata* (Münster *in* Goldfuss 1844) is considerably bigger than *Microschiza pauciornata* and is also easily distinguishable by the more pronounced and wider subsutural shelf and by the clearly different ornamentation. The new species resembles *Littorina minuta* Terquem & Piette 1865 (p. 34, pl. 1, figs 23–25; Cossmann 1925, p. 16, pl. 4, fig. 19) from the upper Hettangian of Nièvre and Sinemurian of the Ardennes. *Littorina minuta* differs in having proportionally higher spire whorls, a more pronounced subsutural shelf and a more adapically placed peripheral angulation of last whorl. The holotype (UCBL-EM 31518; Fig. 17O, P) also has small, irregular nodes along the edge of the subsutural shelf on the final half of the last whorl.

Littorina arduennensis Piette 1856a (p. 204, pl. 10, fig. 19, 19a; Terquem & Piette 1865, p. 33, pl. 1, fig. 20), from the upper Hettangian – Sinemurian of north-eastern France and southern Belgium, is similar to *M. pauciornata*. The type material has not been found in the UCBL-EM collection, but on the basis of the original illustrations *L. arduennensis* is more slender than *M. pauciornata*. Moreover, the outer edge of the sutural shelf is sharper and the periphery is more distinctly angulated. *Phasianella morencyana* Piette 1856a (p. 204, pl. 10, fig. 12) is a coelostylinid from the upper Hettangian of the Ardennes bearing some resemblance to the new species. Four specimens are present in the UCBL-EM collection. None of them seems to correspond

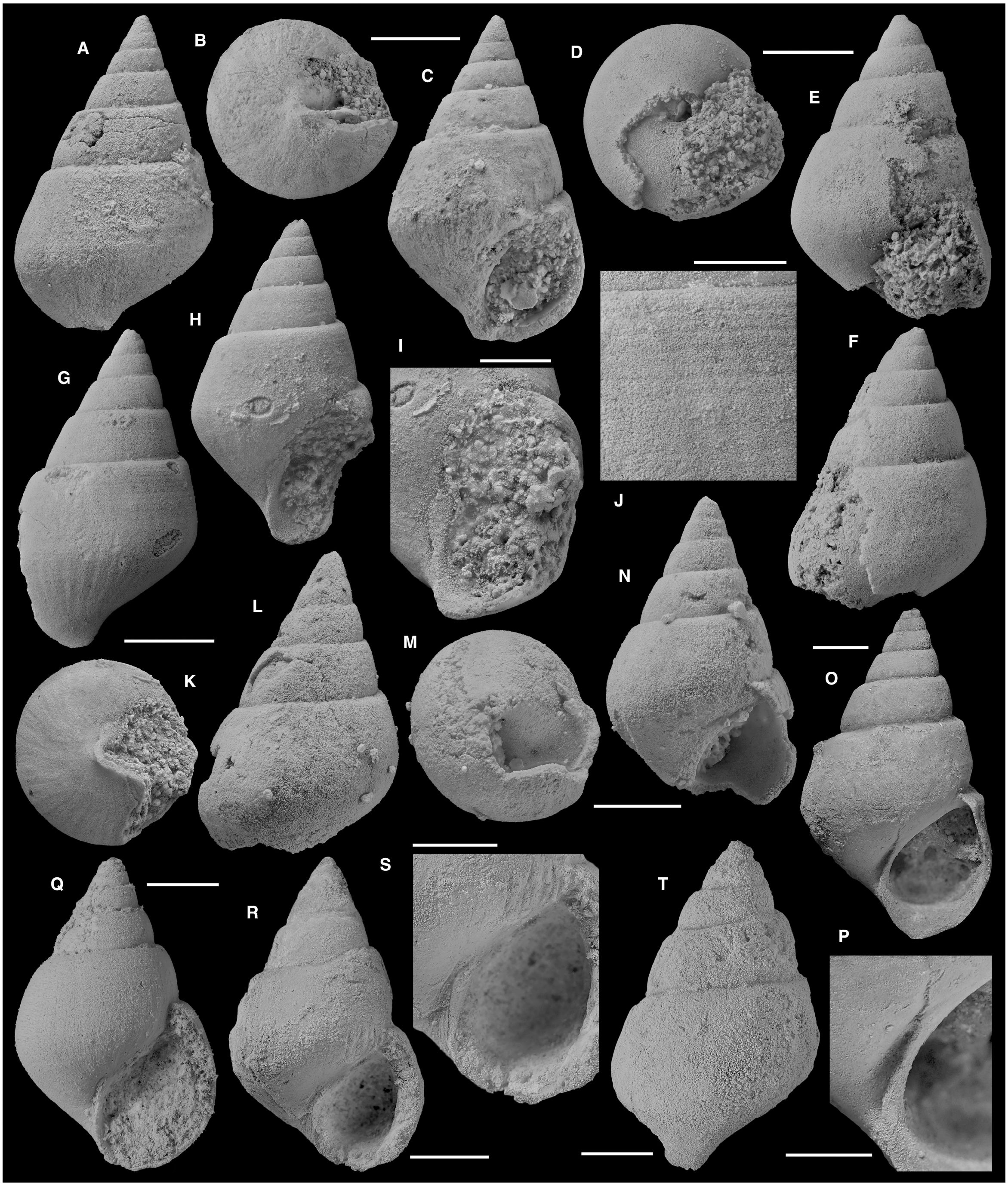

FIG. 17. *Microschiza pauciornata* sp. nov. and possibly related species. A–N, *Microschiza pauciornata* sp. nov.: A–C, paratype MNHNL BR933A in dorsal, basal and apertural views; D–F, paratype MNHNL BR866A in basal, apertural and dorsal views; G–K, holotype MNHNL BR866B in dorsal and apertural views, detail of the aperture, detail of the ornament and basal view; L–N, paratype MNHNL BR933B in dorsal, basal and apertural views. O–P, *Littorina minuta* Terquem & Piette 1865, holotype UCBL-EM 31518 in apertural view, detail of the aperture. Q, *Phasianella morencyana* Piette 1856a, topotype UCBL-EM 31531 in apertural view. R–T, *Coelostylina* (*Omphaloptycha*) *morencyana* (Piette 1856a) *sensu* Dareste de la Chavanne (1912): R–S, UCBL-FSL 27122 in apertural view, detail of the aperture; T, UCBL-FSL 27123 in dorsal view. A–C, L–N, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). D–K, Brouch, Grand-Duchy of Luxembourg, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone). O–P, Étales, Ardennes, France, Sinemurian. Q, Laval-Morency, Ardennes, France, upper Hettangian. R–T, Azy-le-Vif, France, upper Hettangian. Scale bars represent: 5 mm (A–H, K); 2 mm (J, P, Q, S); 3 mm (I, L–O, R, T).

exactly to the type figured by Piette (1856a). The topotype UCBL-EM31531 illustrated by Terquem & Piette (1865, p. 54, pl. 4, figs 9–11) is here refigured (Fig. 17Q). It differs from *M. pauciornata* in lacking a subsutural shelf and in having a convex and not angulated periphery, a straight columella, and a proportionally higher last whorl. The specimens ascribed to Piette's species by Dareste de la Chavanne (1912, p. 377, pl. 16, fig. 8, 8a, b, as *Coelostylina* (*Omphaloptycha*); UCBL-FSL 27122 and 27123, Fig. 17R–T) probably belong to a different taxon. They are similar to *M. pauciornata* in shell shape and apertural characters. However, they have a proportionally higher last whorl and their shell is smooth, as stated by Dareste de la Chavanne (1912).

Stratigraphic & geographic range. Lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone) and upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

?Superfamily STROMBOIDEA Rafinesque 1815

?Family APORRHAIDAE Gray 1850

Genus *Siphonilda* Nützel & Erwin 2004

Type species. Siphonilda pulchella Nützel & Erwin 2004. Upper Norian, Idaho (USA).

Remarks. The protoconch of the type species and only member of the genus *Siphonilda* Nützel & Erwin 2004 is unknown. The genus was placed originally in the family Mathildidae Dall 1889 on the basis of the teleoconch characters. According to Gründel *et al.* (2009), the shape of the shell, the anterior siphonal canal forming a rostrum and the whorls with a sharp middle angulation could indicate a close relationship with members of the stromboidean family Aporrhaidae Gray 1850. This systematic position is here tentatively followed given that mathildoidean shells do not usually have a well-developed rostrum like that of *Siphonilda*.

Siphonilda? *terquemi* (Moore 1867a) comb. nov.

Figure 18

1855 *Pterocera*? Terquem, p. 279, pl. 17, fig. 4.
1865 *Pterocera*?; Terquem & Piette, p. 61.
* 1867a *Fusus Terquemi* Moore, p. 544, pl. 14, fig. 8.

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR232-2.

Description. The shell is medium-sized (height of the preserved two last whorls 9.5 mm) and seemingly high-pagodiform. The last two whorls have a sharp median angulation that corresponds to the periphery. The ramp is oblique and slightly concave. The outer face is almost flat and inclined at an opposite angle to that of the ramp. The suture is inclined. The base is convex, anomphalous and downwards elongated and constricted to form a long neck. The part of the base corresponding to the outer face of the penultimate whorl ends abapically in a rounded and obtuse angulation. On the penultimate whorl the abapical suture runs on this angulation. The siphonal canal is almost half as long as the neck, and seemingly twisted.

The collabral sculpture consists of strong ribs (inferring 10 on the last whorl) separated by intervals that are twice as wide as the ribs. The collabral ribs fade out gradually on the adapical part of the ramp but reach the adapical suture. They vanish abapically just before reaching the basal angulation. The spiral ornament consists of keels and threads overlying the collabral ribs. The peripheral angulation is marked by a sharp spiral keel that forms distinct and pointed nodes at the intersection with the collabral ribs. Another strong spiral keel is present on the lower part of the outer face. It gives rise to low nodes on the collabral ribs. Sharp, evenly distributed spiral threads run on the whorl surface, four on the outer face and 5–6 on the ramp. They make the collabral ribs slightly granulated. On the base, another spiral keel runs close to the basal subangulation and is covered by the suture on the penultimate whorl. The remaining part of the base and the neck are sculptured by numerous and sharp spiral threads that are progressively thinner and more closely spaced towards the termination of the siphonal canal. The growth lines are opisthocline, slightly opisthocyrt on the whorl surface and sinuous on the base, that is, slightly prosocyrt on the abaxial region and slightly opisthocyrt on the neck.

Remarks. All known specimens of *S.*? *terquemi* are incomplete and this hampers confident supraspecific attribution of the taxon. The single available specimen from Luxembourg is partly embedded in matrix and preserves the last two whorls. The specimen described by Terquem (1855) as *Pterocera*? sp. has not been found in the UCBL-EM collection. The species is here ascribed tentatively to the genus *Siphonilda* Nützel & Erwin 2004 on the basis of the close similarity to the type species of this genus, namely *Siphonilda pulchella* Nützel & Erwin 2004 (p. 402, fig. 14A–K; Gründel *et al.* 2009, fig. 6b) from the Norian beds of Idaho (USA). *Siphonilda*? *terquemi* differs from *S. pulchella* in being less slender and in having a less concave ramp and fewer collabral ribs per whorl. The ribs run from suture to suture, whereas in *S. pulchella* they fade out above and below the peripheral keel. *Aporrhais* (*Cuphosolenus*)? sp. from the Upper Triassic of Peru (Haas 1953, p. 255, pl. 16, figs 51, 55) shows some similarity in general shape to *S.*? *terquemi*. However, it is larger, the collabral ribs shorter and the ramp wider.

Fusus jenynsii Moore 1867a (p. 545, pl. 14, figs 6, 7) from the upper Hettangian and lower Sinemurian of Brocastle (Wales, UK) has a general shape and siphonal canal similar to those of *S.*? *terquemi*, but the peripheral keel is placed lower on the whorls, near to the abapical suture. Moreover, the ornament is finely reticulate, without prominent collabral ribs.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Hettange-Grande (Moselle, north-eastern France); Lower Sinemurian

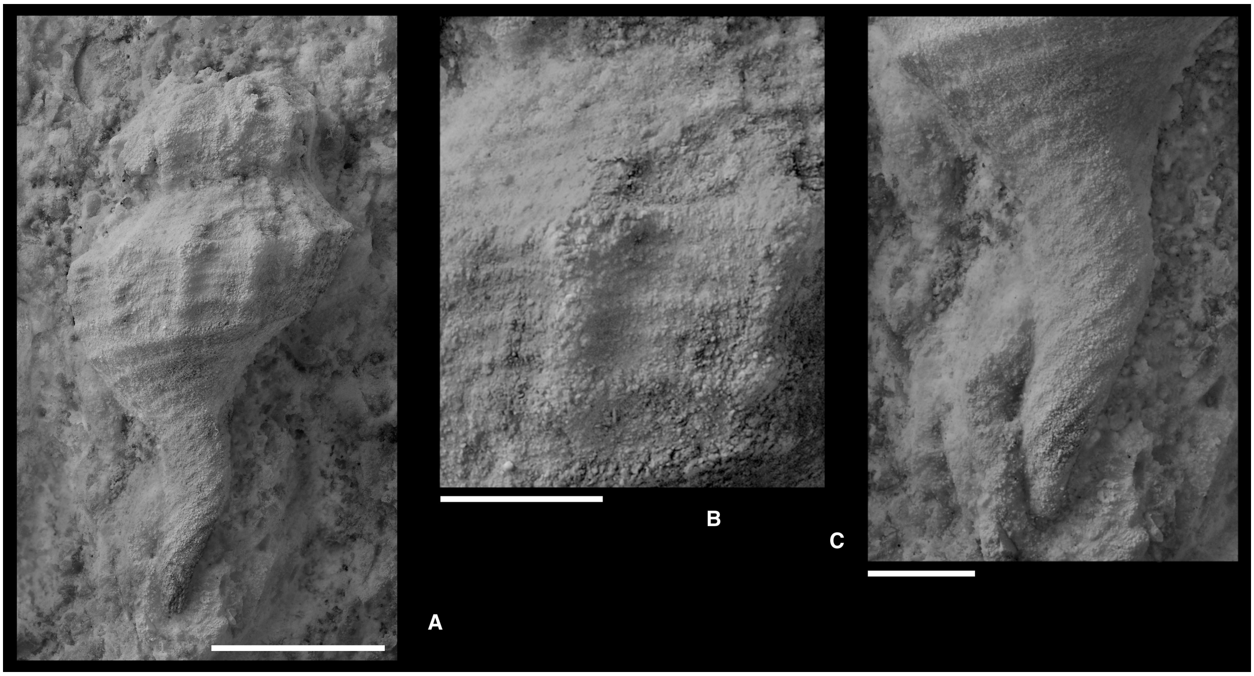

FIG. 18. *Siphonilda*? *terquemi* (Moore 1867a). A–C, MNHNL BR232-2 in subapertural view, detail of the ornament and of the basal rostrum. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 3 mm (A); 1 mm (B, C).

(*Coroniceras* (*Arietites*) *bucklandi* Zone), Brocastle (Glamorgan, Wales, UK).

Order NEOGASTROPODA Wenz 1938
Superfamily uncertain
Family PURPURINIDAE Zittel 1895

Genus *Angularia* Koken 1892

Type species. *Turbo subpleurotomarius* Münster 1841. Lower Carnian, Southern Alps (north-eastern Italy).

Remarks. The distinctive characters of *Angularia* Koken 1892 have been recently redescribed and discussed in detail by Nützel *et al.* (2022) and Bakayeva *et al.* (2024). Bakayeva *et al.* (2024) emended the diagnosis of the genus and described the protoconch characters of *A. pleurotomaria* (Münster 1841), which, as already noted by Bandel (1993), would demonstrate the neogastropod affinity of *Angularia*.

Two citations of Hettangian species were mentioned by Nützel *et al.* (2022). The first citation refers to *Angularia subangulata* (d'Orbigny 1850) in Gründel (2010, p. 9, pl. 2, figs 17, 18, pl. 3, figs 1, 2). This species is here assigned to *Tretospira* Koken 1892 (see below). The second citation refers to *Pleurotomaria obliqua* (Terquem) in Meier & Meiers (1988, p. 31, pl. 6, fig. 13a, b), which is ascribed here to *Angulariopsis* gen. nov. (see below).

Angularia? sp.
Figure 19A–D

Material. 2 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR481, BR885B.

Description. The shell is medium-sized (maximum height *c.* 19 mm), high-spired and gradate. The first preserved whorl seems very weakly angulated whereas the subsequent whorls are distinctly angulated. The periphery corresponds to the angulation and runs at nearly mid-whorl on the early preserved whorls and above the mid-whorl on the penultimate whorl. The ramp is slightly concave to almost flat and strongly inclined. The outer face is almost flat to very slightly convex, sub-vertical on early spire and slightly inclined at the opposite angle to that of the ramp on the later whorls. The base is subconical, rather convex and anomphalous, at least on the juvenile shell. It bears an obtuse and rounded angulation that is slightly exposed on the spire or just covered by the suture. The aperture is seemingly rounded subpentagonal. The peristome of the juvenile shell has a thin parietal inductura that becomes thick on the axial region of the base, and a relatively robust, arched columellar lip.

The ornament is not discernible apart from traces of a spiral keel marking the peripheral angulation. The growth lines are opisthocline and widely opisthocyrt on the spire whorls, and prosocyrt on the base.

Remarks. The material consists of a juvenile shell and an adult shell lacking the apical spire. The shell wall is strongly abraded in both. The general shape of the shell, the few available characters of the aperture and the orientation of the growth lines mean that these specimens are similar to species of the genus *Angularia* Koken 1892. The poor preservation does not permit a species-level assignment.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Genus *Angulariopsis* nov.

LSID. https://zoobank.org/NomenclaturalActs/396f95c8-58dd-46b5-a2dc-e7fa60b8ea41

Derivation of name. From the gastropod genus *Angularia* and the suffix *-òpsis* (Greek: ὄψις), meaning similar to *Angularia*.

Type species. Angularia nivernensis Dareste de la Chavanne 1912. Upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France).

Diagnosis. Biconoidal shell with conoidal subpagodiform spire. Base anomphalous but with axial chink. Whorls angulated at periphery, distinctly below mid-whorl. Ramp wide and rather sloping. Parietal inductura thick in fully adult shell, passing smoothly into columellar lip, with no demarcation between the columellar lip and parietal lip. Shallow and wide outlet on basal lip. Sutural corner of peristome possibly with narrow posterior canal. Ornament consists of a peripheral keel, which bears variably distinct nodes on the last whorl.

Remarks. The type species *Angulariopsis nivernensis* (Dareste de la Chavanne 1912) was originally ascribed to the genus *Angularia* Koken 1892. However, the species included in this genus are much smaller and are distinctly pagodiform gradate with a submedian angulation of the whorls. The base of *Angularia* is swollen and lower than in the new genus, and not conoidal. Moreover, the shell bears sharp and irregular growth lines, making the shell surface rough and forming collabral lamellae or true ribs (e.g. Münster 1841; Klipstein 1843; Laube 1868; Kittl 1891; Bandel 1993, 1994; Bakayeva *et al.* 2024).

Angularia corallina Nützel *et al.* 2022 (p. 294, fig. 20a, b) is here transferred to *Angulariopsis*. Nützel *et al.* (2022) rightly compared their species with the specimen ascribed by Meier & Meiers (1988) to *Pleurotomaria obliqua* Terquem 1855, that is here reassigned to the type species of *Angulariopsis* (see below).

Included species & distribution. The genus is represented by the type species from the upper Hettangian of Nièvre (central-eastern France) and Grand-Duchy of Luxembourg, and *A. corallina* from the Rhaetian (Sevatian) beds of Gaissau (Northern Calcareous Alps, Austria).

Angulariopsis nivernensis (Dareste de la Chavanne 1912) comb. nov.
Figure 19E–K

* v 1912 *Angularia nivernensis* Dareste de la Chavanne, p. 568, pl. 16, fig. 1, 1a.
v 1988 *Pleurotomaria obliqua* Terquem; Meier & Meiers, p. 31, pl. 6, fig. 13a, b.

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR356.

Description. The shell is medium-sized (height *c.* 20 mm), moderately acute, biconical and preserves the last four whorls. The early preserved whorl is moderately convex. The subsequent whorls are distinctly angulated at their lower third. The angulation corresponds to the periphery and becomes slightly sharper during growth. The ramp is wide, strongly inclined and gently concave, apart from a poorly developed subsutural bulge. The outer face is narrow, flat to slightly concave, weakly inclined at the opposite angle to that of the ramp. The base is conoidal, rather convex and anomphalous, with a very weak angulation that, on the preceding whorls, is covered by the suture. The aperture is rather wide, transversally teardrop shaped, distinctly pointed at the sutural corner and with a rounded basal part. The peristome is almost orthocline, obtusely angulated at whorl periphery. The outer lip is sharp and slightly constricted below the sutural corner, presumably to form a narrow posterior furrow. The parietal lip is covered by a moderately thick inductura that extends over the lower part of the inner lip and the axial region of the base. The basal lip is evenly rounded and passes into the inner lip through a shallow and wide concavity reflecting the presence of a lower outlet.

The ornament consists of a prominent and moderately swollen peripheral cord that bears very weak nodes on the last whorl. The growth lines are orthocline and weakly sinuous, that is, prosocyrt on the ramp and base, and slightly opisthocyrt on the peripheral region.

Remarks. The specimen lacks the apical part and the shell surface is strongly abraded. However, it is clearly similar to the holotype of *Angularia nivernensis* Dareste de la Chavanne 1912 (UCBL-FSL 27253) (Fig. 19E–G). Judging from the dimensions and the incompletely developed characters of the peristome, the specimen here described represents a subadult shell. In particular, the parietal inductura is moderately thick and adhering to the base, whereas in the holotype, which is a fully grown shell, the inductura is thicker and partially detached from the base. As observed by Dareste de la Chavanne (1912), the holotype bears low and subregularly distributed collabral undulations of the whorl surface, producing nodes on the peripheral keel. Irregular undulations on the peripheral angulation are present also on the last whorl of the specimen from Luxembourg. These are weaker than in the holotype, probably due to the younger growth stage and to the poor state of preservation of the shell.

Angularia corallina Nützel *et al.* 2022 differs from *A. nivernensis* in having a less acute and gradate spire due to a

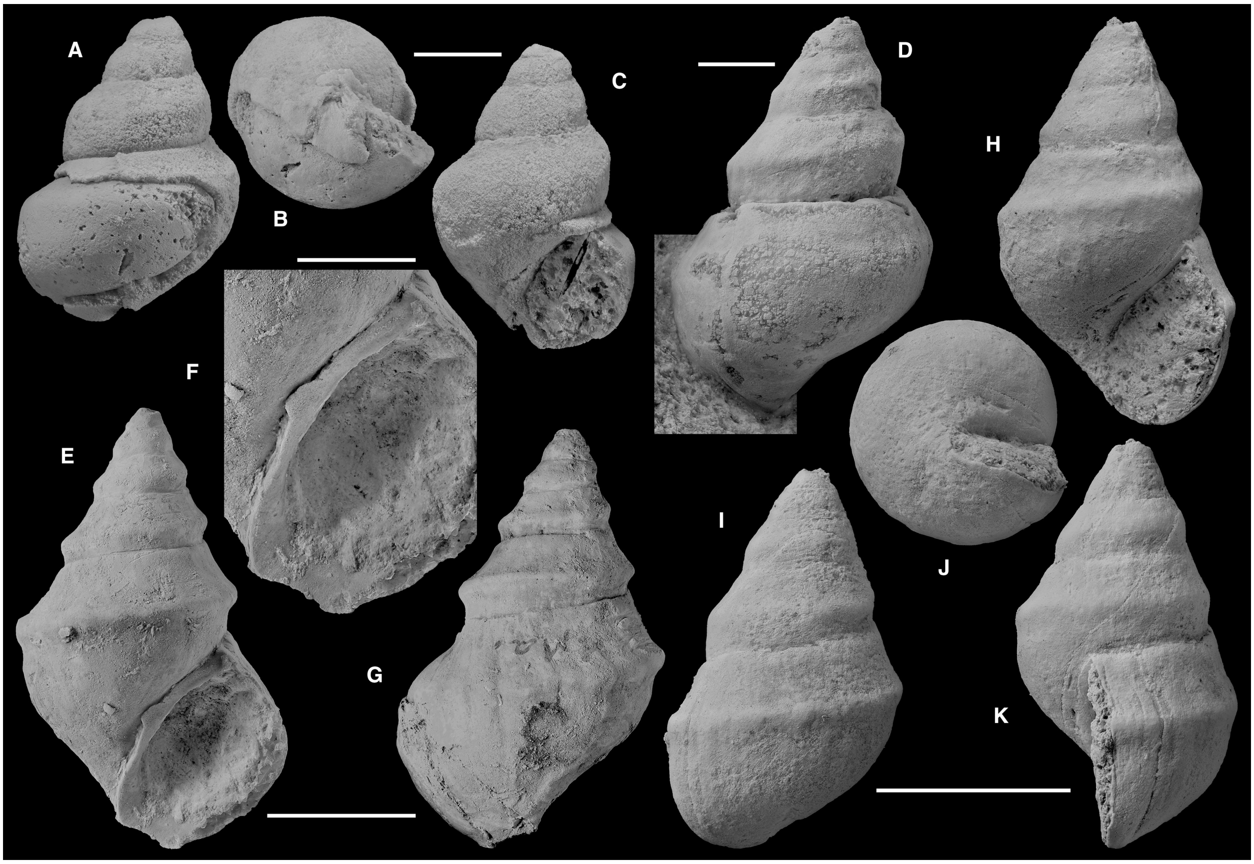

FIG. 19. Family Purpurinidae Zittel 1895. A–D, *Angularia*? sp.: A–C, MNHNL BR885B in dorsal, basal and apertural views; D, MNHNL BR481 in dorsal view. E–K, *Angulariopsis nivernensis* (Dareste de la Chavanne 1912): E–G, holotype UCBL-FSL 27253 in apertural view, detail of the aperture and dorsal view; H–K, MNHNL BR356 in apertural, dorsal, basal and lateral views. A–D, H–K, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). E–G, Azy-le-Vif, France, upper Hettangian. Scale bars represent: 3 mm (A–C); 5 mm (D, F); 10 mm (E, G–K).

less prominent peripheral keel. Moreover, the peripheral nodes are present on the whole shell whereas in *A. nivernensis* they appear only on the last whorl. The characters of the aperture of *A. corallina* are unknown.

Stratigraphic & geographic range. Upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France); upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Genus *Tretospira* Koken 1892

Type species. Melania multistriata Wöhrmann 1889. Carnian, Zirl (Tyrol, Austria).

Remarks. The species described below are here assigned to *Tretospira* Koken 1892 following Cossmann (1909, 1913). As stated by Cossmann (1909, 1913), the Hettangian species differ from the Triassic type species in the larger size and in the absence of a sharp spiral ornament but these differences are not sufficient to place them into a distinct genus. Moreover, as mentioned below, a very weak spiral ornament is occasionally present in one of these species.

The scarcity of distinctive characters of the adult shell, and the lack of information on the protoconch make it difficult to establish the higher taxonomic position of *Tretospira*. According to Zittel (1895), Cossmann (1909), Wenz (1938) and Guzhov (2004), the genus belongs to the family Purpurinidae Zittel 1895, whereas Nützel & Erwin (2004) and Bakayeva *et al.* (2024) assigned it to the family Littorinidae Children 1834. Here we prefer to provisionally retain *Tretospira* in the Purpurinidae on the basis of the sharp median angulation of the whorl making the spire distinctly gradate. However, a general similarity of *Tretospira* to the littorinoidean genera *Purpuroidea* Lycett 1848 (family Purpuroideidae Guzhov 2004) and *Leviathania* Pčelincev 1927 (family Leviathaniidae Harzhauser & Schneider 2014) suggests that the systematic position of this genus is still open to revision.

Tretospira subangulata (d'Orbigny 1850)

Figure 20A–Z

1844 *Ampullaria angulata* Dunker, p. 188.
1847 *Ampullaria angulata* Dkr.; Dunker, p. 110, pl. 13, fig. 4a–c.
* 1850 *Natica subangulata* d'Orbigny, p. 214.
1850 *Ampullaria angulata* Deshayes, p. 45, pl. 72, fig. 23.
v 1855 *Ampullaria carinata* Tqm.; Terquem, p. 248, pl. 13, fig. 2, 2a.
v pars 1855 *Ampullaria angulata* Desh.; Terquem, p. 248, pl. 14, fig. 2; *non* pl. 13, fig. 5, 5a (specimen of pl. 14, fig. 2 is not reported on p. 248 and is wrongly reported as fig. 4 in plates explanation).
1882 *Ampullaria angulata* Dunker; Quenstedt, p. 231, pl. 19, figs 8, 9?
v 1912 *Tretospira azyensis* Dareste de la Chavanne, p. 569, text-figs 3–5.
v pars 1913 *Tretospira carinata* (Terquem); Cossmann, p. 174, pl. 10, figs 14, 15, *non* 16, 17.
v 1988 *Tretospira carinata* (Deshayes); Meier & Meiers, p. 43, pl. 13, fig. 29a, b.
2010 *Angularia subangulata* (d'Orbigny); Gründel, p. 9, pl. 2, fig. 17, 18; pl. 3, figs 1, 2.
2012 *Tretospira carinata* (Terquem); Guérin-Franiatte & Hanzo 2012, p. 181, text-fig. 125E.

Material. 17 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR303B, BR347, BR369, BR733, BR743, BR757, BR768, BR773, BR916, BR984-2, GL479; Altwies, Hettangian, exact stratigraphical level unknown: MNHNL GL278, GL478-2; Côte-d'Eich, Hettangian, exact stratigraphical level unknown: MNHNL GL118B, GL326B; Hesperange, Hettangian, exact stratigraphical level unknown: MNHNL GL273; Hettangian, locality and exact stratigraphical level unknown: MNHNL GL153.

Description. The shell is large-sized (maximum height *c.* 65 mm), globose with a sharply gradate spire and composed of five whorls. The last whorl is large (height of last whorl/height of shell ratio *c.* 0.87) and strongly convex. The earliest preserved whorls are quite convex. Early during growth, a rounded angulation appears on the whorl. The angulation becomes sharper on the subsequent whorls and the penultimate and last whorls are distinctly angulated. On the early shell, the suture is very slightly oblique and draws a regular helicospiral line, but on the last whorl it sometimes deviates in adapical or abapical direction. The ramp is wide and commonly slightly oblique on the spire. It becomes steeper on the last whorl, especially near to the peristome. At the beginning, the ramp is slightly convex and becomes almost flat on the later whorls. The outer face is vertical and almost straight, less commonly weakly convex, almost as wide as the ramp. On the last whorl of fully adult shells this part is evenly convex or slightly concave below the shoulder. It is delimited abapically by a broadly convex to very weakly angular periphery. The base is broadly and evenly convex, slightly constricted in its abapical part, anomphalous or with an axial chink (pseudoumbilicus?). The aperture is broadly elliptical, obtusely angulated at the termination of the shoulder on the peristome. The parietal lip has a moderately thick inductura that passes smoothly into an arched columellar lip. In some specimens the columellar lip appears slightly raised beside a narrow axial chink. In other specimens the axial chink is partially or fully covered by the inductura.

The ornament consists only of a variably distinct spiral keel at the angulation of the mature whorls. This keel can be very slightly prominent to bulge-shaped. The growth lines are coarse, especially on the last whorl. They are distinctly prosocline and almost straight on the ramp, slightly prosocline or orthocline on the base.

Remarks. None of the specimens preserves the protoconch. The apertural and columellar regions are either poorly preserved or embedded in matrix in most of the specimens available. The height of both the spire and the last whorl is moderately variable. In some specimens (e.g. GL278; Fig. 20I–K) the last whorl bears few, very smoothened and widely spaced spiral cords. The occasional occurrence of specimens with this kind of irregular ornament has already been described above for *Globularia obtusa* (Deshayes 1850), and is considered here an aspect of the species variation.

Guzhov (2004) suggested that *Tretospira carinata* (Terquem 1855), here synonymized with *Tretospira subangulata* (d'Orbigny 1850), could belong to *Leviathania* Pčelincev 1927. Harzhauser & Schneider (2014) clearly showed that *Laevithania* is characterized by a large umbilicus with a peculiar morphology of the shell wall. Despite the similarity in shell shape, *T. subangulata* cannot be assigned to *Leviathania* because it lacks an umbilicus.

The nomenclatural status of the present species is complex. The oldest name *A. angulata* Dunker 1844, a species from the lower Hettangian of Halberstadt (Saxony-Anhalt, northern Germany), is a junior homonym of *Ampullaria angulata* Jay 1836, a Recent freshwater species (= *Pomacea scalaris* (d'Orbigny 1835)). *Ampullaria angulata* Deshayes 1850 is another younger homonym of Jay's taxon and both a younger homonym and subjective synonym of Dunker's taxon. D'Orbigny (1850) ascribed Dunker's *A. angulata* to the genus *Natica*, making it a secondary homonym of *Natica angulata* Sowerby *in* Sedgwick & Murchison (1832) from the Upper Cretaceous of the Gosau Group (Austria). D'Orbigny therefore changed Dunker's name to *subangulata*, which is the oldest valid name. Even if the two species are no longer ascribed to the same genus, the name is retained here in accordance with art. 59.3 of ICZN (1999), because it was proposed before 1961 and it has been used, albeit rarely, by subsequent authors (Oppel 1856; Coquand 1860; Parisot 1877; Böhm 1901; Girardot 1905; Gründel 2010). It is worth noting that Dunker (1844, 1847) believed that *A. angulata* was a freshwater species and compared it with *Ampullaria scalaris* d'Orbigny 1835 from Argentina (now *Pomacea*). This remark probably misled Cowie & Thiengo (2003), who assumed that Dunker's *angulata* was a Recent freshwater taxon from South America. These authors also incorrectly interpreted *A. angulata* Deshayes as a Recent taxon. *Ampullaria carinata* Terquem 1855

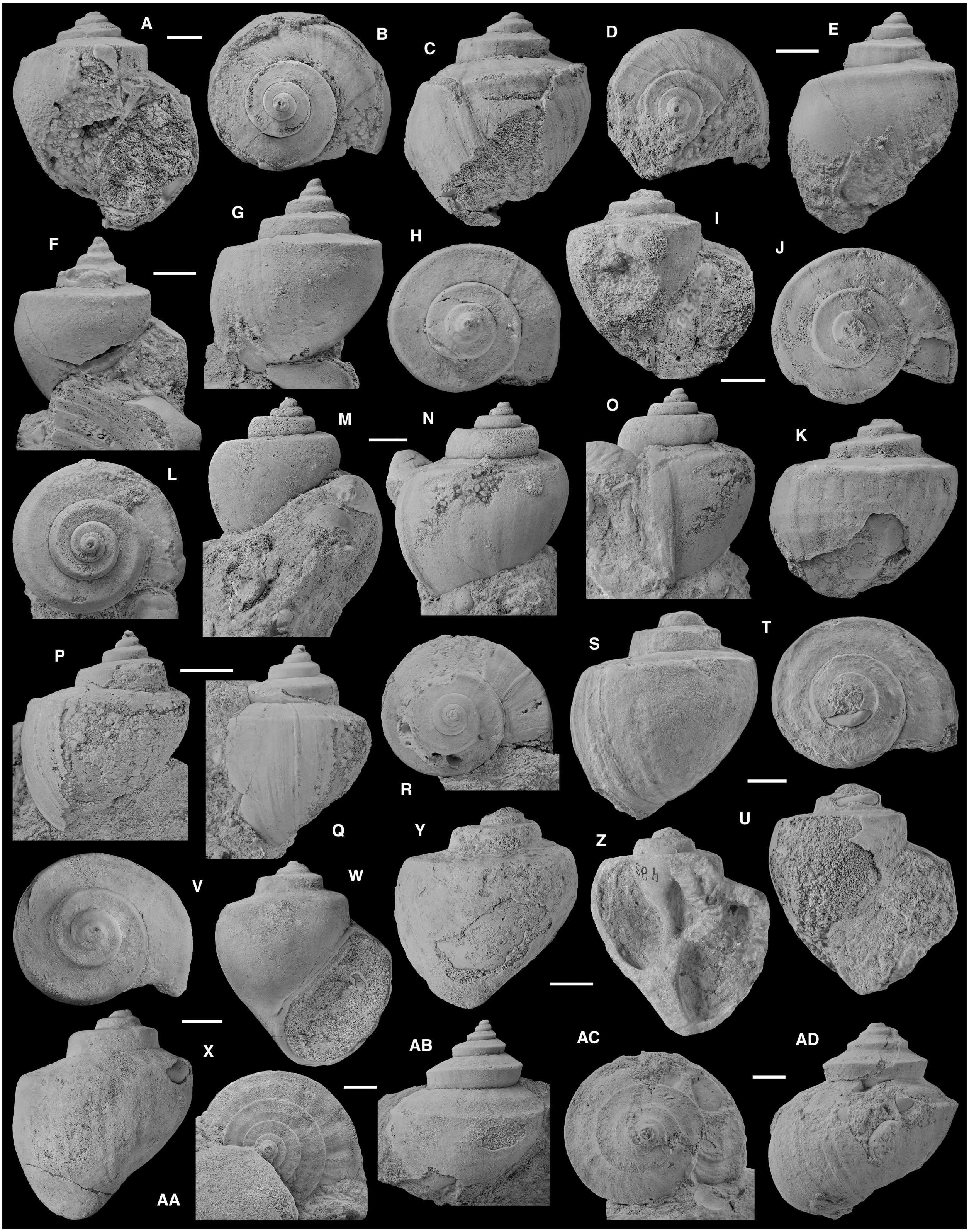
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FIG. 20. *Tretospira* Koken 1892. A–Z, *Tretospira subangulata* (d'Orbigny 1850): A–C, MNHNL BR743 in apertural, apical and dorsal views; D–E, MNHNL BR773 in apical and dorsal views; F–H, MNHNL BR733 in apertural, dorsal and basal views; I–K, MNHNL GL278 in apertural, apical and dorsal views; L–O, MNHNL GL479 in apical, apertural, dorsal and lateral views; P–R, MNHNL BR369 in dorsal, lateral and apical views; S–U, MNHNL GL326B in dorsal, apical and apertural views; V–X, UCBL-EM 31473, lectotype of *Ampullaria carinata* Terquem 1855 in apical, apertural and dorsal views; Y–Z, UCBL-FSL27250, lectotype of *Tretospira azyensis* Dareste de la Chavanne 1912 in dorsal and apertural views. AA–AD, *Tretospira* cf. *subangulata* (d'Orbigny 1850), AA–AB, MNHNL GL478-1 in apical and dorsal views; AC–AD, MNHNL BR434-1 in apical and dorsal views. A–H, L–R, AC–AD, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). I–K, AA–AB, Altwies, Grand-Duchy of Luxembourg, Hettangian. S–U, Côte-d'Eich, Grand-Duchy of Luxembourg, Hettangian. V–X, Hettange-Grande, France, upper Hettangian. Y–Z, Azy-le-Vif, France, upper Hettangian. Scale bars represent 10 mm.

is also an invalid name, being a junior homonym of *Ampullaria carinata* Olivier 1804 (= *Lanistes boltenianus* (Röding 1798)), a Recent freshwater species.

Gründel (2010) proposed the synonymy of both *Ampullaria angulata* figured by Terquem (1855) and *Ampullaria carinata* with *Ampullaria subangulata*. The Deshayes and Terquem collections contain a dozen specimens from the Hettangian of Hettange-Grande referred here to the present species. These collections include the specimen of *A. angulata* figured by Terquem (1855) (UCBL-EM 31476 and 31478), the figured type of *A. carinata* (UCBL-EM 31473; Fig. 20V–X), here selected as lectotype, and the syntypes of *Tretospira azyensis* Dareste de la Chavanne 1912 (UCBL-FSL 27250 and 27251), one of which is here selected as lectotype (UCBL-FSL 27250; Fig. 20Y, Z). It is probable that the specimen of *A. angulata* figured by Deshayes (1850) is also present, but confident identification was not possible. Examination of this material showed that it is not possible to find any significant difference between *A. angulata* Dunker, *A. angulata* Deshayes, *A. carinata* and *T. azyensis*, apart from the larger size and slightly broader spire angle attained by the specimens from France and Luxembourg. Gründel (2010) also included in the synonymy *Ampullospira obliqua* Terquem 1855, which, in contrast, is here treated as a separate species (see *Tretospira obliqua*, below).

Stratigraphic & geographic range. Lower Hettangian, Halberstadt (Saxony-Anhalt, northern Germany); upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France); Hettangian, Hesperange, Altwies, Côte-d'Eich (Grand-Duchy of Luxembourg); Hettangian, Saint-Amand-Montrond (Cher, central France).

Tretospira cf. *subangulata* (d'Orbigny 1850)
Figure 20AA–AD

Material. 2 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR434-1; Altwies, Hettangian, exact stratigraphical level unknown: MNHNL GL478-1.

Remarks. The specimens differ from those here ascribed to *Tretospira subangulata* (d'Orbigny 1850) in the pagodiform shape of the spire due to the inclination of the outer face opposite to that of the ramp. Moreover, the ramp bears shallow and wide, subregularly distributed, prosocline and prosocyrt axial ribs/undulations. In *T. subangulata* the outer face is subvertical and the ramp is smooth. These differences might reflect only infraspecies variations, but the absence of transitional specimens suggests that the provisional separation of this material should be maintained.

Tretospira obliqua (Terquem 1855)
Figure 21

* v	1855	*Ampullaria obliqua* Terquem, p. 249, pl. 13, fig. 6.
v pars	1855	*Ampullaria angulata* Desh.; Terquem, p. 248, pl. 13, fig. 5, 5a; *non* pl. 14, fig. 2.
v	1912	*Tretospira obliqua* Terquem; Dareste de la Chavanne, p. 570, pl. 16, fig. 2.
v pars	1913	*Tretospira carinata* (Terquem); Cossmann, p. 174, pl. 10, figs 16, 17, *non* 14, 15.
	1970	*Tretospira carinata* Terquem; Nagy, p. 87, pl. 1, fig. 2.
v	1988	*Tretospira angulata* (Deshayes); Meier & Meiers, p. 43, pl. 14, fig. 30.
	1992	*Tretospira carinata* (Terquem); Szente, p. 336, pl. 3, fig. 1.
	2012	*Tretospira carinata* (Terquem); Dejax *et al.*, p. 109, text-fig. 77.

Material. 20 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR303A, BR348, BR614-1, BR770, BR853; Altwies, Hettangian, exact stratigraphical level unknown: MNHNL GL140-1, GL 140-2; Bridel, Hettangian, exact stratigraphical level unknown: MNHNL GL425 (5 specimens); Côte-d'Eich, Hettangian, exact stratigraphical level unknown: MNHNL GL118A, GL326A; Hettange-Grande, upper Hettangian: MNHNL GL164A–B, GL330A–C; Hettangian, locality and exact stratigraphical level unknown: MNHNL GL146.

Description. The shell is large-sized (maximum height *c.* 45 mm), pagodiform gradate, taller than wide (height/width ratio of shell *c.* 1.4), with a relatively high spire and composed of 5–6 whorls. The first preserved whorl is strongly convex. On the second whorl a faint angulation appears, which becomes sharper during growth. The last two whorls are distinctly angulated and separated by weakly oblique sutures. The ramp is moderately but distinctly sloping. It becomes steeper during growth. The shoulder corresponds to the periphery and is placed at or slightly above mid-whorl on the spire. The outer face is as wide as the ramp or slightly wider and is very slightly inclined at the opposite angle to that of the ramp. It is straight except for a narrow and weakly concave belt below the periphery. The last whorl is broad and relatively high (height of last whorl/height of shell *c.* 0.75). The base is rather convex, frequently with a median obtuse angulation and an umbilical chink. The aperture is subpentagonal, angular at the periphery. The basal lip is strongly convex. When a basal angulation is present, the basal lip is angularly rounded at its termination on the peristome. On the subadult shell, a moderately thick inductura covers the parietal lip and extends downwards where it forms a sharp and arched columellar lip. The columellar lip is slightly raised, detached from the base and bordering a narrow axial chink, most probably a pseudoumbilicus. The basal lip is slightly reflected outward, presumably corresponding to a shallow lower outlet.

The ornament consists only of a bulge-shaped spiral keel on the shoulder. The keel is weak on the first teleoconch whorls and strengthens during growth. The growth lines are prosocline and prosocyrt on the ramp, nearly orthocline on the concave belt, and strongly opisthocline below it.

Remarks. All of the specimens lack the apical part and some are preserved as inner moulds. The shell is moderately variable in the height of the spire. The spiral keel on the angulation can be variably prominent. The basal angulation can be distinct, although rounded, or just perceptible. Consequently, the basal lip varies from angularly rounded to regularly curved. The ramp is commonly almost as wide as the outer face. Only in specimen BR303A (Fig. 21Q–T) is the ramp much wider and more sloping. However, in the material from Hettange-Grande examined (see below) there are specimens with a transitional morphology.

Cossmann (1913) included *Tretospira obliqua* (Terquem 1855) in the synonymy of *Tretospira carinata* (Terquem 1855) (= *Tretospia subangulata*, see above). Gründel (2010) considered the two species synonyms too. However, the examination of a few dozen specimens from Hettange-Grande in the UCBL-EM collection, including the type figured by Terquem (1855), UCBL-EM 31477, here selected as lectotype (Fig. 21A, B), and the specimen figured by Dareste de la Chavanne (1912) (UCBL-FSL 27258; Fig. 21F, G), suggests that *T. obliqua* is a distinct species. *Tretospira obliqua* and *T. subangulata* have the same gross general shape but it is easy to distinguish one species from the other. *Tretospira subangulata* has a shorter spire and a more globose last whorl. In *T. obliqua* the whorl periphery coincides with the shoulder, whereas in *T. subangulata* it is placed below the shoulder. Moreover, in *T. subangulata* the deviation of the suture is frequent (e.g. Gründel 2010, pl. 3, figs 1, 2). In contrast, none of the many examined specimens of *T. obliqua* shows this deviation. Based on these differences, the specimen UCBL-EM 31476 (Fig. 21C–E), attributed to *Ampullaria angulata* by Terquem (1855, pl. 13, fig. 5), belongs to *T. obliqua*.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch; upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France); upper Hettangian, Hettange-Grande (Moselle, north-eastern France); Hettangian, Altwies, Côte-d'Eich, Bridel (Grand-Duchy of Luxembourg); Hettangian, Pécs (Mecsek Mountains, southern Hungary).

Subclass HETEROBRANCHIA Burmeister 1837
Superfamily MATHILDOIDEA Dall 1889
Family MATHILDIDAE Dall 1889

Genus *Tangarilda* Gründel 2010

Type species. Melania turritella Dunker 1846, *non* Pfeiffer 1840 (= *Cerithium subturritella* d'Orbigny 1850). Hettangian, Halberstadt (Saxony-Anhalt, northern Germany).

Tangarilda trinodulosa (Martin 1860) comb. nov.
Figure 22A–E

* 1860 *Cerithium trinodulosum* Martin, p. 76, pl. 2, figs 15, 16.
1913 *Promathildia trinodulosa* (Martin); Cossmann, p. 225, text-fig. 52.
v 1988 *Turritella* sp.; Meier & Meiers, p. 45, pl. 14, fig. 32a, b.

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR345.

Description. The shell is medium-sized (height *c.* 17 mm), very slender, turritelliform and composed of almost 10 generally convex whorls. The whorls are somewhat high, with a height/width ratio of 0.60 on the early whorls and 0.65 on the adult whorls. Two angulations are visible on the subadult and adult part of the shell. The adapical angulation is peripheral and almost at mid-whorl, whereas the abapical angulation runs at about halfway between the periphery and the abapical suture. The suture is impressed and inclined. The surface of the whorl above the peripheral angulation is quite steep and relatively wide. Its subsutural part is gently concave and becomes slightly convex on the last whorl. The surface of the whorl between the angulations is weakly concave. The base is rounded, anomphalous and the aperture is sub-circular.

The spire whorls bear two spiral keels, each marking the angulations of the whorl surface. A slightly thinner spiral cord runs below the lower angulation and is covered by the suture or just slightly exposed on the spire. Another thin spiral cord runs at some distance from the adapical suture. Additional, faint spiral lines are present. The collabral sculpture consists of prominent and rounded, opisthocyrt ribs, 7–10 on the later whorls, forming spirally elongate nodes at the intersection with the spiral keels. The growth lines are asymmetrically opisthocyrt; they are strongly opisthocyrt above the peripheral angulation and less opisthocyrt and strongly opisthocline below it.

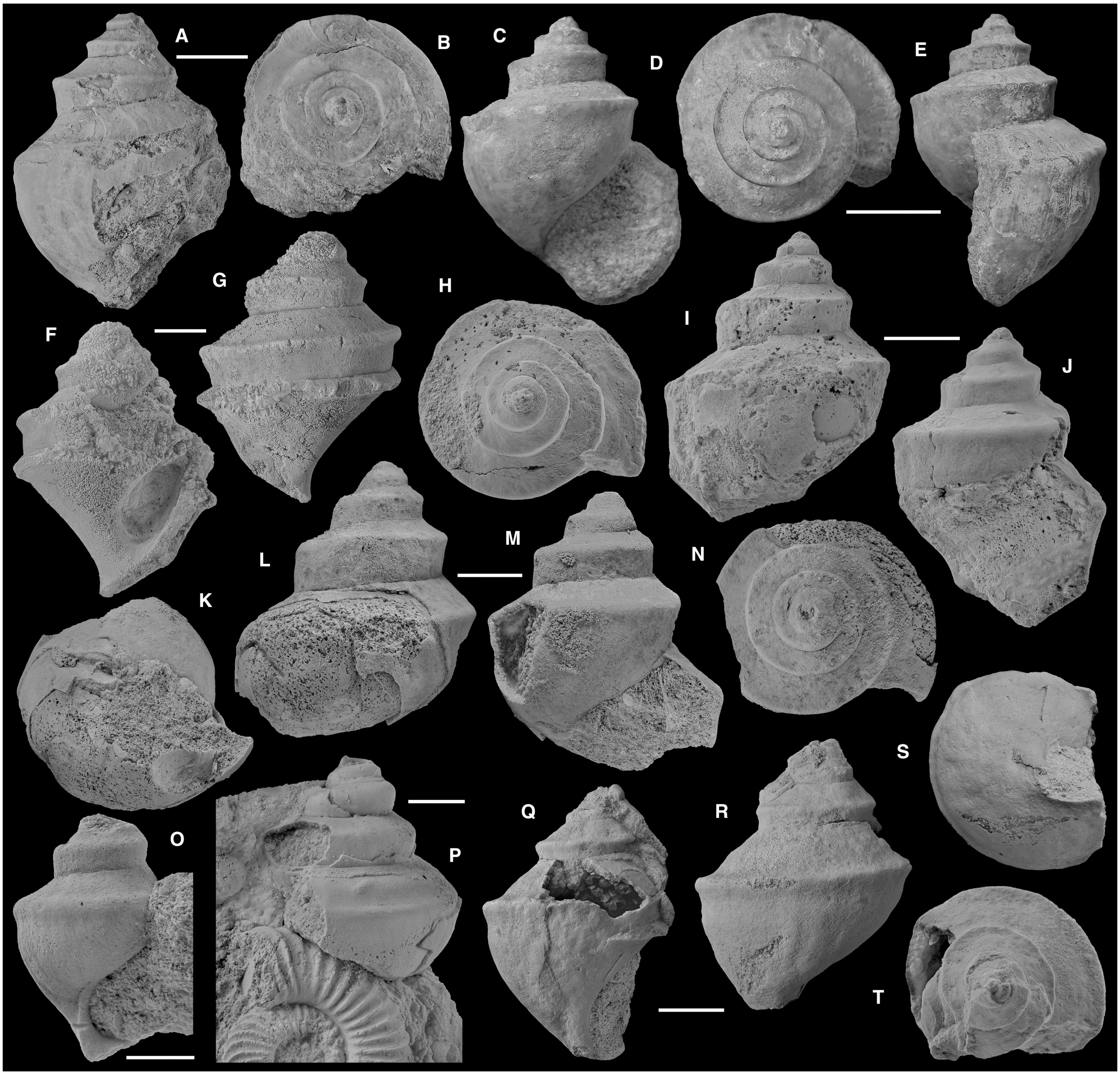

FIG. 21. *Tretospira obliqua* (Terquem 1855). A–B, lectotype UCBL-EM 31477 in apertural and apical views. C–E, UCBL-EM 31476, specimen of *Ampullaria angulata* figured by Terquem (1855) in apertural, apical and lateral views. F–G, UCBL-FSL 27258 in apertural and dorsal views. H–J, MNHNL GL330A in apical, dorsal and apertural views. K–N, MNHNL GL425 in basal, dorsal, apertural and apical views. O, MNHNL BR348 in apertural view. P, MNHNL BR614-1 in lateral view. Q–T, MNHNL BR303A in apertural, dorsal, basal and apical views. A–E, H–J, Hettange-Grande, France, upper Hettangian. F–G, Azy-le-Vif, France, upper Hettangian. K–N, Bridel, Grand-Duchy of Luxembourg, Hettangian. O–T, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 20 mm (A–E); 5 mm (F, G, O, Q–T); 10 mm (H–N, P).

Remarks. The shell of the single specimen is partly dissolved and recrystallized and the details of the ornament are visible only in some parts. Remains of the earliest spire suggest a heterostrophic protoconch with immersed apex. The collabral ribs are well preserved only on the last two whorls; they are seemingly thinner and more closely spaced on the juvenile whorls. The species is here placed in *Tangarilda* Gründel 2010 primarily on the basis of the shape of the growth lines, which is one diagnostic character of the genus according to Gründel (2010) and Gründel & Nützel (2013). *Tangarilda trinodulosa* shows some similarity to the specimen identified as *Cristalloella* sp. by Vitón *et al.* (2020, p. 161, fig. 12.22) from the Upper Sinemurian (*Asteroceras obtusum* Zone) of the Lusitanian Basin, which, however, can be readily distinguished by its single whorl angulation.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Vic-de-Chassenay and Semur (Côte d'Or, north-eastern France).

Tangarilda darestei sp. nov.
Figure 22F–M

1909 *Promathildia turritella* Dunker sp.; Brösamlen, p. 278, pl. 21, figs 6, 7.
v 1912 *Promathildia Terquemi* von Bistram; Dareste de la Chavanne, p. 564, pl. 15, fig. 9, 9a–e.
1997 *Promathilda* (*Promathilda*) *turritella* (Dunker); Hägele, p. 114, text-fig. p. 115.
2003 n. gen. *terquemi* (v. Bistram)? [*sic*]; Gründel, p. 31, pl. 8, figs 1–3, 7–9.
2021 *Turritelloidea terquemi* (Bistram); Valentini & Monari, p. 159, text-fig. 87T.

LSID. https://zoobank.org/NomenclaturalActs/32bccb5b-9d5f-407e-844e-8cd9539d5dd2

Derivation of name. Species dedicated to Jacques Dareste de la Chavanne (1881–1948), Lyonnais geologist and palaeontologist, author of a monograph on the Hettangian fauna of central France.

Type material. Holotype: UCBL-FSL 27128 (Fig. 22F–H). Paratypes: specimens UCBL-FSL 27129–27133, upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France).

Type locality. Azy-le-Vif (Nièvre, central-eastern France).

Type horizon. Upper Hettangian.

Material. Type material and 1 specimen. Brouch, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone): MNHNL BR868A.

Diagnosis. Early shell high-pagodiform with biangulated and bicarinate whorls. Adult shell subturbiniform, with somewhat regularly convex whorls with weak mid-angulation. Aperture elliptical, base low and convex. Ornament of spiral cords and threads, cancellate on early whorls.

Description. The shell is medium-sized (height *c.* 15 mm), slender, made of *c.* 10 relatively low whorls (height/width ratio *c.* 0.45). The suture is distinct and impressed. The initial whorls have two angulations, making the early spire pagodiform. The most adapical angulation is peripheral and runs just above mid-whorl. The abapical angulation is placed at about halfway between the abapical suture and the peripheral angulation. It becomes rapidly less sharp during growth and almost disappears on the last two whorls, changing the shell shape from pagodiform to subturbiniform. The ramp is almost flat on the early preserved whorls and becomes slightly convex on later whorls. The surface below the periphery is very slightly convex. The base is somewhat swollen, anomphalous. The aperture is elliptical, slightly elongate toward the basal lip. The columella is short and straight and forms an obtuse angle with the parietal lip. The inner lip is covered by a thin inductura expanded parietally. The outer lip is simple, obtusely angled at the periphery.

The main ornament of the early whorls is produced by two primary spiral cords, each marking the angulations of the whorls. The peripheral cord is slightly more prominent than the abapical one. A third spiral cord appears between the primary cords. It strengthens gradually and, on the later whorls, it becomes as prominent as the abapical cord. Intercalary spiral threads appear during growth and a fourth cord appears near the abapical suture. Two–three, thin spiral threads are visible on the ramp of the early whorls, the subsutural one being the strongest. These increase up to five on the ramp of last whorl, where they are roughly alternate in strength. Below the periphery, 3–4 evenly spaced spiral cords run on the outer region of the base, while numerous, very thin and dense spiral threads cover the adaxial half of the base. The collabral ornament is produced by thin riblets. These are regularly spaced on the juvenile shell, where they produce a regular cancellate pattern and form small tubercles crossing the spiral elements. The collabral ornament tends to become more irregular and attenuated during growth. The growth lines are generally slightly opisthocline, strongly opisthocyrt on the ramp, slightly opisthocyrt or almost straight below the periphery, becoming widely prosocyrt on the axial region of the base.

Remarks. The species is based on the material (UCBL-FSL 27128–27133; Fig. 22F–J) from the upper Hettangian beds of Azy-le-Vif ascribed by Dareste de la Chavanne (1912) to *Promathildia terquemi* Bistram 1903 (p. 183, pl. 5, figs 9–11). It differs from the latter species in the narrower spire angle, less swollen adult whorls with less impressed suture and, especially, in being much bigger (almost twice as high). The specimen from Brouch here assigned to *Tangarilda darestei* is incomplete and strongly recrystallized. The finest elements of the ornament and the growth lines are just perceptible only in some parts of the shell. Despite its poor state of preservation, direct comparison with the type material indicated only minor differences. This specimen is most probably a subadult shell and differs from the French material only in having a slightly slender shape and a flatter ramp on early preserved whorls. However, the specimens of Dareste de la Chavanne show ample variability in shell shape and ornament. Gründel (2003) suggested that Dareste de la Chavanne's *P. terquemi* and the specimens from the upper Hettangian of Swabia (south-western Germany) classified by Brösamlen (1909) as *Promathildia turritella* (Dunker 1846) (= *Tangarilda subturritella* (d'Orbigny 1850); Gründel 2010) are probably conspecific and ascribed them with doubt to 'n. gen. *terquemi*'. This species was tentatively assigned by Gründel & Nützel (2013) to the genus *Turritelloidea* Walther 1951. However, the ornament pattern of the adult shell is quite different from that of this genus, which is characterized by a somewhat uniform pattern of numerous, strong and subequally sized spiral cords. In contrast, the very well-preserved shells described by Dareste de la Chavanne (1912) clearly show the asymmetrical growth lines typical of the genus *Tangarilda* Gründel 2010.

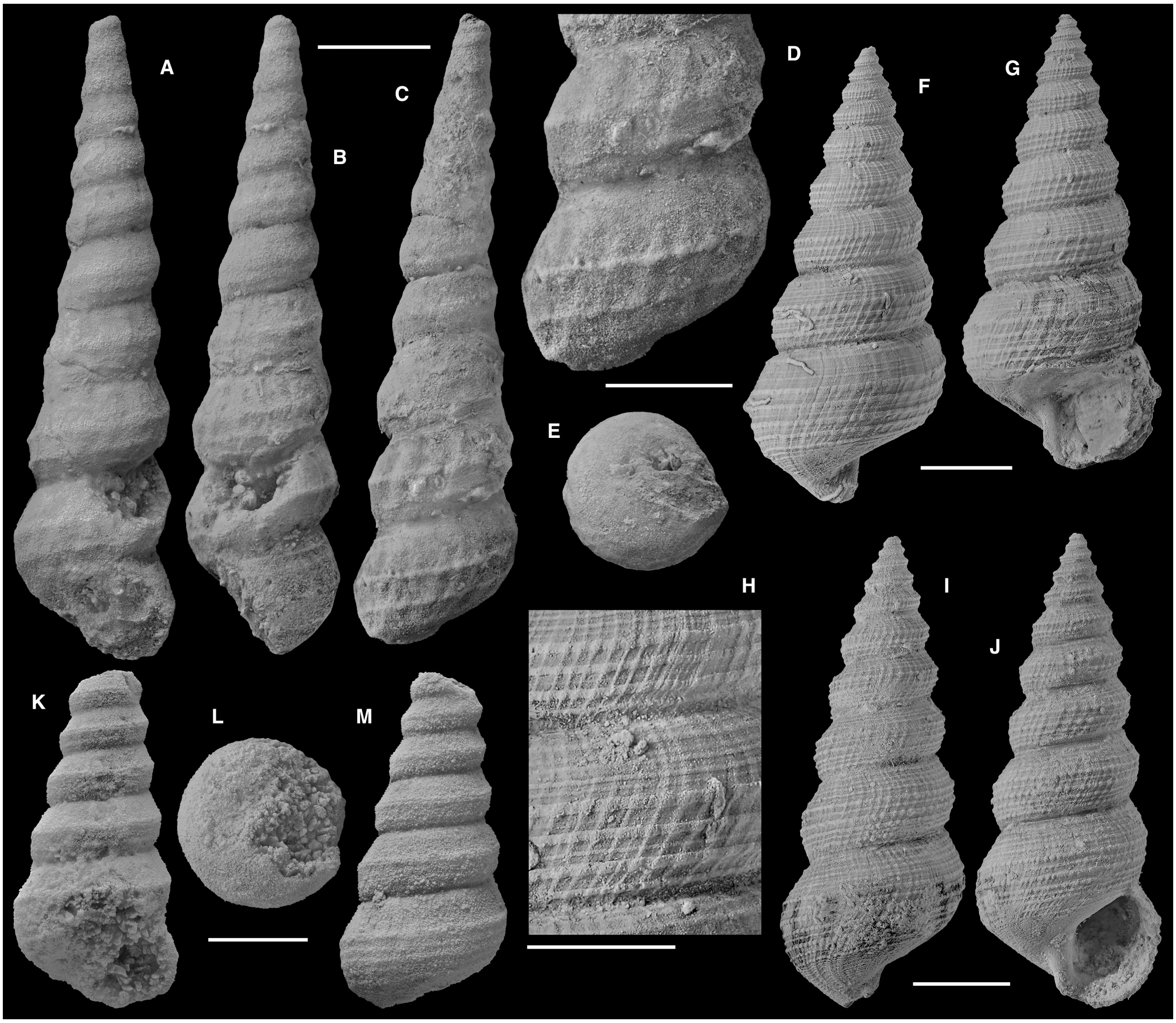

FIG. 22. *Tangarilda* Gründel 2010. A–E, *Tangarilda trinodulosa* (Martin 1860), MNHNL BR345 in apertural, lateral and dorsal views, detail of the ornament on last two whorls and basal view. F–M, *Tangarilda darestei* sp. nov.: F–H, holotype UCBL-FSL 27128 in dorsal and apertural views, detail of the ornament on the penultimate whorl; I–J, paratype UCBL-FSL 27131 in dorsal and apertural views; K–M, MNHNL BR868A in apertural, basal and dorsal views. A–E, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). F–J, Azy-le-Vif, France, upper Hettangian. K–M, Brouch, Grand-Duchy of Luxembourg, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone). Scale bars represent: 3 mm (A–C, E–G, I–M); 2 mm (D, H).

Stratigraphic & geographic range. Lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Göppingen (Baden-Württemberg, south-western Germany); upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France); lower Sinemurian, Semur (Côte-d'Or, north-eastern France).

Genus *Tricarilda* Gründel 1973

Type species. Mathilda (*Tricarilda*) *plana* Gründel 1973. Callovian, Kłęby (Pomerania, Poland).

Tricarilda? *jobae* (Terquem 1855) comb. nov.
Figure 23A, D–M

* v	1855	*Cerithium jobae* Terquem, p. 277, pl. 17, fig. 7a–c.
?	1856a	*Cerithium Terquemi* Piette, p. 201, text-figs 7, 7a.
?	1856a	*Cerithium pleurotoma* Piette, p. 202, text-figs 8, 8a.
pars	1865	*Cerithium jobae* Terq.; Terquem & Piette, p. 65.
v pars	1913	*Promathildia* (*Teretrina*) *jobae* (Terquem); Cossmann, p. 235, pl. 9, fig. 29, *non* 28, ?30–32.

non 1966 *Promathildia jobae* (Terquem) variété *pleurotoma* Cossmann; Bourrouilh, p. 50, text-fig. 26.

Material. 4 specimens. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR301C, BR682-2, GL663, GL664.

Description. The shell is medium-sized (maximum height *c.* 16 mm), high-turbiniform, slightly cyrtoconoidal and composed of six whorls. The whorls are rather convex and separated by a distinctly impressed suture. They are relatively low, with a height/width ratio varying from 0.45 to 0.50. The whorl surface has two very weak angulations. The adapical angulation is at or just above mid-whorl. The abapical angulation is almost halfway between the adapical angulation and the abapical suture. The last whorl is rather inflated, its height being about half the height of the shell. The base is convex, anomphalous. The aperture is oval. The parietal lip has a thin inductura. The columellar lip is moderately stout and slightly arched.

The main ornament consists of two relatively strong, cord-like spiral threads each marking the respective angulations of the whorl surface. Starting from the third last whorl, a third, slightly weaker spiral thread appears in the interspace between the two major threads. A fourth similar thread runs below the second angulation at some distance from the abapical suture, and another one is covered by that suture or just emerging on the penultimate whorl. Additionally, 3–4 faint to very faint spiral threads occur on the ramp. Base ornamented by evenly spaced spiral threads. The growth lines are weakly opisthocline and widely opisthocyrt on the spire whorls, and distinctly prosocyrt on the base.

Remarks. All of the specimens from Luxembourg examined lack the apical whorls and have a broken aperture. The ornamentation is strongly obscured by recrystallization and almost completely smoothened on the early spire whorls. The shell varies moderately in the height of the whorls and, consequently, in the spire angle. Terquem (1855) erected *Cerithium jobae* on specimens from upper Hettangian beds of Hettange-Grande and of Vic-de-Chassenay. One year later, Piette (1856a) erected two species very similar to *C. jobae*, namely *Cerithium terquemi* Piette 1856a and *Cerithium pleurotoma* Piette 1856a on specimens from several French localities of Hettangian age. Subsequently, Terquem & Piette (1865) included these forms in the synonymy of *C. jobae*. As underlined by Cossmann (1913), these authors included also *Cerithium semele* d'Orbigny 1850 from the Sinemurian (?) of Semur (Côte d'Or, north-eastern France), which should have priority. However, Cossmann (1913) maintained that d'Orbigny's species is different from *C. jobae*. He accepted the synonymy of both *C. terquemi* and *C. pleurotoma* with *C. jobae* and assigned this last to the genus *Promathildia* Andreae 1887.

The Terquem collection currently preserves two of the specimens figured by Cossmann (1913) in pl. 9, figs 28 and 29. The specimen of fig. 29 (UCBL-EM 31877, Fig. 23A) is very probably the type figured by Terquem (1855) and is strongly recrystallized. The specimens from Brouch agree well with it. The specimen of fig. 28 (UCBL-EM 31876; Fig. 23B–C) lacks the adult part of the shell (perhaps only the last whorl) but the spire is well preserved and it shows the details of the ornamentation. This specimen has proportionally lower whorls and appears to belong to a different species. Unfortunately, the type material of *C. pleurotoma* and *C. terquemi* has not been found in the UCBL-EM collection. Therefore, the synonymy of these taxa with *T. jobae* cannot be confirmed.

The moderately slender shell, the bicarinate whorls with probably three primary spiral keels, the median keel peripheral, and the ornament pattern of the adult shell makes the species comparable to those belonging to the genus *Tricarilda* Gründel 1973 as emended by Gründel & Nützel (2013). The lack of information on the characters of the protoconch prevents confident genus-level attribution.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian, Vic-de-Chassenay (Côte-d'Or, north-eastern France).

Genus *Brouchilda* nov.

LSID. https://zoobank.org/NomenclaturalActs/62fde2d6-fe22-49ce-bba6-d2f3bcfa12cb

Derivation of name. From Brouch, the type locality of the type species, and the suffix *-ilda* referring to the mathildoidean affinity of the genus.

Type species. Brouchilda laevigata sp. nov. Upper Hettangian, Brouch (Grand-Duchy of Luxembourg).

Diagnosis. Shell very slender and turriculate. Early teleoconch whorls with peripheral angulation almost at mid-whorl. Peripheral angulation moving downwards during early growth. Surface of adult whorls above periphery concave to almost flat, steep to subvertical. Base low and anomphalous. Thin inductura on parietal lip passing smoothly into columellar lip. Ornament of adult whorls consisting of prominent spiral keel on peripheral angulation and less marked spiral keel below suture. Two additional spiral keels below peripheral keel, the lowermost partly or fully covered by the abapical suture. Suture running in a groove between spiral keels. Surface above periphery smooth or with weak spiral ornament. Adaxial half of base ornamented with few spiral threads.

Remarks. The adult teleoconch of *Brouchilda* is similar to those of *Clathrobaculus* Cossmann 1912 and *Gordenella* Gründel 1990, genera that Guzhov (2007) considered as synonymous. The type species of *Clathrobaculus*, namely *Cerithium ziczac* Eudes-Deslongchamps 1842b (p. 198, pl. 11, figs 8, 9; Cossmann 1913, p. 229, pl. 9, figs 18–20) has convex whorls due to the presence of a median angulation marked by a strong spiral keel. In contrast, the whorls of *Brouchilda* are concave to flat and the median keel shifts distinctly on the lower part of the whorl surface. Moreover, *Clathrobaculus* has sharp collabral riblets that make

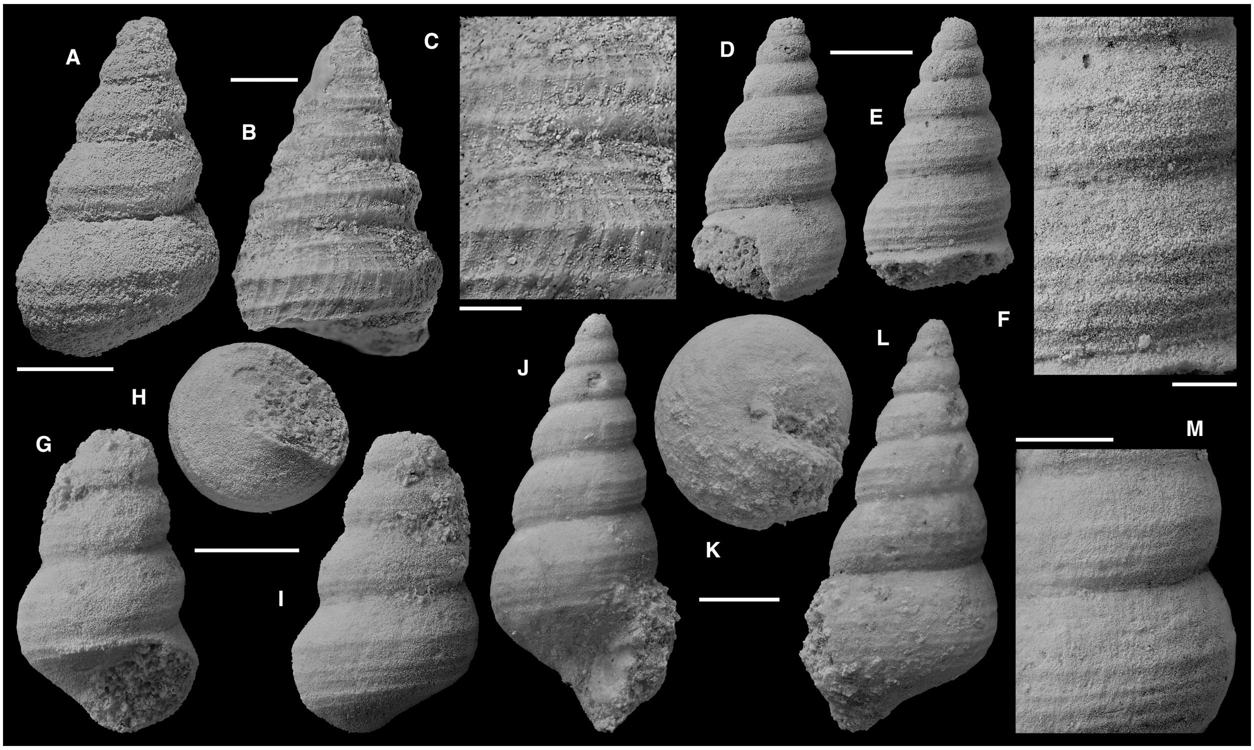

FIG. 23. *Tricarilda*? *jobae* (Terquem 1855). A, UCBL-EM 31877 in dorsal view. B–C, UCBL-EM 31876, specimen ascribed by Cossmann (1913) to *Promathildia* (*Teretrina*) *jobae* (Terquem) in apertural view, detail of the ornament of the two last whorls. D–F, MNHNL GL663 in lateral views, detail of the ornament of two last whorls. G–I, MNHNL GL664 in apertural, basal and dorsal views. J–M, MNHNL BR301C in apertural, basal and dorsal views, detail of the ornament on the two last whorls. A–C, Hettange-Grande, France, upper Hettangian. D–M, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 1 mm (A–B, F); 0.5 mm (C); 3 mm (D, E, G–L); 2 mm (M).

the ornament pattern subreticulate, especially in the juvenile part of the shell. *Brouchilda* is reminiscent of *Gordenella* in concave to straight flank of the adult whorls and in the downwards shifting of the peripheral spiral keel during growth. The main differences are that in new genus the flank between the two major keels is smooth or with very faint spiral elements and that the subsutural keel does not fade with growth (compare with the emended diagnosis of *Gordenella* in Gründel & Nützel 2013, p. 812). In the material available the protoconch is lacking and the early spire not well preserved. In the type species *B. laevigata* the first preserved teleoconch whorl is regularly convex and the second seems to have only one rounded peripheral angulation at mid-whorl. The second keel seems to appear only on later whorls. This would exclude *Brouchilda* from the family Gordenellidae, which according to Gründel (2000) and Gründel & Nützel (2013) is characterized by an early teleoconch with two keels. Therefore, *Brouchilda* is here interpreted as a mathildid genus with an adult teleoconch convergent with that of gordenellids.

Included species & distribution. The genus occurs in upper Hettangian deposits of the central and eastern Paris Basin, Rhône Basin and Luxembourg, and is represented by *Brouchilda laevigata* sp. nov., *Brouchilda mulleri* sp. nov. (described below), from the upper Hettangian of Grand-Duchy of Luxembourg and by *Promathildia bicarinata* Dareste de la Chavanne 1912 (p. 566, pl. 15, fig. 13, 13a–c) from the upper Hettangian of Azy-le-Vif.

In *Turritella grata* Terquem & Piette 1865 (p. 35, pl. 2, figs 16, 17; Dareste de la Chavanne 1912, p. 565, pl. 15, fig. 10, 10a), from the upper Hettangian of Azy-le-Vif and the Sinemurian of Ardennes, the juvenile part of the shell is comparable to that of *Brouchilda*, but the adult whorls become evenly convex.

Brouchilda laevigata sp. nov.
Figure 24A–G

v 1988 *Promathildia unicarinata* (Quenstedt); Meier & Meiers, p. 37, pl. 9, fig. 21.

LSID. https://zoobank.org/NomenclaturalActs/5e9ef2ee-671c-434a-b421-ade055e6c36e

Derivation of name. From the Latin adjective *laevigatus*, meaning ‘smooth’, referred to the absence of spiral ornament on the surface between the spiral keels.

Type material. Holotype: MNHNL HE139 (Fig. 24A–E). Paratype: MNHNL BR350, Brouch (Mersch, Grand-Duchy of

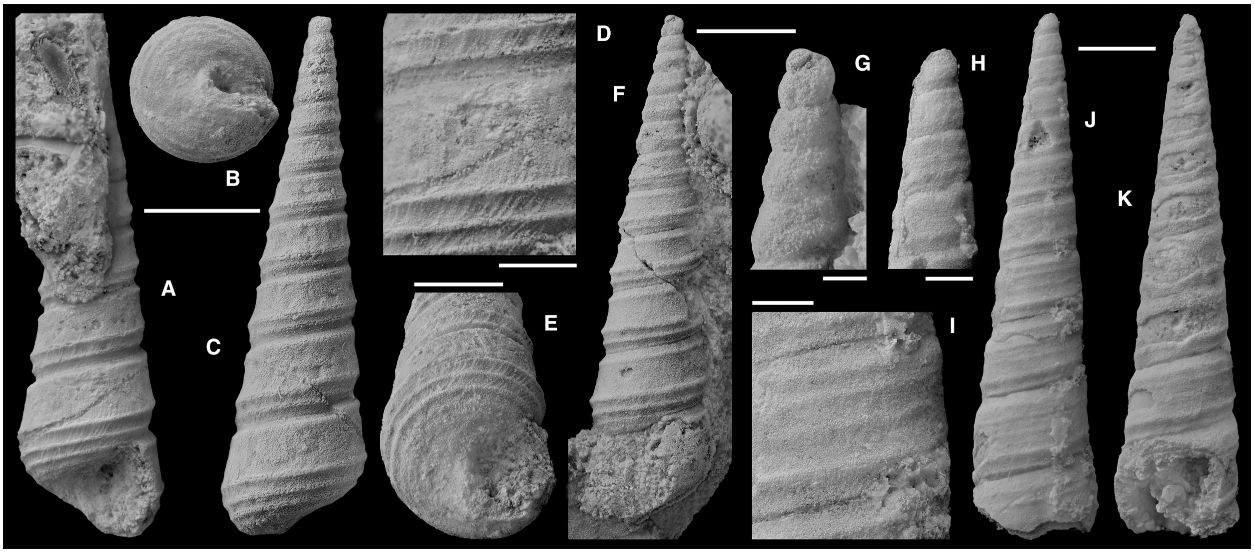

FIG. 24. *Brouchilda* gen. nov. A–G, *Brouchilda laevigata* sp. nov.: A–E, holotype MNHNL HE139 in apertural, basal, dorsal and oblique basal views, detail of the ornament; F–G, paratype MNHNL BR350 in lateral view, detail of the apical whorls. H–K, *Brouchilda mulleri* sp. nov., holotype MNHNL BR420, detail of the apical whorls, detail of the ornament and lateral views. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 3 mm (A–C, F, J, K); 1 mm (D, H, I); 0.5 mm (G); 2 mm (E).

Luxembourg), upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Type material only.

Diagnosis. Spire whorls slightly higher than half of their width. Whorl surface smooth and concave between prominent peripheral and subsutural spiral keels. Third spiral keel running between peripheral keel and abapical suture. Suture edged adapically by a further, thinner spiral keel. Base convex with adaxial part sculptured by 3–4 spiral threads.

Description. The shell is medium-sized (maximum height *c.* 16 mm), very slender, turriculate and composed of *c.* 10 whorls with a height/width ratio *c.* 0.58. The first teleoconch whorl is seemingly regularly convex. The subsequent whorls are angularly rounded. The angulation is peripheral and runs at mid-whorl. During growth, this angulation moves progressively downwards on the whorl surface and in the adult whorls it is placed at the lower third of the whorl. The surface above the angulation is initially slightly concave and becomes almost flat on the later whorls. The suture is moderately inclined and runs in a channelled depression. The base is low and rounded, anomphalous. The aperture is teardrop shaped, distinctly pointed at the sutural corner and rounded at the termination of the periphery on the peristome. The columellar lip is arched. It is slightly reinforced by a narrow marginal callus that extends smoothly into the parietal lip to become a thin inductura.

The ornament consists of a well-developed keel on the peripheral angulation. At about the third whorl, a second slightly thinner keel appears near the adapical suture and a cord-like thread develops in the interspace between the peripheral keel and the abapical suture. The interspace between the peripheral keel and that below it is concave. A further spiral keel edges the abapical suture. The ornament of the base below this keel is produced by 3–4 faint spiral threads. The growth lines are slightly opisthocyrt. They are weakly opisthocline on the whorl surface and become strongly opistocline on the peripheral region of the base. On the last two whorls a dense pattern of sharp and thin growth threads is visible.

Remarks. Both available specimens lack the protoconch and are abraded on the first teleoconch whorls. Compared with the new species, *Brouchilda bicarinata* (Dareste de la Chavanne 1912) is a more slender shell with slightly lower whorls and a less rounded base. It has only one spiral thread visible below the peripheral keel and the subsutural keel runs in a more abapical position, making the interspace below it narrower than in *B. laevigata*. The keel below the periphery runs very near the abapical suture, whereas in *B. laevigata* it is more adapical.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone) Brouch (Grand-Duchy of Luxembourg).

Brouchilda mulleri sp. nov.
Figure 24H–K

LSID. https://zoobank.org/NomenclaturalActs/69c7ba33-920a-4e8e-8013-f5fa7b5237a1

Derivation of name. Species dedicated to geologist Adolphe Muller (1936–2018), who contributed to the knowledge of the geology of Luxembourg.

Holotype. MNHNL BR420 (Fig. 24H–K).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Holotype only.

Diagnosis. Spire whorls distinctly higher than half of their width. Median part of adult whorl surface slightly concave. Adapical and abapical parts weakly swollen. Abapical keel adjacent to or in contact with suture on spire whorls. Surface of whorl between adapical and peripheral keels bearing two widely spaced spiral threads.

Description. The shell is medium-sized (height of incomplete specimen *c.* 20 mm), very slender, turriculate and preserves 11 teleoconch whorls. The height/width ratio is *c.* 0.70 on the early teleoconch whorls and 0.68 on the later whorls. The first preserved whorl is moderately convex and seemingly angularly rounded along its median part. The surface of the adult whorls is slightly concave and almost subvertical on its median part, and weakly swollen, faintly angulated and carinate below and above the suture. The suprasutural keel corresponds to the periphery. The subsutural spiral keel is the abapical edge of a narrow and sloping subsutural shelf. The suture is somewhat inclined and runs in a relatively wide and distinct channel between the spiral keels. The base and apertural characters are unknown.

The main elements of the ornament consist of moderately strong subsutural and peripheral spiral keels. The peripheral keel is slightly stronger. In addition, a spiral thread runs below the periphery in contact with the suture, while two weaker, widely spaced spiral threads ornament the interspace between the keels. The whorl surface between the peripheral and suprasutural keels is concave. Faint secondary spiral threads seem to appear on the last two preserved whorls in the interspaces between the spiral threads and between the spiral threads and the keels. The growth lines are opisthocline and opisthocyrt on the spire whorls.

Remarks. The single available specimen lacks the protoconch. The early teleoconch whorls are poorly preserved and the last whorl is largely incomplete. *Brouchilda mulleri* differs from *Brouchilda laevigata* in being bigger and in having a more acute spire composed of higher whorls with less prominent spiral keels. The side of the whorl is less concave and bears two equally spaced spiral threads. Moreover, the specimen described here has only one spiral thread below the peripheral keel, whereas in *B. laevigata* there is one thread below the peripheral keel and another one just covered by the suture. *Brouchilda bicarinata* (Dareste de la Chavanne 1912) has a more acute shell and distinctly lower whorls. Its subsutural keel is in a more abapical position and there is no clear subsutural shelf. Moreover, *B. bicarinata* has a subtle collabral ornamentation and lacks spiral threads in the interspace between the keels.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone) Brouch (Grand-Duchy of Luxembourg).

Family GORDENELLIDAE Gründel 2000

Genus *Turritelloidea* Walther 1951

Type species. Turritella opalina Quenstedt 1852. Lower Aalenian, Boll (Baden-Württemberg, south-western Germany).

Turritelloidea? *bockfielsensis* sp. nov.
Figure 25

v 1988 *Promathilda turritella* (Dunker); Meier & Meiers, p. 36, pl. 9, fig. 20.

LSID. https://zoobank.org/NomenclaturalActs/dbb61c16-f8ab-4673-8029-b2be76abd47f

Derivation of name. From Bockfiels, the promontory of Luxembourg City where the Count of Ardennes Siegfried built a castle in 963 AD, providing the basis for the development of the town.

Type material. Holotype: MNHNL BR632 (Fig. 25H–J). Paratypes: MNHNL BR301B, BR370, BR419, BR452-2, Brouch (Mersch, Grand-Duchy of Luxembourg), upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Type material and 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL GL666.

Diagnosis. Shell turritelliform with teleoconch composed of fewer than 10 whorls. Early teleoconch whorls with two abapical carinate angulations and subsutural thread. Adult whorls regularly convex and with impressed suture. Two secondary spiral threads appearing between the keels on angulations and between peripheral keel and subsutural thread. Secondary spiral threads

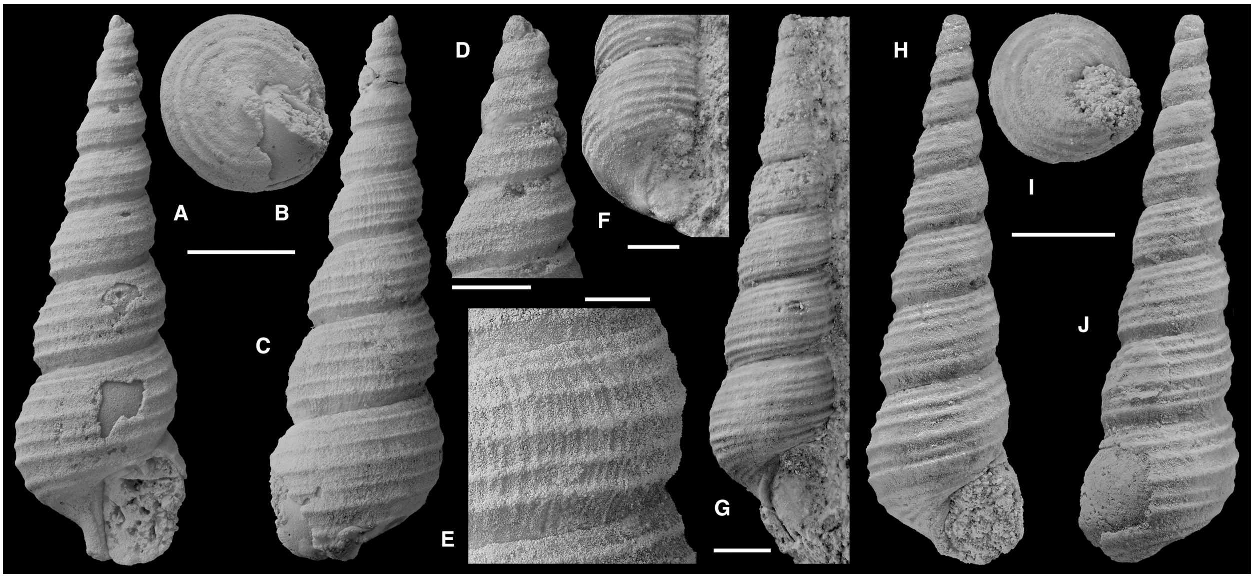

FIG. 25. *Turritelloidea*? *bockfielsensis* sp. nov. A–E, paratype MNHNL BR301B in apertural, basal and dorsal views, detail of apical whorls and detail of the ornament. F–G, paratype MNHNL BR452-2 in oblique basal and apertural views. H–J, holotype MNHNL BR632 in apertural, basal and dorsal views. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 5 mm (A–C, H–J); 2 mm (D); 1 mm (E); 3 mm (F, G).

almost as prominent as primary cords. Adult whorls ornamented by five, evenly distributed spiral cords. Spiral interspaces distinctly wider than cords. Other secondary cords occasionally appearing by intercalation on the last whorl. Opisthocyrt growth lines forming closely spaced, thin and sharp riblets on adult part of shell. Surface of base below primary keels bearing five prominent and equally spaced spiral cords.

Description. The shell is medium-sized (maximum height *c.* 30 mm), high-spired, slender, turritelliform, and composed of nine teleoconch whorls. The early teleoconch whorls are rather high, with a height/width ratio of *c.* 0.65. They are moderately convex and bear two angulations in the abapical half of the whorl. The upper angulation corresponds to the periphery and is placed slightly below mid-whorl. The lower angulation runs distinctly far from the suture. During adult growth, the whorls become more convex and the angulations more rounded, almost indistinct. The suture runs in a furrow between the spiral elements of the ornament and is rather inclined. The base is evenly convex and anomphalous. The aperture is broadly oval, pointed at the sutural angle. The parietal lip has a thin inductura and passes smoothly into an evenly and gently arched columellar lip. The columellar lip has a thin and smooth callus and its outer rim on the axial region of the base is raised. The basal lip seems slightly reflected outward suggesting the presence of a wide and shallow lower outlet.

The first preserved teleoconch whorl bears two primary spiral cords marking the angulations. On the second whorl a third spiral cord, probably worn down by erosion on the previous whorl, is identifiable slightly below the suture. Subsequently, a thinner spiral cord appears between the subsutural and peripheral cord, and another spiral thread appears between the primary keels. They rapidly become almost as prominent as the primary keels. Consequently, the surface of the later whorls is ornamented by five, evenly distributed spiral keels. During the latest growth stage, some additional cord-like spiral threads appear by intercalation or emerge from the adapical and abapical sutures. The collabral sculpture consists of very closely spaced, thin and sharp growth threads. Five, prominent and equally spaced spiral cords ornament the surface of the base below the primary keels. The growth lines are slightly opisthocline and distinctly and symmetrically opisthocyrt on the whorl surface. They are prosocyrt on the base.

Remarks. The specimens lack the protoconch and part of the peristome. The beginning of the teleoconch is badly preserved. *Turritelloidea*? *bockfielsensis* shares with the species of the genus *Turritelloidea* Walther 1951 the ontogenetic change in the ornament and in the shape of the whorls, that is, whorls initially bicarinate becoming regularly convex and with numerous, strong and subequally prominent spiral cords. The tentative attribution to *Turritelloidea* is in accordance with the opinion of Gründel & Nützel (2013) who maintained that the specimen MNHNL BR370 figured by Meier & Meiers (1988) as *Promathilda turritella* (Dunker 1846), which is included in the material studied here, probably represents a species of the genus *Turritelloidea*. However, the lack of information on the protoconch characters does not permit a confident genus attribution. Moreover, in the typical *Turritelloidea* species the shell is more slender and multispiral. The ornament pattern of *T.*? *bockfielsensis* does not fully fit the diagnosis of the genus by Gründel (2005) and Gründel & Nützel (2013). In the species of *Turritelloidea* the adult ornament consists of broad spiral cords separated by thin interspaces, whereas in *T.*? *bockfielsensis* the spiral cords are narrower than the interspaces. In this respect, the species approaches *Turritella* (*Mathilda*) *abbas* Hudleston 1892 (p. 230, pl. 17, fig. 2a–c) from the upper Aalenian beds of Dorset (England) and Baden-Württemberg, a species that Gründel *et al.* (2011a, p. 109, pl. 4, figs 1–4), Gründel & Nützel (2013) and Gründel 2019 (p. 49, figs 7–10) assigned only tentatively to *Turritelloidea*. *Turritelloidea*? *bockfielsensis* differs from *T. abbas* in the smaller and less slender shell and in the greater spire angle. The whorls are less numerous and slightly more inflated. The spiral cords are less prominent and the width of the interspaces more irregular than in *T. abbas*.

Turritelloidea sp. in Gründel (2019, p. 50, figs 11–13), from the upper Pliensbachian of Franconia (southern Germany), is also similar to *T.*? *bockfielsensis* but has a much smaller size and the spiral cords are denser and more prominent.

Turritelloidea? *bockfielsensis* is closely reminiscent of *Tricarilda schoberti* Nützel & Gründel 2015 (p. 28, pl. 15, figs A–I; Gründel & Nützel 2015, p. 67, pl 5, figs 18, 19), from the upper Pliensbachian beds of Franconia (southern Germany) in the general shape of the shell and in the development of the ornament. However, the shell of *T.*? *bockfielsensis* is almost three times bigger and its spiral ornaments is coarser.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone) Brouch (Grand-Duchy of Luxembourg).

?Superfamily MATHILDOIDEA Dall 1889
Family uncertain

Genus *Gruendelifusus* nov.

LSID. https://zoobank.org/NomenclaturalActs/85670a70-d5ed-4787-980f-0e9f48b97f47

Derivation of name. Genus dedicated to Joachim Gründel, Institut für Geowissenschaften, Fachbereich Paläontologie, Freie Universität Berlin.

Type species. Gruendelifusus melusinae sp. nov. Upper Hettangian, Brouch (Grand-Duchy of Luxembourg).

Diagnosis. As for type and only species.

Remarks. The genus is ascribed tentatively to the Mathildoidea on the basis of the general shape of the spire and the ornamentation. However, the relatively high last whorl and the distinct siphonal canal reminiscent of that of most caenogastropods are unusual in the Mathildoidea. The lack of information on the protoconch morphology prevents a confident suprageneric attribution.

Protuba Cossmann 1912 is reminiscent of *Gruendelifusus* in the general morphology. Its type species is *Protuba intermittens* (Kittl 1894) (p. 216, pl. 9, fig. 1) from the Carnian beds of the S. Cassian Formation (Southern Alps, north-eastern Italy). This genus differs from *Gruendelifusus* in lacking a distinct anterior canal. The columellar lip is thin, not adherent to the base and edges an axial chink. The basal lip forms a lower outlet rather than a canal. According to Bandel (1995), *P. intermittens* has a caenogastropod protoconch and is not mathildoidean.

Included species & distribution. The genus is represented only by the type species from the upper Hettangian of Grand-Duchy of Luxembourg.

Gruendelifusus melusinae sp. nov.
Figure 26

LSID. https://zoobank.org/NomenclaturalActs/53ba7743-9812-4995-a74a-945cab5be11e

Derivation of name. From *Melusina*, a mythological figure of European medieval legends, linked to the foundation of Luxembourg.

Type material. Holotype: MNHNL BR885A (Fig. 26A–G). Paratype: MNHNL BR875, Brouch (Mersch, Grand-Duchy of Luxembourg), upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Type material only.

Diagnosis. Shell moderately slender, fusiform and with pagodiform spire. Last whorl rather high, base conoidal, anomphalous, with moderately long neck. Spire whorls low, biangulated. Adapical angulation peripheral, almost at mid-whorl. Peristome with robust, moderately wide siphonal canal. Parietal lip covered by thin inductura passing smoothly into and forming callus on columellar lip. Spiral ornament produced by cords on angulations, and by threads. Collabral ornament of variably distinct and sized riblets producing low nodes at intersection with spiral cords.

Description. The shell is medium-sized (maximum height *c.* 17 mm), moderately slender, fusiform on the whole and composed of five whorls delimited by impressed sutures. The spire is pagodiform and the whorls are rather low (height/width ratio *c.* 0.42). The height of the last whorl is about two-thirds of the total height of the shell. Starting from the first preserved teleoconch whorl, the whorl surface bears two angulations. The first angulation is peripheral, sharp and placed just below mid-whorl. The second angulation is placed halfway between the periphery and abapical suture. It is less defined and almost disappears on the last two whorls. The sutural ramp is wide and rather inclined. It is weakly convex on the early spire, becoming almost flat on later whorls, and reversing to convex just before the peristome. The base is conoidal, anomphalous, with a slightly convex surface and short but well-defined neck. The aperture is obliquely oval, with acute sutural angle. The peristome is orthocline. The parietal lip forms a continuous wide arch with the columellar lip. The outer lip is simple and evenly arched. A thin parietal inductura extends onto the columella where it becomes

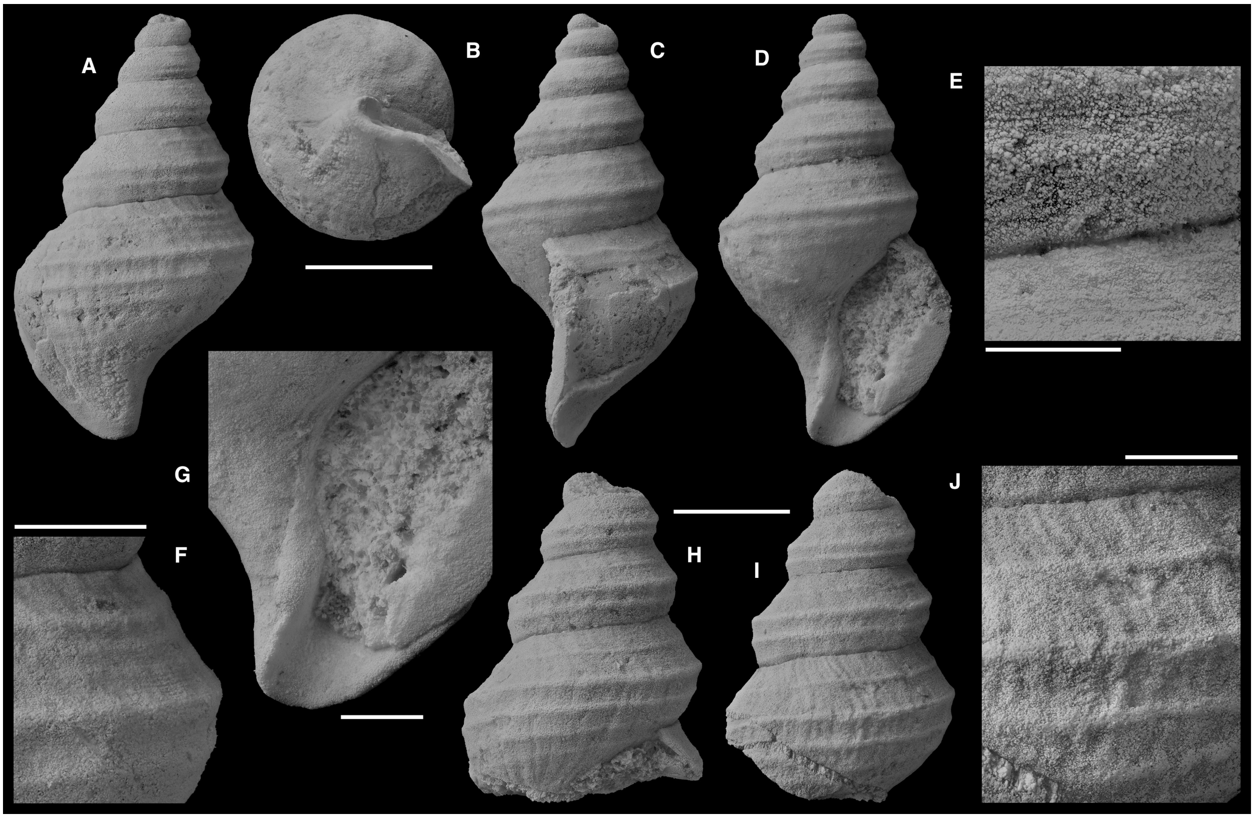

FIG. 26. *Gruendelifusus melusinae* gen. et sp. nov. A–G, holotype MNHNL BR885A in dorsal, basal, lateral and apertural views, detail of the micro-ornament and detail of the siphonal canal. H–J, paratype MNHNL BR875 in apertural and dorsal views, detail of the ornament of the last whorl. Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Scale bars represent: 5 mm (A–D, H, I); 2 mm (E–G, J).

a thickened callus. The aperture extends into a rather wide, shallow and inclined siphonal canal.

The most prominent elements of the ornament are two strong spiral keels, each corresponding to the whorls' angulations. The spiral keel of the peripheral angulation is stronger than the lower one. A third, thinner spiral thread runs just above mid-ramp. Two other poorly defined and equally spaced threads may be present below it on the ramp. On the base, a spiral cord is present below the abapical keel. This is initially covered by the suture, becoming partially exposed on the last whorl. Below it, the base seems ornamented with equally spaced and sized spiral threads. The surface of the shell bears also a micro-ornamentation of closely spaced, very thin spiral striae. The collabral ornament consists of faint opisthocyrt riblets that cause the surface of the spiral keels to be wavy. On the first whorls, the riblets are low and poorly defined and become a little sharper, thinner and of variable strength on the last whorl. The growth lines are widely opisthocyrt on the ramp and outer face, bending at the periphery. They become prosocyrt on the neck.

Remarks. The holotype lacks the apical part and the teleoconch was presumably composed of six whorls. Both available specimens are slightly smoothened by dissolution and maybe abrasion and the spiral micro-ornament is visible only in a few patches. *Teretrina canaliculata* Nützel & Erwin 2004 (p. 405, fig. 14O) from the upper Norian of the Wallowa Terrane (Idaho, USA) is similar to *Gruendelifusus melusinae* in the fusiform, biconical shape of the shell and in the presence of a siphonal canal. It differs in the higher and less pagodiform spire, in the presence of a distinct sutural channel and in the absence of collabral ornaments. *Promathilda* (*Teretrina*) *eucycloides* Haas 1953 (p. 201, pl. 13, figs 10, 19–21, 27, 29) from the Norian–Rhaetian beds of Pucará Basin (Peru) differs from *G. melusinae* in the more pagodiform shape, stronger spiral ornament and less distinct siphonal canal. According to Haas (1953), his species could belong to *Protuba*.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

?Superfamily CIMOIDEA Warén 1993
?Family CIMIDAE Warén 1993

Genus *Kaimella* nov.

LSID. https://zoobank.org/NomenclaturalActs/6a619e35-d67a-448f-b688-b23b4a7f5d7a

Derivation of name. Genus dedicated to Andrzej Kaim, Institute of Paleobiology, Polish Academy of Sciences.

Type species. Kaimella tenuilineata sp. nov. Upper Hettangian, Brouch (Grand-Duchy of Luxembourg).

Diagnosis. As for type and only species.

Remarks. The lack of information on the protoconch of *Kaimella* prevents confident suprageneric assignment of this genus. The biangulated bicarinate shape of the early teleoconch whorls is reminiscent of that of several members of the superfamily Mathildoidea Dall 1889. However, the subturbiniform conoidal shape of the shell is unusual in this group. Taxa with similar shells, such as *Conusella* Gründel 1999a, were placed by Gründel & Nützel (2013) into the family Tofanellidae Bandel 1995 (= Cimidae Warén 1993, according to Bouchet *et al.* 2017) on the basis of the protoconch morphology. With regard to the teleoconch, *Conusella* differs from *Kaimella* in the lack of angulations in the whorls and in the much smaller shell (*c.* 3 mm vs *c.* 15 mm for the type species *K. tenuilineata*).

Included species & distribution. The genus is represented only by the type species from the upper Hettangian of Grand-Duchy of Luxembourg.

Kaimella tenuilineata sp. nov.
Figure 27

LSID. https://zoobank.org/NomenclaturalActs/d4ae6c56-af9a-48ad-b2d7-395dea31f777

Derivation of name. From the Latin adjectives *tenuis*, meaning 'thin/weak', and *lineatus*, meaning 'threaded', referring to the attenuated spiral ornament of the species.

Type material. Holotype: BR858F (Fig. 27A–C). Paratypes: MNHNL GL390B–C, HE143, Brouch (Mersch, Grand-Duchy of Luxembourg), upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Type locality. Brouch (Mersch, Grand-Duchy of Luxembourg).

Type horizon. Luxembourg Sandstone Formation, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Material. Type material only.

Diagnosis. Shell moderately high-turbiniform and cyrtoconoidal. Whorls moderately convex and with pendent outline. Juvenile part of shell with two narrowly carinate angulations in lowermost part of whorl. Angulations delimiting narrow peripheral outer face and disappearing on adult part of shell. Base low and anomphalous. Parietal lip with thin inductura passing smoothly into short and arched columellar lip. Basal lip seemingly forming barely defined lower outlet.

Description. The shell is medium-sized (maximum height *c.* 15 mm), moderately high-turbiniform, cyrtoconoidal and composed of 5–6 teleoconch whorls. The whorls are rather low, with a height/width ratio of *c.* 0.45. The last whorl is rather high, its height being a little more than half the height of the shell. The first two teleoconch whorls show a first obtuse angulation a little below mid-whorl. A second, less clear angulation runs just above the suture. These two angulations define a peripheral narrow, almost flat and vertical outer face. The sutural ramp leading to the first angulation is weakly convex. During growth the angulations fade and the whorl surface becomes convex and moderately pendent. The suture is impressed and only slightly inclined. The base is low and convex, anomphalous. The aperture is transversely ovate and pointed at the sutural angle. The parietal lip is covered by a very thin inductura that passes smoothly into the columellar lip. The columellar lip is relatively stout, short and arched and passes smoothly to the parietal lip. The basal lip is rounded, seemingly slightly reflected outward, probably indicating the presence of a barely defined lower outlet.

On the early teleoconch whorls the ornament is represented by two thin spiral threads that mark the angulations. A third, thinner spiral thread appears between them and rapidly strengthens to match the other two. Faint spiral threads are present on the ramp. They are seemingly relatively closely and regularly spaced. Some faint, regularly spaced, thin spiral threads are present also on the base. All spiral ornament loses definition on the last whorl, but that on the periphery and base remains distinct. The growth lines are moderately opisthocline and gently opisthocyrt on the spire whorls. They are distinctly prosocyrt on the base.

Remarks. The new species vaguely resembles *Conusella* sp. described by Gründel (2006, p. 9, pl. 3, figs 13, 14), a species from the upper Bathonian of Calvados assigned only tentatively to the genus *Conusella* by Gründel & Nützel (2013). However, the Bathonian species is considerably smaller (it is less than 2 mm high) and its early teleoconch is not biangulated. Similarly, the late Oxfordian *Conusella* sp. from Kłęby (Poland) is much smaller than *K. tenuilineata* and not biangulated, despite the presence of faint and irregular spiral lineation (Gründel & Kaim 2006, p. 148, fig. 23).

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg).

Superfamily ACTEONOIDEA d'Orbigny 1842
Family CYLINDROBULLINIDAE Wenz 1938

Genus *Cylindrobullina* von Ammon 1878

Type species. Tornatella fragilis Dunker 1846. Hettangian, Halberstadt (Saxony-Anhalt, northern Germany).

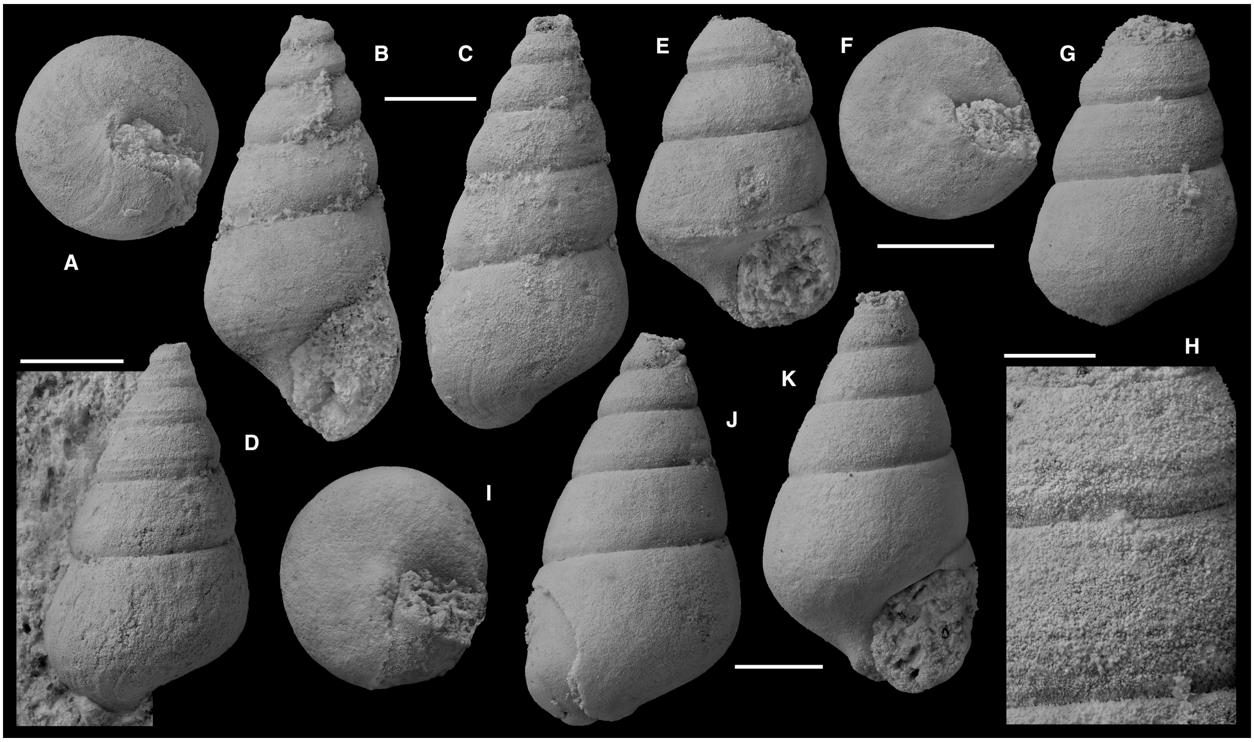

FIG. 27. *Kaimella tenuilineata* gen. et sp. nov. A–C, holotype MNHNL BR858F in basal, apertural and dorsal views. D, paratype MNHNL HE143 in dorsal view. E–H, paratype MNHNL GL390B in apertural, basal and dorsal views, detail of the whorl surface. I–K, paratype MNHNL GL390C in basal, dorsal and apertural views. A–D, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). E–K, Luxembourg Sandstone Fm., locality and stratigraphical level unknown, Hettangian. Scale bars represent: 3 mm (A–G; I–K); 1 mm (H).

Cylindrobullina inermis (Terquem 1855)
Figure 28A–F

* 1855 *Tornatella inermis* Terquem, p. 258, pl. 15, fig. 4.
v 1988 *Cylindrobullina secale* (Terquem); Meier & Meiers, p. 46, pl. 15, fig. 34a, b.

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR343.

Description. The shell is medium-sized (height *c.* 12 mm), ovate cylindrical and composed of four teleoconch whorls. The spire is prominent, somewhat slender and subgradate. The last whorl is subcylindrical and its height is *c.* 80% of the height of the shell. The spire whorls have a sloping ramp delimited abapically by a rounded shoulder. The ramp is seemingly slightly and evenly convex on the early whorls. On the last two whorls, a very weak spiral depression appears on the middle of the ramp. On the last whorl, the shoulder becomes slightly sharper. The surface of the spire whorls below the shoulder is as wide as the ramp or slightly wider, almost straight and subvertical on the penultimate whorl. The suture is impressed and slightly inclined. The flank of the last whorl is very slightly convex. The aperture is narrow, much higher than wide, its height being slightly more than twice its width. The parietal lip is covered by a thin inductura that continues into a thick columellar lip. The columellar lip is detached from and slightly reflected towards the axial region of the base. Traces of growth lines are visible only on the base where they are opisthocyrt.

Remarks. The specimen has the shell wall strongly altered by recrystallization. The columellar callus is damaged at the junction with the parietal lip and this gives the false impression that there is a columellar fold. The type specimen of *Tornatella inermis* Terquem 1855 from the upper Hettangian of Hettange-Grande was not found in the UCBL-EM collection. Based on the original illustration, the specimen seems to differ from the shell described here only in having more evenly convex whorls. However, Terquem (1855) specified that the whorls are obtusely angulated, rather than convex, and that this angulation becomes slightly sharper on the last whorl. This is exactly the case of the specimen from Luxembourg. Cossmann (1895a) treated *C. inermis* as a synonym of *Cylindrobullina fragilis* (Dunker 1846) (p. 169, Dunker 1847, p. 11, pl. 13, fig. 19a, b; Gründel 2010, p. 18, pl. 4, figs 2–8 and references therein) from the Hettangian beds of Halberstadt (Saxony-Anhalt, northern Germany). However, in *C. fragilis* the last whorl is higher, the spire whorls lower and less inflated and the shoulder less defined.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch

(Grand-Duchy of Luxembourg); upper Hettangian Hettange-Grande (Moselle, north-eastern France).

Family TUBIFERIDAE Cossmann 1895b

Genus *Striactaeonina* Cossmann 1895b

Type species. Orthostoma avena Terquem 1855. Upper Hettangian, Hettange-Grande (Moselle, north-eastern France).

Striactaeonina buvignieri (Terquem 1855)
Figure 28G–M

- * v 1855 *Tornatella Buvignieri* Terquem, p. 257, pl. 15, fig. 1, 1a, b.
- v 1895a *Striactaeonina buvignieri* Terq.; Cossmann, p. 27, pl. 1, figs 38–39.
- non 1903 *Cylindrobullina Bouvignieri* [*sic*] Tqm. sp.; Bistram, p. 77, pl. 6, fig. 7.
- v 1912 *Striactaeonina Buvignieri* Terquem; Dareste de la Chavanne, p. 556, pl. 15, fig. 1, 1a, b.
- non 1954 *Cylindrobullina bouvignieri* [*sic*] Terquem; Conti, p. 178, pl. 8, figs 2, 3.
- v 1988 *Cylindrobullina buvignieri* (Terquem); Meier & Meiers, p. 46, pl. 15, fig. 33a, b.

Material. 1 specimen. Brouch, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone): MNHNL BR344.

Description. The shell is medium-sized (height *c.* 17 mm), cylindrical, much higher than wide, and is composed of at least four teleoconch whorls. The spire is rather prominent, slender, slightly cytoconoidal, narrowly and sharply gradate. The spire whorls are rather high, with a height/width ratio of *c.* 0.5, and separated by an impressed and distinctly inclined suture. The height of the last whorl is *c.* 70% of the reconstructed height of the shell. The whorls have a narrow, somewhat sloping and slightly convex ramp. The surface of the spire whorls below the shoulder is about three times wider than the ramp and is subvertical and almost flat. The shoulder is slightly bulged, cord shaped. It is edged abapically by a distinct furrow whereas its adapical edge is sharp. The flank of the last whorl is vertical and almost flat. The aperture is rather high, narrow in its upper part and broader, compressed, teardrop shaped in its lower half. The columellar lip is thin, sharp, regularly arched and slightly detached from the axial region of the base.

In addition to the spiral bulge of the shoulder and its marginal spiral furrow, the ornament consists of very thin, dense spiral striae on the base that vanish approximately at the line where the suture runs. A pair of spiral striae seems to be present on the ramp. The growth lines are opisthocline and slightly prosocyrt on the spire whorls. On the body whorl they are widely prosocyrt and become slightly opisthocyrt in the lower part of the base.

Remarks. The shell lacks the apical part but it does not show substantial differences to the holotype of *Tornatella buvignieri* Terquem 1855 in Terquem's collection (UCBL-EM 31485; Fig. 28G). The specimen ascribed by Bistram (1903, p. 77, pl. 6, fig. 7) to this species differs in the less slender shell and lower whorls. The sutural ramp is flat and with sharp outer edge, and the spiral furrow below the shoulder is lacking.

Stratigraphic & geographic range. Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Azy-le-Vif (Nièvre, central-eastern France); upper Hettangian, Hettange-Grande (Moselle, north-eastern France).

Striactaeonina sinemuriensis (Martin 1860)
Figure 28N–V

- pars 1855 *Orthostoma frumentum* Terquem, p. 261, *non* pl. 15, fig. 7, 7a, b.
- * 1860 *Acteon sinemuriensis* Martin, p. 70, pl. 1, figs 9, 10.
- 1864 *Orthostoma scalaris* Dumortier, p. 126, pl. 20, fig. 12.
- pars 1895a *Striactaeonina sinemuriensis* Mart.; Cossmann, p. 27, pl. 4, fig. 42; *non* pl. 1, figs 40, 41.
- non 1903 *Cylindrobullina sinemuriensis* Mart.; Bistram, p. 191, pl. 4, figs 3–4.
- 1907a *Striactaeonina turgida* (Terquem); Cossmann, p. 19, pl. 4, fig. 17.
- 1912 *Striactaeonina sinemuriensis* Martin; Dareste de la Chavanne, p. 557, pl. 15, fig. 2, 2a.
- non 1954 *Cylindrobullina sinemuriensis* Martin; Conti, p. 177, pl. 7, figs 21, 22.
- 2003 *Cylindrobullina scalaris* (Dumortier); Gründel, p. 32, pl. 8, figs 4–6.
- 2010 *Cylindrobullina* sp. Gründel, p. 18, pl. 4, figs 9–14.

Material. 1 specimen. Brouch, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone): MNHNL BR864.

Description. The strongly fragmentary specimen is 6.3 mm high and represents a subovate shell with a prominent, sharply gradate spire. The ramp is narrow, almost flat or very slightly convex, and slightly sloping. On the penultimate whorl, the surface below the shoulder is rather high. It extends almost twice the width of the ramp. The suture seems to be slightly more inclined on the last whorl than on the preceding one. The shoulder is slightly bulged, cord shaped. Its abapical edge is marked by a distinct groove, whereas its adapical margin, corresponding to the outer edge of the ramp, is sharp. The last whorl is ovate and its periphery is located somewhat below the line of the suture. The base is elongate, gently convex and anomphalous. The columellar lip seems to be strengthened by a smooth callus. The growth lines are not visible.

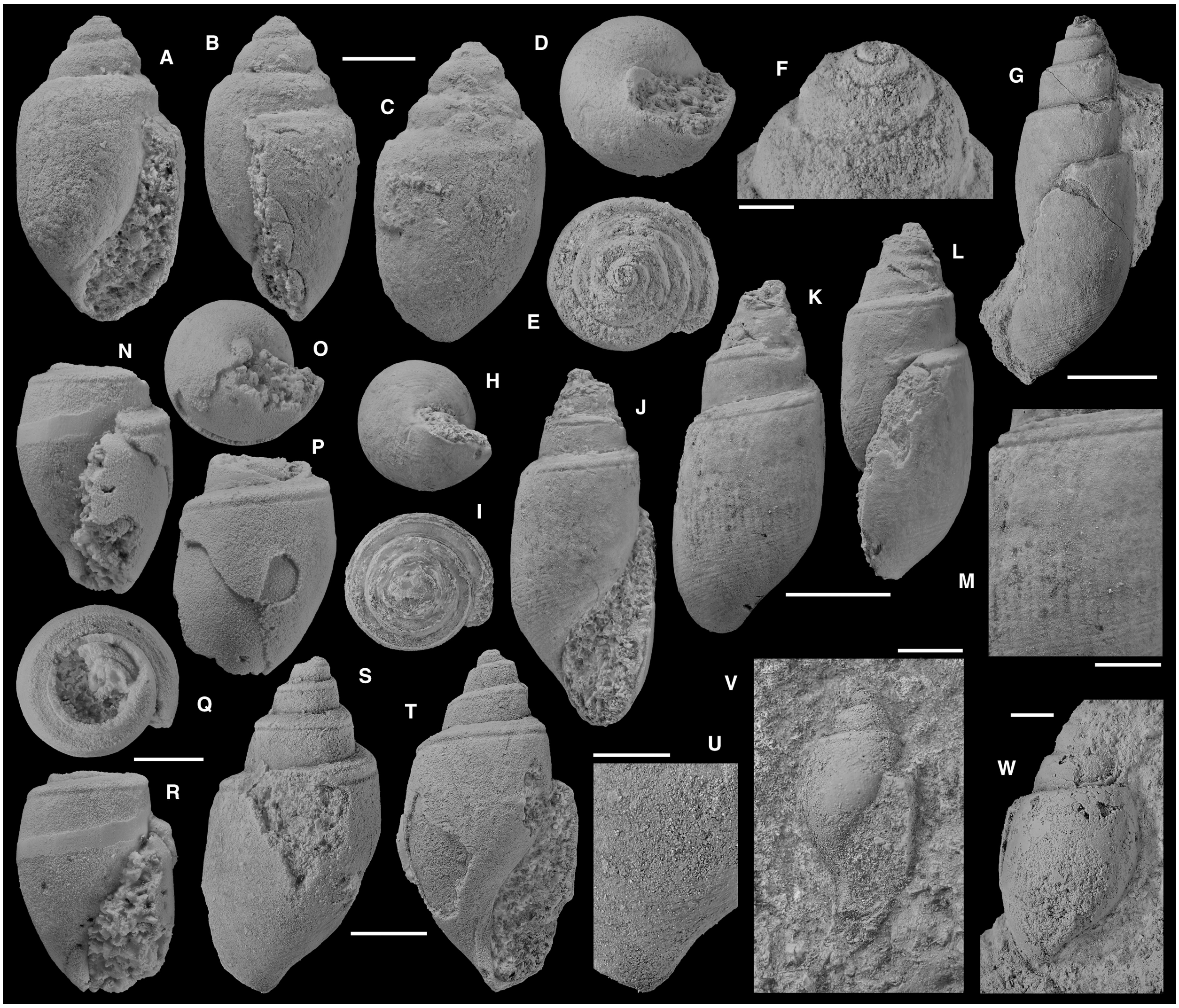

FIG. 28. Acteonoidea d'Orbigny 1842. A–F, *Cylindrobullina inermis* (Terquem 1855), MNHNL BR343 in apertural, lateral, dorsal, basal and apical views, detail of the apical whorls. G–M, *Striactaeonina buvignieri* (Terquem 1855): G, holotype UCBL-EM 31485 in lateral view; H–M, MNHNL BR344 in basal, apical, apertural, dorsal and lateral views, detail of the ornament on the last whorl. N–V, *Striactaeonina sinemuriensis* (Martin 1860): N–R, MNHNL BR864 in lateral, basal, dorsal, apical and apertural views; S–U, UCBL-EM 33414 in dorsal and apertural views, detail of the ornament on the base; V, UCBL-EM 31487b in apertural view. W, *Orthostoma frumentum* Terquem 1855, lectotype UCBL-EM 31487a in dorsal view. A–F, H–M, Brouch, Grand-Duchy of Luxembourg, upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). G, S–W, Hettange-Grande, France, upper Hettangian. N–R, Brouch, Grand-Duchy of Luxembourg, lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone). Scale bars represent: 3 mm (A–E); 1 mm (F, U–W); 5 mm (G–L); 2 mm (M–T).

Remarks. The single specimen available preserves only the last one and half whorls. The peristome is incomplete. The shell wall is strongly recrystallized and its external layer is lacking on most of the shell surface. The general shape of the specimen, albeit strongly fragmentary, and the characters of the ramp and shoulder match those of *Acteon sinemuriensis* Martin 1860 from the upper Hettangian of Semur. This species has extremely fine spiral striae on the last whorl's surface, but these are not present on the specimen from Luxembourg here described (MNHNL BR864), probably due to its poor state of preservation. One specimen in Terquem's collection (UCBL-EM 33414; Fig. 28S–U) from the upper Hettangian of Hettange-Grande labelled *Orthostoma avena* Terquem 1855 (p. 260, pl. 15, fig. 8, 8a, b) is identical in shape to the specimen here described but is better preserved and has a very thin spiral ornament on the basal part of the last whorl. It clearly does not belong to *O. avena*, a species with a much more elongated and subcylindrical shell (Cossmann 1895a, p. 26, pl. 1, figs 36, 37; Cossmann 1895b, p. 59, pl. 1, fig. 22; Cossmann 1902, p. 167, pl. 3, figs 3, 4; Cossmann 1907a, p. 18, pl. 4, figs 27, 28; all as *Striactaeonina*).

The specimen from Luxembourg here described (MNHNL BR864) is also similar to the shell from the upper Hettangian of

Provenchères-sur-Meuse figured as *Striactaeonina turgida* (Terquem 1855) by Cossmann (1907a, p. 19, pl. 4, fig. 17). The type material of *Orthostoma turgida* was not found in the UCBL-EM collection. However, the original illustration in Terquem (1855, p. 260, pl. 15, fig. 6, 6a, b) shows a shell that differs from both *S. turgida sensu* Cossmann (1907a) and *S. sinemuriensis* in having a lower and less distinctly gradate spire and a more cylindrical last whorl. Cossmann (1895a, 1902, 1907a) included *Orthostoma triticum* Terquem 1855 (p. 261, pl. 15, fig. 5, 5a, b) and *Orthostoma frumentum* Terquem 1855 (p. 261, pl. 15, fig. 7, 7a, b), both from the upper Hettangian of Hettange-Grande, in the synonymy of *S. turgida*, attributing to this taxon a very high morphological variability. The type material of *O. triticum* is absent from the Terquem UCBL-EM collection. In contrast, the type material of *O. frumentum* is represented by two specimens poorly preserved and partially embedded in matrix. They clearly belong to two different species and the description of *O. frumentum* given by Terquem (1855) is very probably a composite one. The specimen UCBL-EM 31487a (Fig. 28W) is here designated as lectotype of the species because it is a better match to the original illustration. This specimen does not have a groove below the shoulder. Consequently, *O. frumentum*, as defined by the lectotype, does not belong to *Striactaeonina*. The other specimen (UCBL-EM 31487b; Fig. 28V) is a juvenile that probably belongs to *S. sinemuriensis*.

According to Cossmann (1895a) and Dareste de la Chavanne (1912), *Orthostoma scalaris* Dumortier 1864 (upper Hettangian, Rhône Basin, southern France) is a junior synonym of *S. sinemuriensis*. In the species description, Dumortier stated that the shell surface of *O. scalaris* is smooth, but Cossmann (1895a) observed that the type specimen of Dumortier is abraded. Bistram (1903, p. 76, pl. 6, figs 3, 4) recorded *Cylindrobullina sinemuriensis* in the Hettangian beds of Val Solda (Lombardy, northern Italy). However, this attribution is probably wrong, because the specimens figured by him have a cylindrical and not ovate last whorl, and the spire is shorter and with lower whorls.

Stratigraphic & geographic range. Lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone), Brouch (Grand-Duchy of Luxembourg); upper Hettangian, Semur (Côte d'Or, north-eastern France); upper Hettangian, Hettange-Grande (Moselle, north-eastern France); upper Hettangian, Rhône Basin (southern France); upper Hettangian, Provenchères-sur-Meuse (Haute-Marne, north-eastern France).

COMPARISONS WITH THE HETTANGIAN GASTROPOD FAUNA OF HETTANGE-GRANDE

The systematic analysis identified 33 species, 11 of which are new. Five species are classified in open nomenclature and four of them (*Torusanina* sp., *Trypanostylus*? sp., *Anulifera* sp. and *Angularia*? sp.) are distinct from the others recognized in the material. Fourteen families belonging to nine superfamilies (i.e. Caenogastropoda superfamily indet., Campaniloidea, Pseudozygopleuroidea, Littorinoidea, Stromboidea?, Neogastropoda superfamily indet., Mathildoidea, Cimoidea? and Acteonoidea) are represented in the material. All species come from the *Schlotheimia angulata* Zone except *Tangarilda darestei* and *Striactaeonina sinemuriensis* (Martin 1860), which are present only in the lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras johnstoni* Subzone), and *Globularia obtusa* (Deshayes 1850) found in undifferentiated Hettangian deposits. Species coming from both ammonite zones are *Bourguetia bipartita*, *Microschiza semiornata* and *Microschiza pauciornata*. Together with the Patellogastropoda, Vetigastropoda and Neritimorpha described by Monari *et al.* (2011), the whole gastropod fauna of Luxembourg consists of 55 species (Table 1).

Terquem (1855) and Terquem & Piette (1865) described 69 gastropod species from the *Schlotheimia angulata* Zone of the nearby locality Hettange-Grande. The taxonomic revision in Monari *et al.* (2011) and in this study reduces the list to 61 species and the number is probably lower, given that part of the fauna from Hettange-Grande still needs to be revised. Therefore, the species richness of the gastropod fauna from the Luxembourg Sandstone Formation is only slightly lower than that from Hettange-Grande. About 50% of the species recognized in the Luxembourg Sandstone Formation are lacking at Hettange-Grande (Table 1). However, at higher taxonomic rank the differences are much less marked. At the family level the material from the *Schlotheimia angulata* Zone of Brouch and that published by Terquem (1855) shows a very high taxonomic diversification and few differences (Fig. 29). The taxonomic diversity at Hettange-Grande is higher but the most diversified families at the two sites are almost the same. All of the families that occur in a single locality, apart from the Ataphridae, are represented by single species. Palaeoecological interpretation and comparison between the two sites are made difficult by the fact that the gastropods of Brouch come mainly from storm beds and that the exact levels from which the gastropods of Hettange-Grande were collected are unknown.

PALAEOBIOGEOGRAPHICAL ANALYSIS OF EARLY JURASSIC WESTERN TETHYAN GASTROPODS

The aim of the palaeobiogeographical analysis was primarily to investigate the relationship between the Hettangian gastropod fauna of the Luxembourg Sandstone Formation and other coeval faunas of western Tethys. In a more general context, the analysis has been expanded to a longer time interval to study the tempo and mode of the Early Jurassic gastropod recovery in the western Tethys and to evaluate the effects that the wide-scale

TABLE 1. List of species from the Luxembourg Sandstone and number of specimens for each species.

	Luxembourg Sandstone													Hettange-Grande
	Brouch			Hesperange	Bridel	Itzig	Altwies	Côte-d'Eich	Mamer	Burmerange	Steiford	Kopstal	Loc. unknown	
	a	b	c	Undifferentiated Hettangian										
Subclass PATELLOGASTROPODA Lindberg 1986														
?Superfamily LOTTIOIDEA Gray 1840														
?Family ACMAEIDAE Forbes 1850														
Scurriopsis (_Scurriopsis_) _schmidti_ (Dunker 1844**)**		16	2											*
Scurriopsis (_Hennocquia_) _hettangiensis_ (Terquem 1855**)**		33	3										8	*
Subclass VETIGASTROPODA Salvini-Plawen 1980														
Superfamily PLEUROTOMARIOIDEA Swainson 1840														
Family PLEUROTOMARIIDAE Swainson 1840														
Pleurotomaria wanderbachi Terquem 1855		5							1					
Pleurotomaria hettangiensis Terquem 1855		5		1										*
Pleurotomaria cf. _hettangiensis_ Terquem 1855		1												
Pleurotomaria hennocquii Terquem 1855		1												*
Pleurotomaria cognata Chapuis & Dewalque 1854										3				
Pleurotomaria sp.										1				
Anodomaria schroederi Monari _et al._ 2011		1												
Family TROCHOTOMIDAE Cox 1960c														
Trochotoma vetusta Terquem 1855		33												*
Trochotoma clypeus Terquem 1855		2												*
Superfamily PTYCHOMPHALOIDEA Wenz 1938														
Family PTYCHOMPHALIDAE Wenz 1938														
Cryptaenia rotellaeformis (Dunker 1847**)**		2												*
Ptychomphalus caepa (Eudes-Deslongchamps 1849a**)**	2	5			14				1		5	1		*
Angulomphalus wehenkeli (Terquem & Piette 1865**)**		40	1											
Superfamily TROCHOIDEA Rafinesque 1815														
Family TURBINIDAE Rafinesque 1815														
Meiersia disarmata Monari _et al._ 2011		7												
Superfamily EUCYCLOIDEA Koken 1897														
Family EUCYCLIDAE Koken 1897														
Eucyclus sp.													1	
Family CIRRIDAE Cossmann 1916														
Spirocirrus weisi Monari _et al._ 2011		2												
Platyacra aff. _sinistrorsa_ (Terquem 1855**)**		2												
Subclass NERITIMORPHA Koken 1897														
Superfamily NERITOIDEA Rafinesque 1815														
Family NERIDOMIDAE Bandel 2008														
Neridomus liasina (Dunker 1844**)**		10												*
Neridomus cannabis (Terquem 1855**)**		5												*
Superfamily NERITOPSOIDEA Gray 1847														
Family uncertain														
Bandelopsis? cf. _exigua_ (Terquem 1855**)**		4												?
Bandelopsis? sp.		1												
Subclass CAENOGASTROPODA Cox 1960b														
Superfamily uncertain														

(continued)

TABLE 1. (Continued)

	Luxembourg Sandstone													Hettange-Grande
	Brouch			Hesperange	Bridel	Itzig	Altwies	Côte-d'Eich	Mamer	Burmerange	Steiford	Kopstal	Loc. unknown	
	a	b	c	Undifferentiated Hettangian										
Family PSEUDOMELANIIDAE Hoernes 1884														
***Pseudomelania inornata* (Terquem & Piette 1865)**		3												
***Bourguetia deshayesea* (Terquem 1855)**		6		1										*
***Bourguetia bipartita* sp. nov.**	2	73											1	
***Bourguetia? dubia* (Terquem 1855)**		2												*
***Torusanina* sp.**		1												
Family COELOSTYLINIDAE Cossmann 1908														
***Coelostylina paludinare* (Terquem 1855)**		4												*
***Trypanostylus?* sp.**		1												
Superfamily CAMPANILOIDEA Douvillé 1904														
Family AMPULLINIDAE Cossmann *in* Cossmann & Peyrot 1919														
***Globularia obtusa* (Deshayes 1839)**				2										*
***Globularia delsatei* sp. nov.**		1												
***Oonia feidtorum* sp. nov.**		2												
***Oonia haasi* sp. nov.**		4												
Superfamily PSEUDOZYGOPLEUROIDEA Wenz 1938														
Family ZYGOPLEURIDAE Wenz 1938														
***Jurazyga theodori* (Terquem 1855)**		1												*
Family PROTORCULIDAE Bandel 1991														
***Anulifera verrucosa* (Terquem 1855) comb. nov.**		25												*
***Anulifera* sp.**		1												
Superfamily LITTORINOIDEA Children 1834														
Family PURPUROIDEIDAE Guzhov 2004														
***Microschiza semiornata* (Münster *in* Goldfuss 1844)**	2	108	1	2	2	2	1						2	*
***Microschiza pauciornata* sp. nov.**	3	2												
?Superfamily STROMBOIDEA Rafinesque 1815														
?Family APORRHAIDAE Gray 1850														
***Siphonilda? terquemi* (Moore 1867a)**		1												*
NEOGASTROPODA														
Superfamily uncertain														
Family PURPURINIDAE Zittel 1895														
***Angularia?* sp.**		2												
***Angulariopsis nivernensis* Dareste de la Chavanne 1912**		1												
***Tretospira subangulata* (d'Orbigny 1850)**		11		1			2	2					1	*
***Tretospira* cf. *subangulata* (d'Orbigny 1850)**		1					1							
***Tretospira obliqua* (Terquem 1855) comb. nov.**		5			5		2	2						*
Subclass HETEROBRANCHIA Burmeister 1837														
Superfamily MATHILDOIDEA Dall 1889														
Family MATHILDIDAE Dall 1889														
***Tangarilda trinodulosa* (Martin 1860)**		1												
***Tangarilda darestei* sp. nov.**	1													

(continued)

TABLE 1. (Continued)

	Luxembourg Sandstone													Hettange-Grande
	Brouch			Hesperange	Bridel	Itzig	Altwies	Côte-d'Eich	Mamer	Burmerange	Steiford	Kopstal	Loc. unknown	
	a	b	c	Undifferentiated Hettangian										
***Tricarilda? jobae* (Terquem 1855)**		4												*
Family GORDENELLIDAE Gründel 2000														
***Brouchilda laevigata* gen. et sp. nov.**		2												
***Brouchilda mulleri* gen. et sp. nov.**		1												
***Turritelloidea? bockfielsensis* sp. nov.**		6												
?Superfamily MATHILDOIDEA Dall 1889														
Family uncertain														
***Gruendelifusus melusinae* gen. & sp. nov.**		2												
?Superfamily CIMOIDEA Warén 1993														
?Family CIMIDAE Warén 1993														
***Kaimella tenuilineata* gen. et sp. nov.**		4												
Superfamily ACTEONOIDEA d'Orbigny 1843														
Family CYLINDROBULLINIDAE Wenz 1938														
***Cylindrobullina inermis* (Terquem 1855)**		1												*
Family TUBIFERIDAE Cossmann 1895b														
***Striactaeonina buvignieri* (Terquem 1855)**		1												*
***Striactaeonina sinemuriensis* (Martin 1860)**	1													*

The list includes the Patellogastropoda, Vetigastropoda and Neritimorpha described by Monari *et al.* (2011), and the Caenogastropoda and Heterobranchia studied here. Asterisks mark species co-occurring at Hettange-Grande. a, *Psiloceras planorbis* Zone. b, *Schlotheimia angulata* Zone. c, undifferentiated Hettangian.

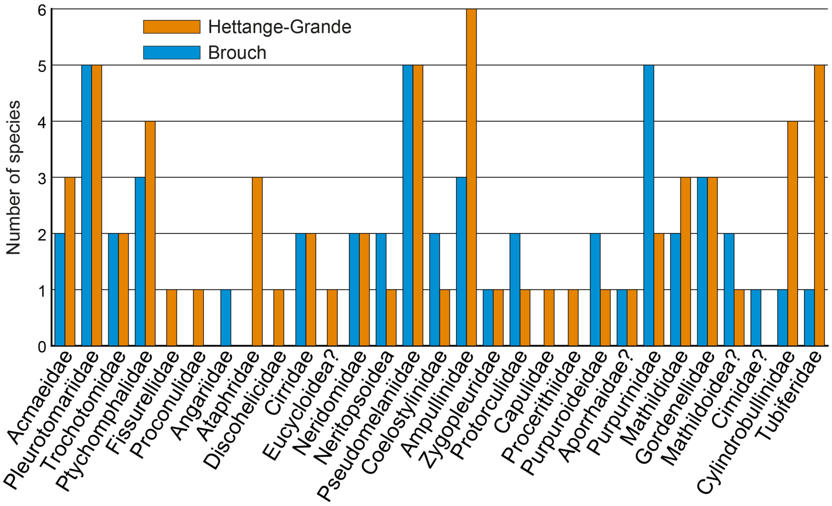

FIG. 29. Comparison of taxonomic composition at family level between the gastropod fauna from the *Schlotheimia angulata* Zone of Brouch and that from the upper Hettangian of Hettange-Grande described by Terquem (1855).

palaeogeographical and environmental changes had on this process.

The database includes the species known for the European epicontinental seas, the central part of western Tethys and the North African continental margin. Two stratigraphic intervals have been considered, namely Hettangian – lower Sinemurian and upper Sinemurian – Pliensbachian. The corresponding time spans are longer than those used in similar analyses based on other western Tethyan invertebrate groups such as, for example, ammonites (Dommergues *et al.* 2009) and belemnites (Neige *et al.* 2021). However, the quality of stratigraphic information in most of the data examined is not presently sufficient to provide greater detail. Moreover, the gastropod species generally have a fairly long stratigraphic range (one or two stages).

Two considerations justify the selection of these intervals. First, many Hettangian species (i.e. almost 30%) occur also in the lower Sinemurian, whereas only 12 out of 665 species present in the Hettangian and lower Sinemurian extend to the upper Sinemurian to Pliensbachian (i.e. 1% of *c.* 1400 species listed in the database). The second point concerns the geodynamic history of the western Tethys in the Early Jurassic. During this time, a tectonic extensional regime caused by the ongoing Neo-Tethyan rifting led to the dismemberment of extensive, shallow-water carbonate platform systems and the formation of a complex configuration of horsts and intervening basins where pelagic sedimentation took place (Bernoulli & Jenkyns 1974; Channel *et al.* 1979; D'Argenio *et al.* 1980; Santantonio 1993, 1994; Santantonio & Carminati 2011; Masetti *et al.* 2016; Jenkyns 2020). This event deeply changed the environmental conditions of the intra-Tethyan region, whereas the European epicontinental shelf was hardly affected. Although the timing of this event is diachronous, most of the Lower Jurassic gastropod-bearing pelagic limestones of the central part of western Tethys have a late Sinemurian to Pliensbachian age.

Sixteen OGUs have been identified for the Hettangian – early Sinemurian interval (Table 2) and 21 OGUs for the late Sinemurian – Pliensbachian interval (Table 3). The Grand-Duchy of Luxembourg has been considered part of the eastern Paris Basin.

RESULTS

Hettangian – early Sinemurian. The dataset consists of 665 species, of which 181 species are shared by two or more OGUs (Appendix S1). Two main clusters result from the cluster analysis, which correspond to the two main clades identified in the single maximum parsimony cladogram retained by the parsimony analysis (Fig. 30). They represent the faunas of the European epicontinental shelf and those of the intra-Tethyan carbonate platforms, respectively. According to the analysis, the faunas of the eastern High Atlas carbonate platform are closely related to those of the intra-Tethyan region and belong to the same main cluster/clade. Shared aspects in all the dendrograms are the northern Aquitanian basin at the root of the main cluster of the European shelf, and the presence of the following clusters: Mecsek–northern Germany, Rhone Basin–southern Paris Basin and Northern Calcareous Alps–Lombardy. However, the position of these clusters and the relationships between the OGUs in the respective main clusters change in relation to the coefficient of similarity used. The results of the cluster and parsimony analyses are confirmed by the ordination analysis

TABLE 2. OGUs identified for palaeobiogeographical analysis of Hettangian – early Sinemurian gastropods and references used to assemble the database.

Hettangian – early Sinemurian

OGU	Locality	Reference
Northern Aquitanian Basin	Vendée, Deux-Sevres	Cossmann (1895a, 1902, 1913), Fischer & Weber (1997), Guérin-Franiatte & Hanzo (2012), Pieroni *et al.* (2021), Cougnon & Gendry (2024)
Rhone Basin	Rhone, Mont d'Or, Haute-Savoie, Ardeche, Gard, Isere, Lozere, Ain, Saone-et-Loire, Jura, Doubs	d'Orbigny (1850, 1851–60); Martin (1860), Dumortier (1864, 1867), Henry (1876), Cossmann (1895a, 1913), Fischer & Weber (1997), Guérin-Franiatte & Hanzo (2012), pers. data (MV-RG-SM)
Southern Paris Basin	Niévre, Cher, Yonne, Cote d'Or, Haute-Saone, Haute-Marne	d'Orbigny (1850, 1851–60), Terquem (1855), Martin (1859, 1860), Dumortier (1864, 1867), Eudes-Deslongchamps (1864), Cossmann (1895a, 1907a), Thevenin (1907), Dareste de la Chavanne (1912), Fischer & Weber (1997), Guérin-Franiatte & Hanzo (2012), Valentini & Monari (2021), pers. obs. (MV-SM)
Eastern Paris Basin	Luxembourg, Meuse, Moselle, Meurthe-et-Moselle, Ardenne	Eudes-Deslongchamps (1849a), Deshayes (1839–1857), d'Orbigny (1851–60), Chapuis & Dewalque (1854), Terquem (1855), Piette (1856a), Terquem & Piette (1865), Cossmann (1895a, 1913), Joly (1907, 1936), Haber (1932), Meier & Meiers (1988), Fischer & Weber (1997), Monari *et al.* (2011), Gründel (2012), this paper and pers. data (MV-RG-SM)
SW England – S Wales	Glamorganshire (South Wales), Dorsetshire, Worcestershire, Gloucestershire (south-western England)	Sowerby (1818–21), Tawney (1866), Moore (1867a), Tate (1870, 1871), McDonald & Trueman (1921), Haber (1932), Melville (1956), Lindström & Peel (2010), Todd & Munt (2010), Munt *et al.* (2019)
Cleveland Basin	Redcar, Milligton, Cliff, Marske Bay, Leppington, Robin Hood's Bay, Foxton, Northallerton (Yorkshire)	Tate & Blake (1876), McDonald & Trueman (1921), Gründel *et al.* (2011b), Munt *et al.* (2019)
Southern Germany	Gmünd, Trossingen, Göggingen, Ostdorf, Balingen, Schanbach, Böblingen, Unterböbingen, Oberbettringen, Vaihingen, Mögglingen, Ofterdingen, Hechingen (Baden-Württemberg), Bamberg (Franconia)	Quenstedt (1852, 1856, 1865–67, 1881–1884), Sieberer (1907), Brösamlen (1909), Haber (1932), Kuhn (1934), Hägele (1997), Gründel (2003)
Northern Germany	Halberstadt (Sassonia-Anhalt)	Dunker (1846, 1847), Bronn (1851–52), Quenstedt (1881–84), Cossmann (1895b), Haber (1932), Huckriede (1967), Gründel (2010)
Mecsek Mountains	Pécsbánya (southern Hungary)	Nagy (1970), Szente (1992)
Northern Calcareous Alps	Hochfelln (Bavaria, southern Germany), Achensee (Tyrol, Austria)	Neumayr (1879), Clark (1887), Ammon (1893), Seuß *et al.* (2005), pers. obs. (RG-SM)
Lombardy	Albenza Mountain, Saltrio, Val Solda	Parona (1894), Bistram (1903), Sacchi Vialli (1964), Conti (1954), Berini (1957), Gaetani (1970)
Tuscany	Pisano Mountain, Apuane Alps, La Spezia, Gerfalco	Canavari (1882, 1888), Simonelli (1883), Fucini (1895, 1906), Arthaber (1935), Pieroni *et al.* (2021)
Central Apennine	Umbria, Marche, Abruzzo	Canavari (1879, 1886), Parona (1883), Bellini (1905), Haber (1932), Conti & Monari (1995), Fischer *et al.* (2002), pers. obs. (SM)
Trapanese Platform	Rocca Busambra (north-western Sicily)	Gemmellaro (1878, 1879), De Gregorio (1886), Carapezza & Tagliarini (1895), Tagliarini (1895), Fucini (1913), Pieroni *et al.* (2021), pers. obs. (SM)
Calabrian Arc	Peloritani Mountains (north-eastern Sicily), Rossano (northern Calabria)	Di Stefano (1887), Greco (1893), Onetti (1915), Lentini (1973), Pieroni *et al.* (2021), pers. obs. (SM)
Eastern High Atlas	El-Hameïret, Nord du jbel Araira, Rosfet-er-Rjem, Daïet-el-Hamir, jbel Tamsahelt, jbel El-Haïmer, Hassi-Khriouia	Bourrouilh (1966), Pieroni *et al.* (2021)

OGU, operational geographical unit.

TABLE 3. OGUs identified for palaeobiogeographical analysis of late Sinemurian – Pliensbachian gastropods and references used to assemble the database.

Late Sinemurian – Pliensbachian		
OGU	**Locality**	**Reference**
Northern Aquitanian Basin	Vendée	Cossmann (1895a, 1907b, 1915), Fischer & Weber (1997)
NW Paris Basin	Fontaine-Etoupefour, May-sur-Orne, Landes-sur-Ajon, Feuguerolles (Calvados)	Eudes-Deslongchamps (1842a, 1842b, 1842c, 1842d, 1842e, 1842f, 1842g, 1849a, 1849b), d'Orbigny (1851–60), Eudes-Deslongchamps (1860, 1864, 1866), Dumortier (1869), Cossmann (1895a, 1909, 1913, 1916), Fischer (1961), Fischer & Weber (1997), Gründel (2007b)
Southern Paris Basin	Haute Saone, Haute Marne, Cote d'Or, Cher	d'Orbigny (1850, 1851–60), Dumortier (1867, 1869), Cossmann (1913), Fischer & Weber (1997)
Rhone Basin	Rhone, Ain, Isere, Gard, Ardeche, Lozere, Saone-et-Loire, Jura	d'Orbigny (1851–60), Dumortier (1857, 1867, 1869), Cossmann (1895a, 1908, 1913, 1916), Fischer & Weber (1997), Gatto *et al.* (2015b)
Southern England	Somersetshire, Dorset, Gloucestershire, Leicestershire, Lincolnshire, Northamptonshire	Moore (1867b), Tate (1870, 1871, 1875), Wilson (1887), Richardson (1918), McDonald & Trueman (1921), Cox (1928, 1936, 1955), Melville (1956), Hickman & McLean (1990), Lindström & Peel (2010), Todd & Munt (2010), Gründel *et al.* (2011b), Monari & Gatto (2013), Munt *et al.* (2019)
Cleveland Basin	Hawsker, Eston, Upleatham, Belman Bank, Hob Hill, Skinningrove, Northcote, Hutton Mines, Huntcliff, Staithes, Robin Hood's Bay, Maske Mill, Saltburn, Coathan, Wood End, Ayton, Chop Gate, Bilsdale, Hummersea, Rockcliff, Down Cliff, Hawsker, Upsall, Kettleness, Grosmont (Yorkshire)	Tate & Blake (1876), McDonald & Trueman (1921), Young & Bird (1828), Gründel *et al.* (2011b), Munt *et al.* (2019)
Swabia	Endingen, Reutlingen, Eislingen, Maitis, Mögglingen, Kirchheim/Teck, Hechingen, Hinterweiler, Geislingen, Balingen, Weidach, Göppingen, Unterböbingen, Nehren, Iggingen, Salach, Erzingen, Aalen, Westhausen, Ostdorf (Baden-Württemberg)	Zieten (1832), Oppel (1856), Quenstedt (1852, 1856, 1881–84), Sieberer (1907), Brösamlen (1909), Hägele (1997), Gründel (2007a)
Franconia	Berg (Neumarkt), Kalchreuth, Buttenheim, Stauf, Neumarkt, Bamberg, Amberg, Dörlbach, Banz (Bamberg), Heidenheim, Trimeusel, Creez (Bayreuth), Ehenfeld, Thurnau, Unterstürmig, Sendelbach (Bamberg), Staffelstein, Marloffstein, Burgkundstadt, Lentersheim, Lichtenfels, Prezfels, Altdorf, Schnaittach	Zieten (1832), Goldfuss (1844), Schlosser (1901), Sieberer (1907), Kuhn (1935, 1936, 1938), Schnittmann (1966), Nützel & Kiessling (1997), Nützel (1998, 2008), Gründel & Nützel (1998, 2015), Gründel (1999b, 2011, 2014), Nützel & Hornung (2002), Nützel & Gründel (2007, 2015)
NW Germany	Herford (Renania-Westfalia); Markoldendorf, Hainberges, Goslar, Wenzen, Göttingen, Hambühren, Schneflingen (Lower Saxony); Hildesheim, Hüttenberg (Hesse)	Roemer (1836, 1839), Koch & Dunker (1837), Dunker (1847), Brauns (1871), Sieberer (1907), Schröder (1995), Hägele (1997), Gründel (1999c, 1999d), Schubert (2004), Gründel (2005), Schubert *et al.* (2008)
Western Pomerania	Usedom, Grimmen, Zarrenthin	Schröder (1995), Gründel (1997, 1999a, 1999b, 2007c), Gründel & Buchholz (1999), Gründel & Koppka (2007), Buchholz (2012), Nützel & Gründel (2015)
Northern Calcareous Alps	Hierlatz, Schafberg (Austria)	Reuss (1852), Hauer (1853), Stoliczka (1861), Vörös *et al.* (2003), Szabó (2008, 2009, 2016, 2018, 2019), Gatto & Monari (2010), Gatto *et al.* (2015a), pers. obs. (SM)
Bakony Mountains	Sümeg, Szentgál, Herend, Hárskút, Lókút, Eplény, Zirc, Tés	Böckh (1874), Szabó (1979, 1980, 1981, 1982, 1983, 1984, 1995, 2008, 2009, 2016), Gatto & Monari (2010), Gatto *et al.* (2015a), pers. obs. (SM)

(continued)

TABLE 3. (Continued)

Late Sinemurian – Pliensbachian

OGU	Locality	Reference
Belluno Basin	Vedana (Venetian Alps, northern Italy)	De Toni (1912), Haber (1932), Gatto & Monari (2010)
Trento Platform	Venetian Alps (northern Italy)	Schauroth (1865), Benecke (1866), Lepsius (1878), Böhm (1884), Tausch (1890), Dal Piaz (1909), Fabiani (1911)
Umbria-Marche	Catria Mountain, Sasso di Pale, Nerone Mountain, Cimitelle Mountain, Martani Mountains, Montecelio (Umbria-Marche Apennine)	Conti & Monari (1995), pers. obs. (SM)
Sicani Mountains	Chiusa-Sclafani, Giuliana (south-western Sicily)	Gemmellaro (1874), Conti *et al.* (2007)
Calabrian Arc	Rocche Rosse, Ziretto Mountain, Santa Teresa di Riva (Peloritani Mountains, north-eastern Sicily)	Gemmellaro (1911), Maugeri Patanè (1924), Monari *et al.* (2008), Gatto & Monari (2010), pers. obs. (SM)
Eastern Tellian Atlas	Guelma (north-eastern Algeria)	Dareste de la Chavanne (1920), pers. obs. (SM)
Eastern High Atlas	jbel Bou-Mokhta, jbel Bou Dahar (Morocco)	Gardet & Gérard (1946), Dubar (1948), Bourrouilh (1966)
Western Pontides	Bilecik area (north-western Turkey)	Conti & Monari (1991)
Lusitanian Basin	S. Pedro de Moel, Coimbra and Peniche areas (Portugal)	Sharpe (1850), Böhm (1901), Choffat (1903), Fischer & Palain (1971), Mouterde & Rocha (1981), Vitón *et al.* (2020)

OGU, operational geographical unit.

(Fig. 31). In the scatter plot obtained with the Dice coefficient, the faunas of the European shelf fall in the field of negative values of principal coordinate 1 (PCo1), while those of the intra-Tethyan carbonate platforms fall in the field of positive values. The opposite occurs in the scatter plot based on the Raup–Crick coefficient. Most probably, PCo1 represents the palaeoenvironmental conditions reflected by the different facies. The network analysis further corroborates the identification of the two main OGU aggregations (Fig. 32A) and shows that they are connected through only five species.

The Raup–Crick dendrograms recover three relatively distinct faunal groups in the European epicontinental region: the faunas of southern France (Rhone Basin and southern Paris Basin), those distributed along a belt extending from eastern France to Germany and Mecsek (eastern Paris Basin, southern Germany, northern Germany and Mecsek), and the faunas of the England basins (SW England–South Wales and Cleveland Basin). The northern Aquitanian basin is at the root of the European shelf main cluster whereas in the parsimony analysis it forms a terminal clade with the faunas of the Rhone Basin. This contrast depends on the different computational algorithms used by the two methods. Analysis of both the character (species) and apomorphy distribution in the cladogram from the parsimony analysis shows that the relationship between the northern Aquitanian basin and the Rhone Basin and the position of this clade are almost fully determined by reversals (i.e. by disappearance of species rather than by species co-occurrence).

In the Raup–Crick dendrogram, the Mecsek–northern Germany cluster is in terminal position and forms a larger cluster with the southern Germany and eastern Paris Basin. Instead, in the Dice dendrogram the Mecsek–northern Germany cluster has a basal position in the main cluster of the European shelf. This position is probably determined by scarcity of data, given that the faunas of northern Germany and Mecsek are those with the smallest number of species overall.

The position of the eastern Paris Basin fauna is noteworthy. In the Raup–Crick dendrograms, it is included in a poorly supported cluster with the faunas of southern Germany, northern Germany and Mecsek. Instead, the Dice dendrogram and the minimum spanning tree of the corresponding ordination analysis show that the fauna of the eastern Paris Basin is more closely linked to those of southern France (Rhone Basin and southern Paris Basin). In the parsimony analysis cladogram, it is also included in the clade of the French basins. The fluctuating position of the eastern Paris Basin could reflect the fact that this

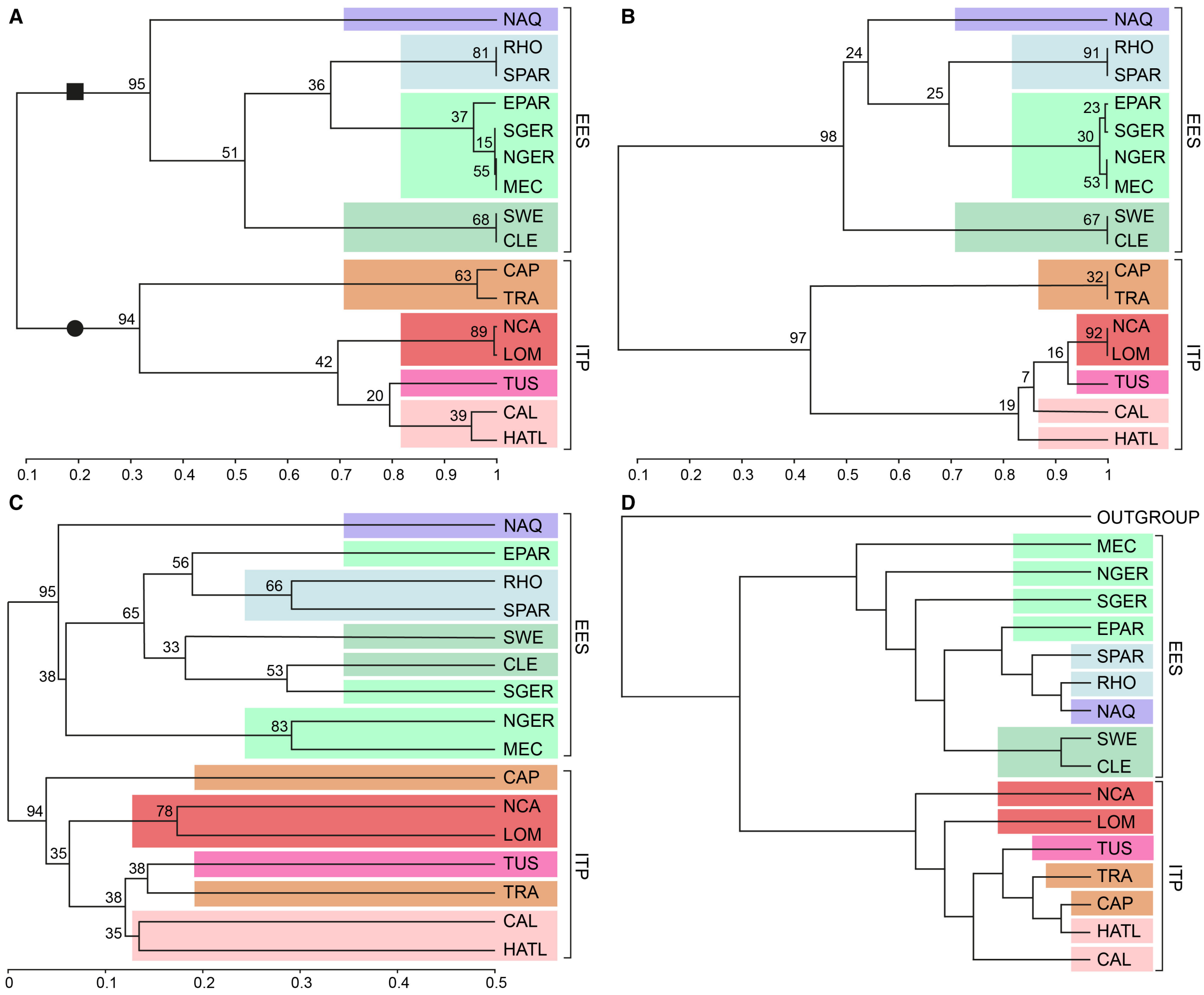

FIG. 30. Results of cluster analysis and parsimony analysis of endemicity (PAE) applied to the Hettangian – early Sinemurian database. A–C, dendrograms based on: A, the matrix including singletons and Raup–Crick similarity coefficient, cophenetic correlation coefficient 0.825; B, the matrix without singletons and Raup–Crick similarity coefficient, cophenetic correlation coefficient 0.826; C, the matrix including singletons and Dice similarity coefficient, cophenetic correlation coefficient 0.883; support values of branches based on 1000 bootstrap replicates. D, single maximum parsimony tree obtained from PAE (score = 498, consistency index = 0.3655, retention index = 0.8719). Colours indicate the clusters identified in the Raup–Crick dendrogram based on the dataset with singletons. Symbols mark the major clusters and serve to facilitate comparison with principal coordinates analysis scatter plots and palaeogeographical maps. *Operational geographical unit abbreviations*: CAL, Calabrian Arc; CAP, central Apennine; CLE, Cleveland Basin; EPAR, eastern Paris Basin; HATL, Eastern High Atlas; LOM, Lombardy; MEC, Mecsek Mountains; NAQ, northern Aquitanian Basin; NCA, Northern Calcareous Alps; NGER, northern Germany; RHO, Rhone Basin; SGER, southern Germany; SPAR, southern Paris Basin; SWE, SW England–S Wales; TRA, Trapanese Platform; TUS, Tuscany; EES, European epicontinental shelf; ITP, intra-Tethyan carbonate platforms including the North African margin.

OGU was intermediate between the German and southern France basins and probably acted as an area of exchange. This interpretation finds support also in the network diagram, in which the eastern Paris Basin has an almost central position in the subnetwork of the European shelf and is surrounded by the other French basins and the southern Germany Basin as satellites. The cluster composed by SW England–South Wales and Cleveland Basin is well supported in the Raup–Crick dendrograms. The close relationships between these faunas are less clear in the Dice dendrogram. However, the minimum spanning tree of the corresponding ordination analysis shows that they are directly connected.

The main cluster comprising the faunas of the intra-Tethyan and North African carbonate platforms has the same general structure in all of the cluster analysis

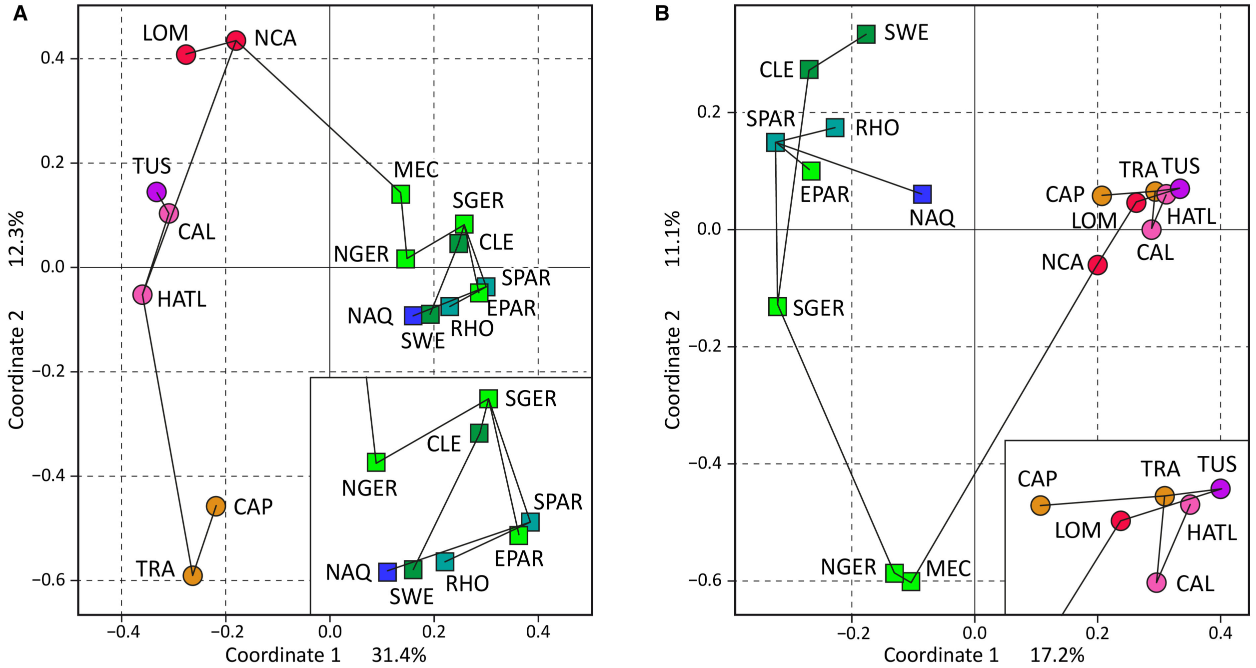

FIG. 31. Scatter plots and minimum spanning tree resulting from the principal coordinates analysis applied to the Hettangian – early Sinemurian database with singletons (insets show details of areas with crowded datapoints). A, Raup–Crick similarity coefficient. B, Dice similarity coefficient. Operational geographical unit abbreviations, symbols and colours as in Figure 30.

dendrograms. The Dice dendrogram differs from the Raup–Crick dendrogram only in the position of the Trapanese Platform, which does not form a distinct cluster with the Central Apennine. In contrast, a direct link between these OGUs is evidenced by the minimum spanning tree of the corresponding PCoA. This cluster has a somewhat high support value in the Raup–Crick dendrogram based on the complete dataset (with singletons) and is also present, in the same position, in the Raup–Crick dendrogram based on the reduced dataset (without singletons), albeit with a rather low support value. The relationship between the faunas of the Northern Calcareous Alps and those of Lombardy is quite robust, this cluster being present and well-supported in all dendrograms. The Eastern High Atlas–Calabrian Arc cluster is also present both in the Dice dendrogram and in the Raup–Crick dendrogram based on the complete dataset, whereas the Raup–Crick dendrogram based on the reduced matrix shows a pectinate shape. Other relationships are not well-supported. This is probably due to the widespread distribution of many species, which tends to equalise the similarity among OGUs, making the results of the cluster analysis unstable. The cladogram from the parsimony analysis of the intra-Tethyan main clade is also uninformative. Figure 30D shows a fully pectinate topology, which is rather different from that obtained in the cluster analysis. Assuming that the distribution of faunas in this region was regulated largely by dispersal rather than vicariance, this method does not seem suitable in this case to correctly discriminate the internal relationships.

Late Sinemurian – Pliensbachian. The dataset referred to this time span consists of 736 species, of which 145 are present in at least two OGUs (Appendix S1). The parsimony analysis retained two maximum parsimony trees. In all dendrograms, in the strict consensus tree and in the network graph a third main group appears in addition to the two groups already present in the Hettangian – early Sinemurian time span (Figs 32, 33). This group represents the faunas inhabiting the areas with pelagic deposition that originated from the drowning of the intra-Tethyan carbonate platforms. The subdivision into three main groups is also well highlighted by the PCoA (Fig. 34). As for the Hettangian – early Sinemurian interval, PCo1 probably represents the set of environmental parameters reflected by the differences in facies.

The cluster and principal coordinates analyses (Figs 33A–C, 34) show that the European shelf main cluster is subdivided into three distinct subclusters corresponding to the faunas of the French basins, German basins and English basins, respectively. The only exception concerns the position of Swabia in the Raup–Crick dendrogram based on the reduced dataset. The Raup–Crick dendrogram based on the complete dataset differs from the Dice dendrogram and cladogram obtained by the parsimony analysis mainly in the position of the

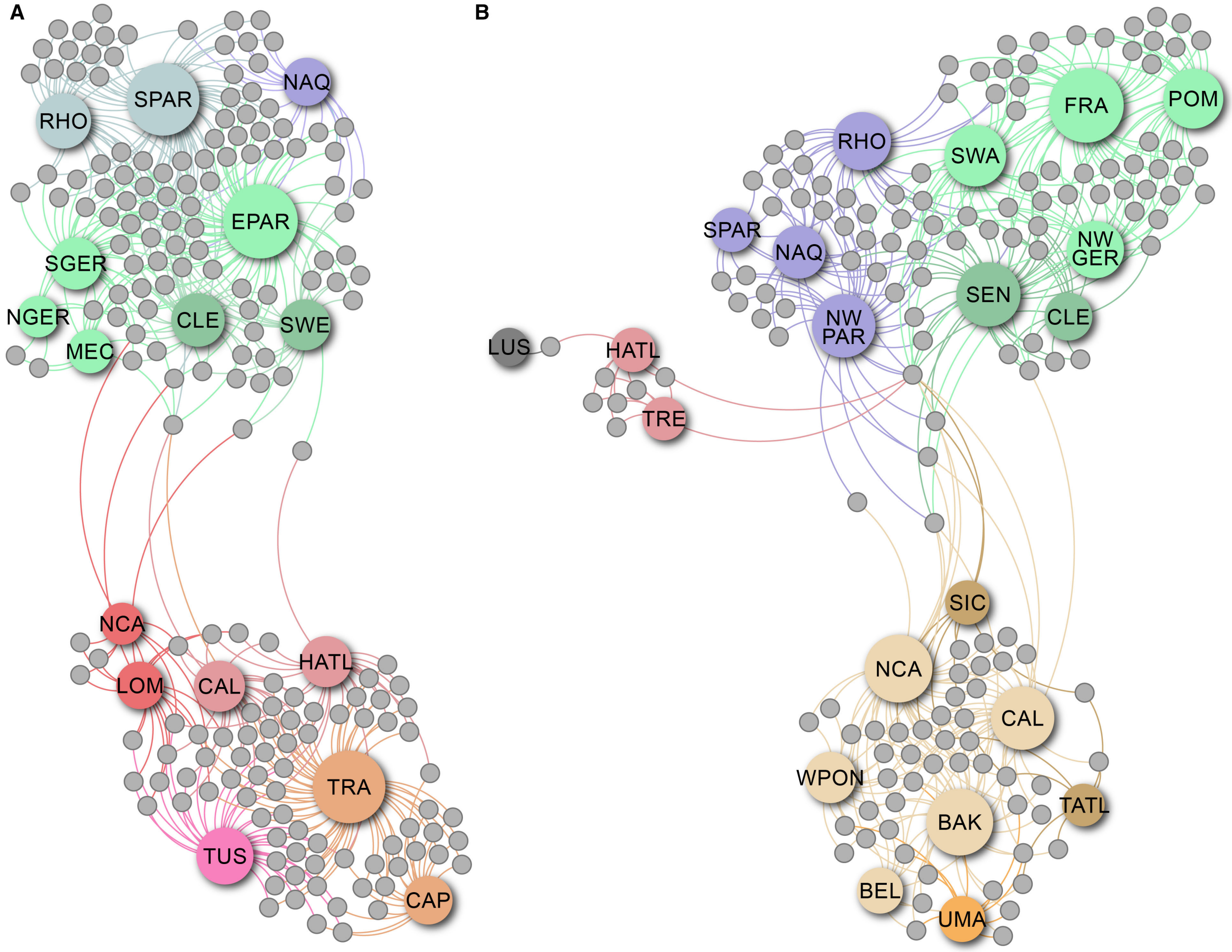

FIG. 32. Bipartite network diagrams generated using the Gephi software (Bastian *et al.* 2009) illustrating the connections between the operational geographical units (OGUs; coloured circles with shadow) in the two time slices considered. The size of the OGU circles is proportional to the number of species present. Small grey circles without shadow are species shared between two or more OGUs. A, Hettangian – early Sinemurian (OGU abbreviations and colours as in Fig. 30). B, late Sinemurian – Pliensbachian (OGU abbreviations and colours as in Fig. 33).

faunas of the German basins and in minor differences within the cluster of the French basins, where the southern Paris Basin clusters with the north-western Paris Basin. Instead, in the Dice dendrogram, the southern Paris Basin is in a basal position. This is presumably determined by the unbalanced distribution of the data, the southern Paris Basin having the smallest number of species among the faunas of the European shelf. The network graph also shows that the main cluster of the European shelf can be subdivided in three groups represented by the French, English and German basins, respectively, even if they do not form well-defined subclusters (Fig. 32B).

The parsimony analysis retained two maximum parsimony trees, and the consensus (Fig. 33D) shows the same basic tripartition, but the faunas of the French basins form a grade at the root of the European shelf clade. The German clade has the same topology as the corresponding cluster in the Dice dendrogram. Both show a close relationship between the Franconia and western Pomerania faunas. The Raup–Crick dendrogram based on the reduced matrix does not show this cluster and Swabia is more strictly connected to the England basins than to the rest of Germany. This relationship is not easily explained. The Raup–Crick dendrogram based on the complete dataset also differs from the Dice dendrogram and from the cladogram in the parsimony analysis in lacking a strict connection between Franconia and western Pomerania. However, this part of both Raup–Crick dendrograms is marked by low support values. In addition, the minimum spanning tree of the ordination analysis based on the Raup–Crick coefficient is similar to that obtained using the Dice coefficient, and both show the affinity of the Franconia faunas with western Pomerania faunas, as

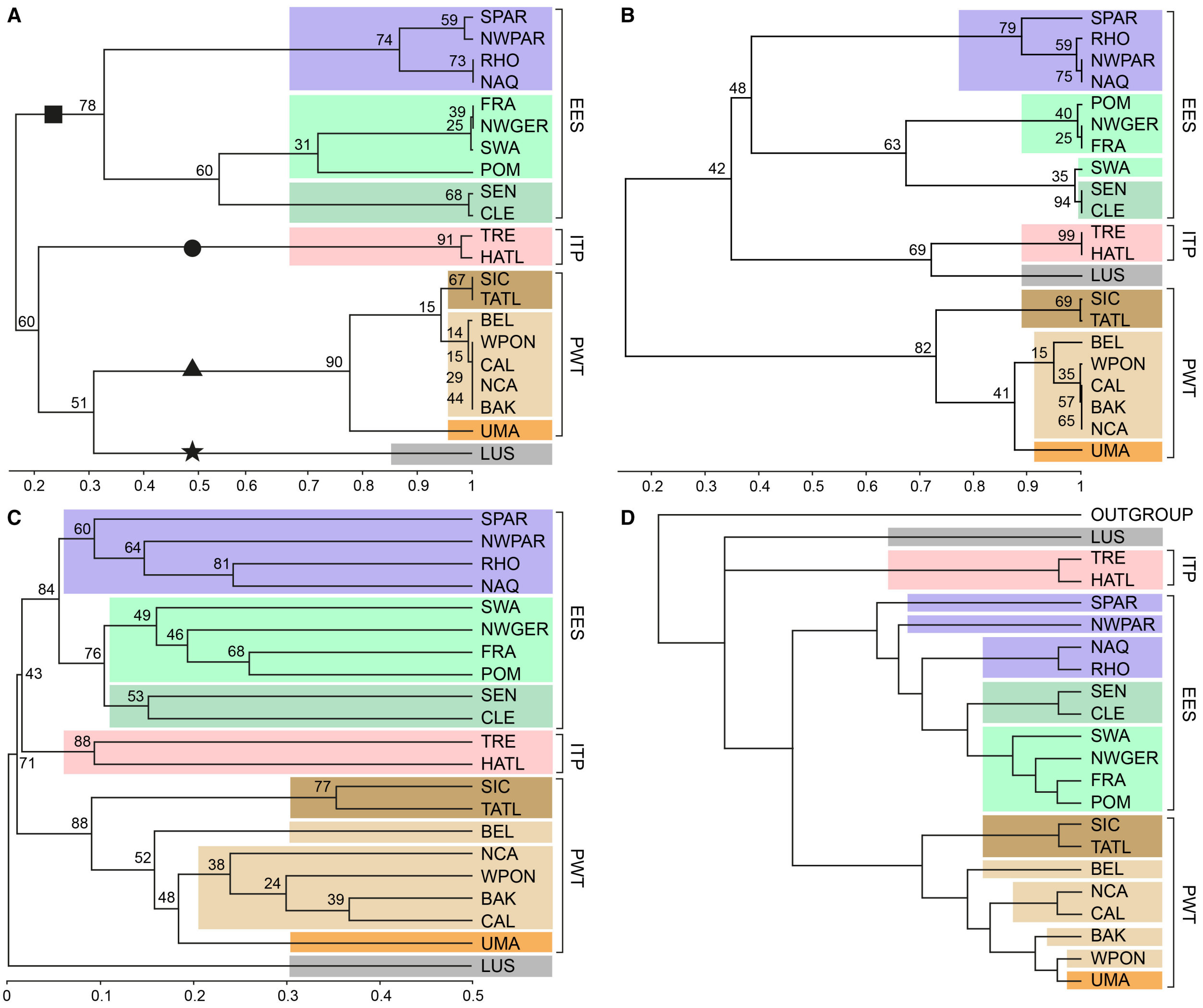

FIG. 33. Results of cluster analysis and parsimony analysis of endemicity (PAE) applied to the late Sinemurian – Pliensbachian database. A–C, dendrogram based on: A, the matrix with singletons and Raup–Crick similarity coefficient, cophenetic correlation coefficient 0.807; B, the matrix without singletons and Raup–Crick similarity coefficient, cophenetic correlation coefficient 0.836; C, Dice coefficient, cophenetic correlation coefficient 0.916; support values of branches based on 1000 bootstrap replicates. D, strict consensus of two maximum parsimony trees retained by PAE (score = 411, consistency index = 0.3528, retention index = 0.8991). Colours indicate the clusters identified in the Raup–Crick dendrogram based on the dataset with singletons. Symbols mark the major clusters and serve to facilitate comparison with principal coordinates analysis (PcoA) scatter plots and palaeogeographical maps. *Operational geographical unit abbreviations*: BAK, Bakony Mountains; BEL, Belluno Basin; CAL, Calabrian Arc; CLE, Cleveland Basin; FRA, Franconia; HATL, Eastern High Atlas; LUS, Lusitanian Basin; NAQ, northern Aquitanian Basin; NCA, Northern Calcareous Alps; NWGER, northwestern Germany; NWPAR, northwestern Paris Basin; POM, Western Pomerania; RHO, Rhone Basin; SEN, Southern England; SIC, Sicani Mountains; SPAR, southern Paris Basin; SWA, Swabia; TATL, eastern Tellian Atlas; TRE, Trento Platform; UMA, Umbria-Marche; WPON, Western Pontides; EES, European epicontinental shelf; ITP, intra-Tethyan and North African carbonate platforms; PWT, intra-Tethyan pelagic deposits.

suggested also by the network graph. In this case, the Dice dendrogram seems to represent the probable relationships within the German cluster better than the Raup–Crick dendrograms.

The cluster comprising the gastropod faunas of the western Tethyan pelagic facies is well supported in all dendrograms, as also demonstrated by the rather tight distribution of the respective OGUs in the scatter plots of the PCoA (Fig. 34). The dendrograms and the strict consensus tree from the parsimony analysis show different and poorly supported internal relationships between these OGUs. The only sufficiently supported cluster recovered in all dendrograms is the one including the faunas of the Sicani Mountains and of the eastern Tellian Atlas. The

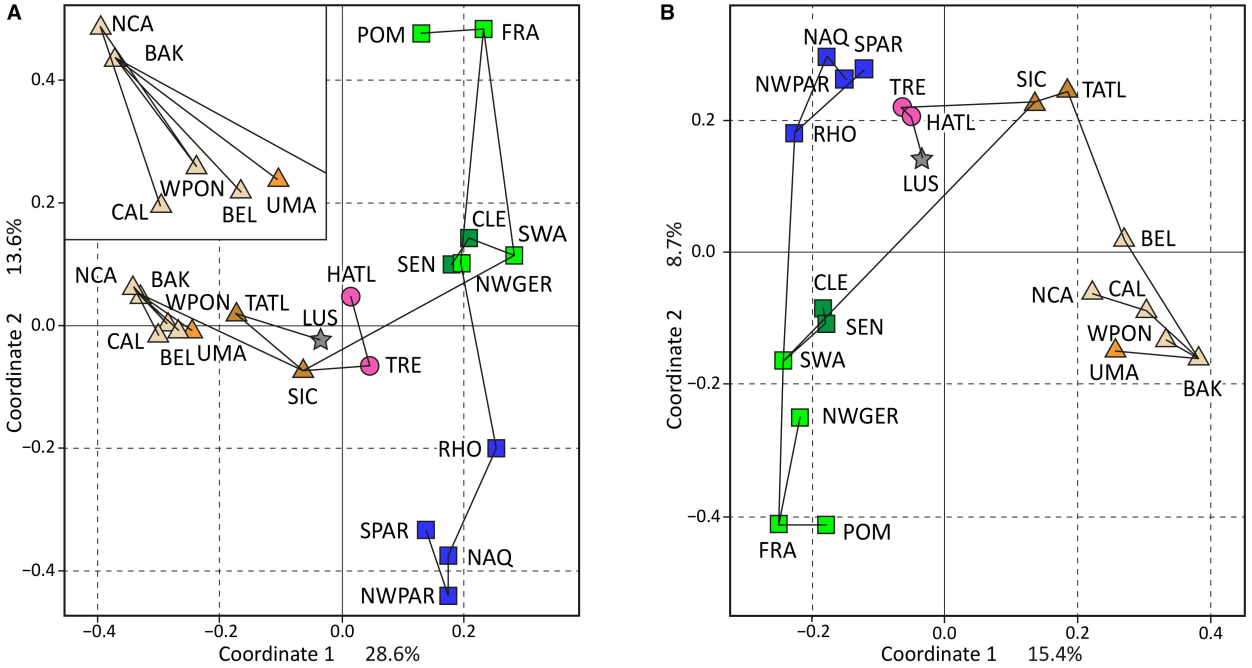

FIG. 34. Scatter plots and minimum spanning tree resulting from the principal coordinates analysis applied to the late Sinemurian – Pliensbachian database including singletons. A, Raup–Crick similarity coefficient. Inset shows detail of area with crowded datapoints. B, Dice similarity coefficient. Operational geographical unit abbreviations, symbols and colours as in Figure 33.

network diagram also fails to show any structure within this subnetwork. However, the principal coordinates scatter plots seem to show a weak differentiation of these faunas along PCo1.

The fauna of the Trento Platform is the only OGU representing the intra-Tethyan carbonate platforms in the database for the late Sinemurian – Pliensbachian time span. The analysis shows its close relationship with the fauna of the Eastern High Atlas. In the Raup–Crick dendrogram based on the complete matrix this cluster is linked to the main cluster representing the faunas of the western Tethyan pelagic facies. The minimum spanning trees show the same structure. In contrast, the Dice dendrogram and the Raup–Crick dendrogram based on the dataset without singletons show this cluster to be related to the faunas of the European shelf. From the network graph it is clear that this cluster is connected to the other two through a single common species, and this may explain the mismatch in the multivariate analysis. The parsimony analysis is not indicative because the relationship between the clade of the carbonate platforms and the other two main clades is unresolved.

Finally, the Lusitanian basin is represented by only nine species, eight of which are endemic. This explains its position at the root of the Dice dendrograms and probably also of the parsimony analysis cladogram. Its connection with the Eastern High Atlas shown by the minimum spanning tree of the Dice PCoA and by the network analysis is determined only by the co-occurrence of a single species, *Bohemiola exilis*. Although poorly supported, this link could be reasonable from a palaeogeographical point of view because the Eastern High Atlas was the westernmost among the considered OGUs and presumably connected to the proto-Atlantic region.

Interpretation of the analysis

Our investigation shows that the distribution of the gastropods at the beginning of the Jurassic reflects the subdivision of the western Tethys into two distinct sectors distinguished by different environmental conditions, depositional processes and geodynamic histories: the European epicontinental shelf characterized by a mixed carbonate and siliciclastic sedimentation, and the central part of the western Tethys, more or less corresponding to the intertropical belt, where a vast system of carbonate platforms extended to the North African margin (Fig. 35). During the Hettangian and early Sinemurian, several areas of endemism began to emerge within the European shelf. They correspond to the basins of southern France, the belt extending from the eastern part of the Paris Basin to the Germany and Mecsek, and the English basins ranging from South Wales and SW England to Yorkshire. The analysis suggests that the eastern part of the Paris Basin, although characterized by gastropod

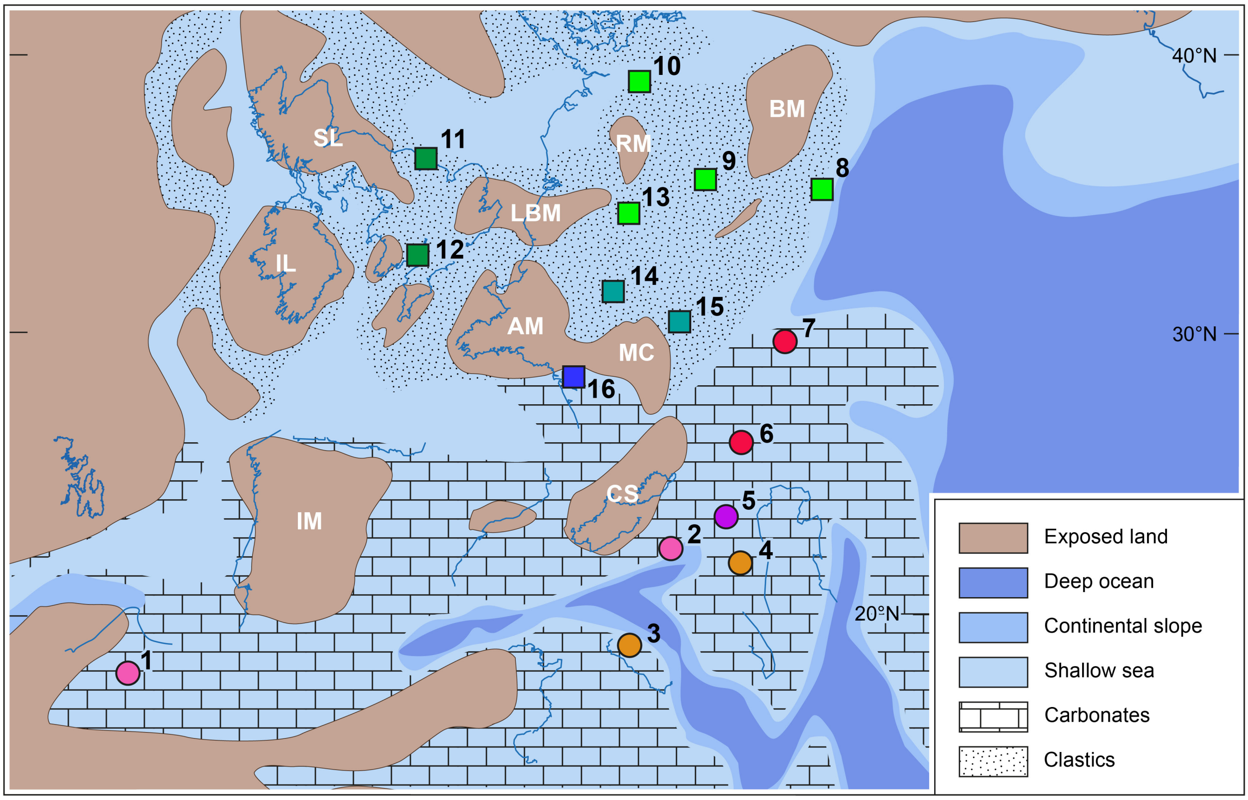

FIG. 35. Palaeogeographical map of the Hettangian – early Sinemurian interval showing the distribution of the operational geographical units listed in Table 2. Symbols and colours as in Figure 30. 1, Eastern High Atlas. 2, Calabrian Arc. 3, Trapanese Zone. 4, Central Apennine. 5, Tuscany. 6, Lombardy. 7, Northern Calcareous Alps. 8, Mecsek Mountains. 9, southern Germany. 10, northern Germany. 11, Cleveland Basin. 12, SW England–S Wales. 13, eastern Paris Basin. 14, southern Paris Basin. 15, Rhone Basin. 16, northern Aquitanian Basin. *Abbreviations:* AM, Armorican Massif; BM, Bohemian Massif; CS, Corsica–Sardinia; IL, Irish Landmass; IM, Iberian Massif; LBM, London–Brabant Massif; MC, Massif Central; RM, Rhenish Massif; SL, Scottish landmass. Base map redrawn and modified from Scotese & Schettino (2017).

faunas more similar to those of Germany than to southern France, constituted an exchange zone between these two adjacent areas. The gastropod faunas of the England basins were relatively distinct from those of the other areas of western Europe, although subject to faunal exchanges with both Germany and France. The Cleveland Basin seems to have played a greater role than the SW England and southern Wales regions in the faunal relationships with the German basins. Data concerning the gastropods of the Aquitanian basin are available only for its northern part. The analysis shows that the fauna of this region was different from the other western European faunas, although a few species occurred also in the basins of the southern France.

The three areas of endemism in the European shelf, which in the Hettangian and early Sinemurian were poorly differentiated, became distinct during the late Sinemurian and Pliensbachian. They correspond to the French, German and English basins, respectively (Fig. 36). Compared with the previous time interval, the fauna of the northern Aquitanian Basin strengthened its connection with those of the Rhone Basin. The faunas of the English basins also became more distinct and the affinities between the faunas of Southern England and those of Cleveland more defined. In contrast to the preceding interval, during which the English faunas maintained relationships with those of both the French and German basins, in the late Sinemurian to Pliensbachian interval they exchanged preferentially with the faunas of Germany.

The Hettangian – early Sinemurian gastropod faunas of the intra-Tethyan carbonate platforms are somewhat similar to each other. Distinct areas of endemism in this sector are not clearly recognizable, except for a separation between the faunas of the northern platforms (Northern Calcareous Alps and Southern Alps), and those of the other, southernmost platforms. This could indicate the existence of a latitudinal gradient controlling the distribution of gastropods. In contrast, despite their considerable palaeogeographic distance, the Eastern High Atlas and the

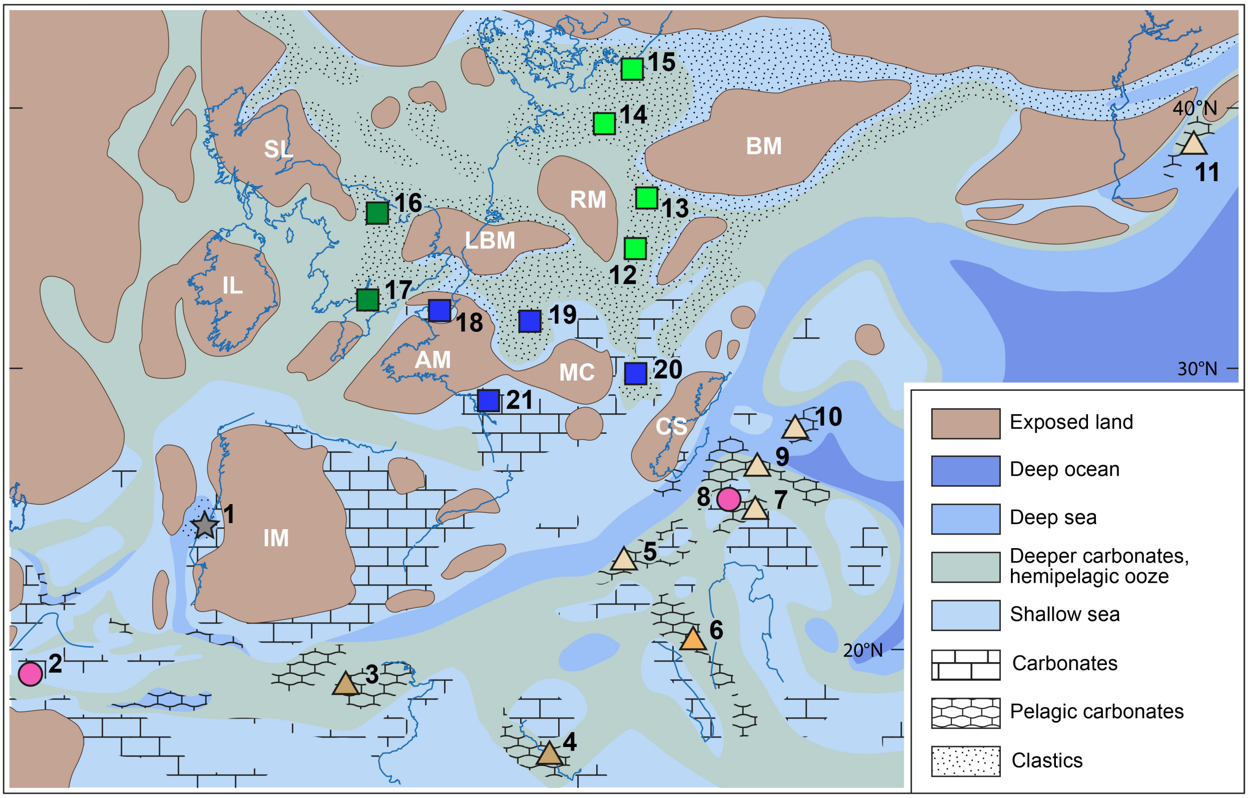

FIG. 36. Palaeogeographical map for the late Sinemurian to Pliensbachian interval showing the distribution of the operational geographical units (OGUs) listed in Table 3. Symbols and colours as in Figure 33. 1, Lusitanian Basin. 2, Eastern High Atlas. 3, eastern Tellian Atlas. 4, Sicani Mountains. 5, Calabrian Arc. 6, Umbria-Marche. 7, Belluno Basin. 8, Trento Platform. 9, Bakony Mountains. 10, Northern Calcareous Alps. 11, Western Pontides. 12, Swabia. 13, Franconia. 14, northwestern Germany. 15, Western Pomerania. 16, Cleveland Basin. 17, Southern England. 18, northwestern Paris Basin. 19, southern Paris Basin. 20, Rhone Basin. 21, northern Aquitanian Basin. Acronyms of exposed lands as in Figure 35. Base map redrawn and modified from Dercourt *et al.* (2000).

intra-Tethyan carbonate platforms show evident faunal similarities that indicate a strong facies control on the distribution of the gastropods.

As mentioned earlier, during the Early Jurassic large parts of the carbonate platforms of the central region of the western Tethys were progressively drowned as an effect of the Neo-Tethyan rifting. This event clearly had an influence on the biogeographical and evolutionary history of the western Tethyan gastropod faunas and may have modulated the Early Jurassic recovery in this region. While the gastropod faunas of the still active carbonate platforms (e.g. Trento Platform) and of the European epicontinental region were derived from their respective Hettangian to early Sinemurian faunal complexes, the drowned areas that underwent pelagic deposition record the emergence of a new faunal stock (Szabó 1988, 1992, 1994; Conti & Monari 1991, 1995; Monari *et al.* 2008; Gatto & Monari 2010; Gatto *et al.* 2015a; Szabó *et al.* 2021), especially in those areas of morpho-structural high characterized by condensed deposition termed pelagic carbonate platforms (PCP; Santantonio 1993, 1994; Santantonio *et al.* 1996; Santantonio & Carminati 2011). This event is clearly recorded in the analysis (Fig. 36) and has already been recognized in the distribution of other invertebrate groups such as brachiopods (Vörös 2016 and references therein) and ammonites (Dommergues *et al.* 2009; Dera *et al.* 2011).

Vörös (2016), who applied statistical methods of analysis similar to those used here, recognized two biochores (*sensu* Westermann 2000) in the distribution of the Pliensbachian western Tethyan brachiopods, namely the Euro-Boreal and the Mediterranean, to which he attributed the rank of faunal provinces. Vörös (2016) also recognized two subprovinces in the Mediterranean province, the peri- and intra-Mediterranean. Subsequently, Vörös & Escarguel (2020) carried out a more refined analysis confirming this subdivision and adding more detail about the palaeobiogeographic structure of the western Tethyan brachiopods. All of the data reported here for the gastropods refer to localities that fall within the intra-Mediterranean province of Vörös (2016) and Vörös & Escarguel (2020). The only localities with gastropods belonging to their peri-Mediterranean subprovince are the upper Pliensbachian deposits of the external Subbetic zone (Inesta *et al.* 1990) and Gozzano (southern Alps, Italy) (Parona 1880, 1893; Sacchi Vialli & Cantaluppi 1967). These localities have been excluded from our analysis due to the very low number of gastropod species. In any case, the presence of *Worthenia superstes* Szabó 1980, *Ambercyclus alpinus* (Stoliczka 1861) and *Eucyclomphalus hierlatzensis* (Ammon 1893) clearly relates the Subbetic zone to the Mediterranean province (Inesta *et al.* 1990). Only one species is known from Gozzano, *Oonia pennina* (Parona 1893), which Sacchi Vialli & Cantaluppi (1967) erroneously synonymized with *Bourguetia*? *dubia* (Terquem) (see also Szabó 1983, 2009). This species has been tentatively recognized also in the Subbetic zone (Inesta *et al.* 1990).

Palaeobiogeographical units based on Early Jurassic gastropods were already suggested by Szabó (1988, 1992, 1994) who recognized, within the Mediterranean province, an Alpine subprovince, constituted by the late Sinemurian – Pliensbachian faunas of the pelagic sectors, and a Sicilian subprovince, already present in the early Sinemurian and including the faunas of the intra-Tethyan and North-African carbonate platforms. Given that this subdivision is clearly controlled by the facies, the Sicilian and Alpine faunas should be considered as different faunal stocks of the same biogeographic unit, rather than markers of true subprovinces (Westermann 2000).

The late Sinemurian and Pliensbachian gastropods of the Sicilian stock are represented here by the faunas of the Trento Platform and of the Eastern High Atlas. Their strong similarity highlighted by the palaeobiogeographic analysis demonstrates that the relationships recorded in the early Sinemurian between the Moroccan fauna and those of the intra-Tethyan carbonate platforms persisted also into the late Sinemurian – Pliensbachian interval. Other evidence supporting a temporal continuity of the carbonate platform faunal stock is that several early Pliensbachian taxa identified by Dubar (1948) in the Eastern High Atlas are very close to, or the same as, those recognized by Gemmellaro (1878, 1879) in the lower Sinemurian beds of the Trapanese Platform. Considering that the drowning of the intra-Tethyan platforms fragmented the environmental continuity of this area, the similarity between the Eastern High Atlas and Trento Platform faunas confirms even more the strong environmental control on the distribution of the gastropods.

The gastropod faunas of the areas characterized by pelagic deposition are rather homogenized, although the palaeobiogeographical analysis hints at some kind of latitudinal differentiation (Fig. 36). The affinities between the gastropods of the Western Pontides and those of the drowned areas of the intra-Tethyan region represent a further example of the strong facies control on the distribution of this group (Conti & Monari 1991; Gatto & Monari 2010). The Western Pontides were located far from the central area of western Tethys (Koçyiğit *et al.* 1991; Dercourt *et al.* 2000). In spite of this distance, the deposits yielding gastropods of this area show exactly the same facies as those characterizing the pelagic sequences of the intra-Tethyan region (Altiner *et al.* 1991; Nicosia *et al.* 1991). As emphasized by Gatto & Monari (2010), this demonstrates that the Alpine stock appeared wherever pelagic deposition took place, independent of palaeogeographic position.

DYNAMICS OF THE EARLY JURASSIC GASTROPOD RECOVERY

The palaeobiogeographic analysis provides a general picture of the changes in the relationships between the gastropod faunas of the western Tethys during the Early Jurassic recovery. Data at substage or biozone levels extracted from our database can provide some additional hints on the dynamics of the recovery, although the amount of information available at this level of stratigraphical detail is limited. Data on the lower Hettangian are scarce. The earliest gastropod faunas known for the European shelf come from the Psilonoten-Schichten of Halbertstadt (northern Germany) studied by Dunker (1844, 1846, 1847) and Huckriede (1967), and revised by Gründel (2010). Despite the low number of species, this fauna shows a remarkable supraspecific diversification, represented by the Acmaeidae, Pleurotomarioidea, Neritoidea, Pseudomelaniidae, Coelostylinidae, Palaeorissoinidae, Purpurinidae, Mathildoidea, Architectonicoidea and Acteonoidea.

Data concerning the late Hettangian of the European shelf are more abundant and widely distributed. Diversified gastropod assemblages are known especially in the southern and eastern Paris Basin and Swabia. The gastropod faunas of the eastern Paris Basin are certainly the richest and their distribution extends from Lorraine to the western side of the London–Brabant–Ardennes landmass. In contrast, the gastropods from the upper Hettangian of SW England, South Wales and the Cleveland Basin are less diversified, but their richness increases noticeably in the early Sinemurian. Data excluded from our database due to poor documentation could prospectively contribute to define the picture of gastropod diversity in this area. For example, a consistent number of species from Hettange-Grande are mentioned also by Dumortier (1864) from the *Schlotheimia angulata* Zone of the Rhone Basin and by Moore (1867a) from the upper Hettangian – lower Sinemurian deposits of Glamorganshire (South Wales). If these records were confirmed, the fauna of Lorraine (Luxembourg and Hettange-Grande) should be considered representative of a highly diversified (Fig. 29) and widespread faunal stock that characterized the late Hettangian – early Sinemurian gastropods of the western European epicontinental region.

The most ancient Hettangian gastropod fauna of the intra-Tethyan carbonate platforms comes from the *Psiloceras planorbis* Zone and the lower part of the *Alsatites liasicus* Zone of the Southern Alps (Bistram 1903; Conti 1954) and shows an evident taxonomic diversification. The gastropods are represented by the Trochoidea, Eucycloidea, Coelostylinidae, Pseudomelaniidae, Zygopleuriidae, Palaeorissoinidae?, Procerithiidae, Mathildoidea and Actaeonoidea. Further insights that could confirm a local high taxonomic diversity of the early Hettangian gastropod faunas of the intra-Tethyan carbonate platforms are provided by Capellini (1862, 1866) who described the 'Infralias' of the Tuscany Zone. This material has been excluded from our analysis because its exact stratigraphical position is unknown. Rigo *et al.* (2013) recognized the Triassic–Jurassic boundary in some of the outcrops from which this material comes. According to Rigo *et al.* (2013), gastropod-rich beds occur both below and above this boundary and the material studied by Capellini was probably collected from both the Rhaetian and the Hettangian beds. Late Hettangian gastropods are rare and documented only in the Southern Alps (Conti 1954; Gaetani 1970), whereas early Sinemurian gastropod faunas are widespread and recorded in many carbonate platforms of the intra-Tethys region. The fauna of Rocca Busambra (western Sicily, Italy) described by Gemmellaro (1878, 1879) and subsequent authors (Table 3) coming from the *Arietites bucklandi* Zone (Gugenberger 1935, 1936a, 1936b; Pignatti *et al.* 2019) consists of *c.* 200 species, of which *c.* 50 are also known from other intra-Tethyan carbonate platforms. This attests to the very high diversity reached during the early Sinemurian.

The trend of rediversification described above is exemplified by the change in number of species of the European shelf through three substages/biozones (Fig. 37): the taxonomic diversity plotted by family rank is moderate in the *Psiloceras planorbis* Zone, much higher in the *Schlotheimia angulata* Zone and stable in the lower Sinemurian. This trend supports a fast recovery of gastropods subsequent to the end-Triassic crisis, as suggested by Monari *et al.* (2011) on the basis of qualitative considerations and described quantitatively by Ferrari & Hautmann (2022). Comparable timings are also documented in other marine invertebrate groups (Tomašových & Siblík 2007; Guex *et al.* 2012; Damborenea *et al.* 2017; Atkinson & Wignall 2019) indicating that the absence of the lag phase was a distinctive aspect of the recovery (Erwin 1998, 2001; Hautmann *et al.* 2015; Kropf *et al.* 2024).

Another feature clearly emerging from our investigation is the extremely high proportion of taxa occurring in only one OGU (Table 4). These values are certainly not directly representative of the real degree of endemism. They are probably artificially inflated by the strict criteria used in assembling our database, which excluded any unverifiable citation. This left out many cited-only or poorly documented species that, if confirmed, would increase the number of shared taxa with a consequent reduction in the degree of endemism. In fact, in older literature it was quite common to report the species already known only in faunal lists and to describe and illustrate only new or rare species. Significant examples are the papers by Dumortier (1864, 1867, 1869), Moore (1867a), Joly (1907, 1936), Tate & Blake (1876) and Tutcher & Trueman (1925). In addition, many other difficult-to-verify single citations are scattered throughout the literature listed in Tables 2 and 3.

Although the percentage of singletons could not be considered a direct proxy of the real degree of endemism, the overall trend of its variation could provide significant hints at the process of rediversification. In our analysis we found gradually better defined areas of endemism, at least in the European epicontinental region. The ratio of the number of species exclusive to single OGUs to that of the total number of species increases by 7.5% between the Hettangian – early Sinemurian and the late Sinemurian – Pliensbachian intervals. If one considers only the areas with similar facies occurring in both time intervals, all belonging to the European shelf, the increment reaches 17%. A similar comparison cannot be done for the intra-Tethyan region, mainly due to its high structural dynamism. Gastropod faunas of the pelagic facies appeared in the late Sinemurian and, consequently, there are no terms of comparison for the Hettangian – early Sinemurian time span. Furthermore, OGUs present in both time intervals (e.g. the Northern Calcareous Alps) are represented by faunas of different facies. The increment of endemism calculated for the faunas of the intra-Tethyan carbonate platforms (18%), which is similar to that of the European shelf faunas, is misleading because it is driven by the unbalanced distribution of OGUs between the two time-slices considered. In fact, the Hettangian – early Sinemurian dataset includes a higher number of OGUs than the late Sinemurian – Pliensbachian dataset. The latter dataset comprises only the Eastern High Atlas and Trento Platform, and the great majority of species come from a single locality of the Eastern High Atlas. Therefore, a high number of singletons is expected, which surely does not represent the real degree of endemism.

The apparent low cosmopolitanism of the gastropod faunas here considered may shed some light on the palaeoecological context of the early Jurassic recovery of benthic communities. Established ecological models

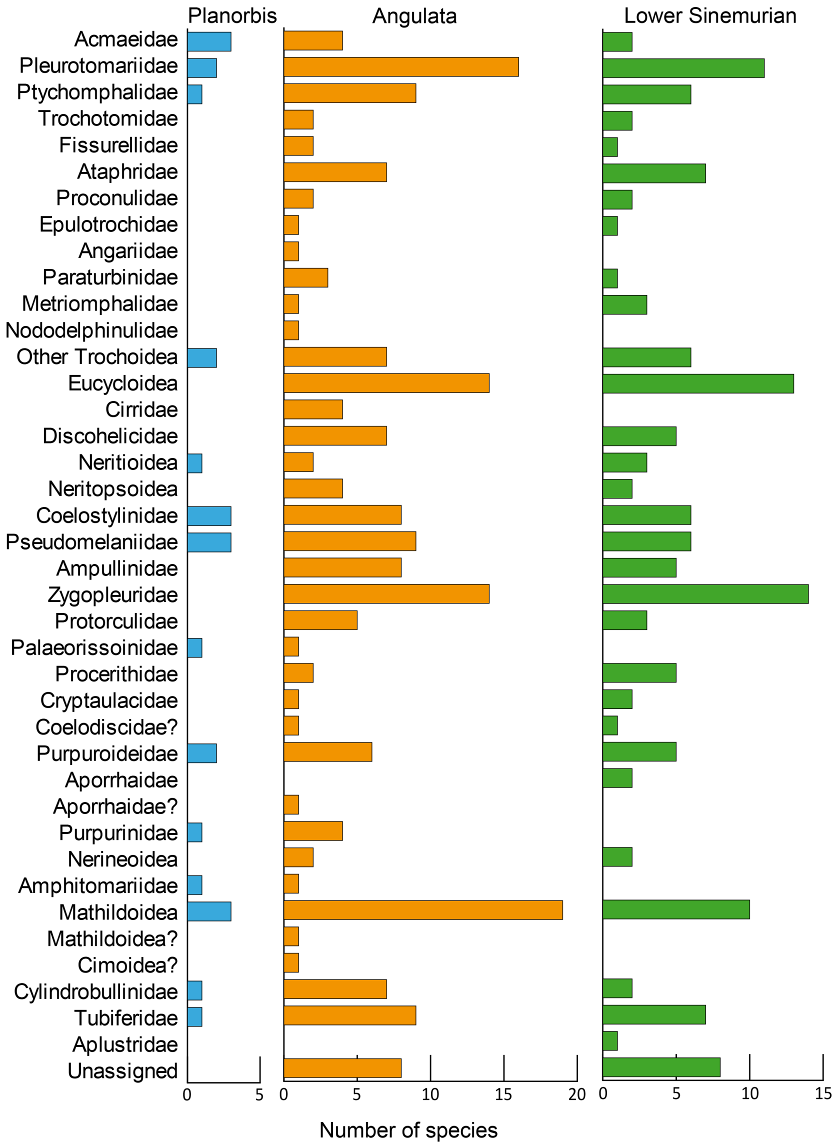

FIG. 37. Variation in the taxonomic composition of gastropods (represented by the number of species per family/superfamily) from the early Hettangian to early Sinemurian interval. Only species with known biozone occurrence have been considered. Superfamily rank used for species for which the family attribution is uncertain.

postulate that the immediate aftermath of a mass extinction is characterized by cosmopolitan taxa derived from disaster taxa (e.g. Hallam & Wignall 1997; Erwin 2001; Fraiser & Bottjer 2005; Brayard *et al.* 2006; Petsios & Bottjer 2016). Hautmann *et al.* (2015) and Kropf *et al.* (2024) explained the delay of rediversification subsequent to major mass extinction events as due to the low competition in environments poor in biodiversity. This would enable a wider species dispersal that would homogenize the composition of the early post-extinction faunas. The recovery would substantially result from an increase in species competition over time, promoting diversification. According to Erwin (1998), the lag phase of the Early Jurassic recovery of marine ecosystems in the European shelf does not show a transition from eurytopic to stenotopic taxa. Our data seem to confirm this: in the European shelf, only 10% of the Hettangian – early Sinemurian species show a concomitant distribution in three or more OGUs, which are commonly adjacent and similar in facies, and this also applies to the gastropod faunas of the intra-Tethyan carbonate platforms. True eurytopic gastropod species, widespread and occurring in different facies, and homogeneous assemblages dominated by these species are absent even in the earliest Jurassic communities. From this perspective, the high degree of endemism also fits well with a fast recovery and a

TABLE 4. Species richness and degree of endemism of the Early Jurassic gastropods of western Tethys.

		Hettangian – early Sinemurian			Late Sinemurian – Pliensbachian			D (%)	E (%)
		A	B	C (%)	A	B	C (%)		
All OGUs		665	484	72.8	736	591	80.3	+7.5	+10.7
EES OGUs		328	225	68.6	426	336	78.9	+10.3	+29.9
Selected EES OGUs		232	130	56.0	307	224	73.0	+16.9	+32.3
ITP OGUs		342	259	75.7	143	135	94.4	+18.7	−58.2
PWT OGUs		–	–	–	166	112	67.5	–	–
Vetigastropoda	All OGUs	209	151	72.2	345	257	74.5	+2.2	+65.1
	ESS	118	80	67.8	182	132	72.5	+4.7	+54.2
	ITP	95	71	74.7	33	31	93.9	+19.2	−65.3
	PWT	–	–	–	135	93	68.9	–	–
Neritimorpha	All OGUs	36	27	75.0	15	10	66.7	−8.3	−58.3
	ESS	10	7	70.0	2	1	50.0	−20.0	−80.0
	ITP	26	20	76.9	6	4	66.7	−10.3	−76.9
	PWT	–	–	–	7	5	71.4	–	–
Caenogastropoda	All OGUs	270	196	72.6	213	185	86.9	+14.3	−21.1
	ESS	113	81	71.7	119	98	82.4	+10.7	+5.3
	ITP	158	115	72.8	75	73	97.3	+24.5	−52.5
	PWT	–	–	–	16	10	62.5	–	–
Heterobranchia	All OGUs	96	66	68.8	144	122	84.7	+16.0	+50.0
	ESS	57	35	61.4	109	92	84.4	+23.0	+91.2
	ITP	39	31	79.5	25	23	92.0	+12.5	−35.9
	PWT	–	–	–	7	4	57.1	–	–

A, total number of species. B, number of species exclusive to a single operational geographical unit (OGU). C, percentage of endemic species (i.e. no. of species exclusive to a single OGU relative to the total no. of species). D, percentage change of degree of endemism over time. E, percentage change of species richness over time. Selected OGUs are OGUs present in both time intervals and in similar facies, i.e. northern Aquitanian Basin, Rhone Basin, southern Paris Basin, Southern England and South Wales, Cleveland Basin, southern Germany (Swabia and Franconia) and northwestern Germany. EES, European epicontinental shelf. ITP, intra-Tethyan and North African carbonate platforms. PWT, intra-Tethyan pelagic deposits.

diversification driven by interspecies competition, as predicted by the model proposed by Hautmann *et al.* (2015).

A strong endemism at species level was recorded also by Vörös (2016) and Vörös & Escarguel (2020) for the Pliensbachian brachiopods of western Tethys, which they justified as due to the low dispersal capability of this group as a result of its short planktotrophic larval phase. In the present case, the gastropod species known only from single areas belong to a wide range of taxonomic groups with diversified modes of larval development and varying dispersal capability. The Neritimorpha, many caenogastropod groups and the Heterobranchia have planktotrophic larval development with a pelagic larval stage of variable duration, whereas the Vetigastropoda are non-planktotrophic (lecitotrophic) (Nützel 2014). Predictably, the endemism of the Hettangian – early Sinemurian heterobranchs of the European shelf is lower than that of the vetigastropods. In contrast, endemism is higher in the caenogastropods and in the late Sinemurian – Pliensbachian heterobranchs. Seemingly, our data cannot be explained by the direct application of the paradigm, which assumes a wider geographic distribution for the groups with planktotrophic larval development due to their higher dispersal potential (Shuto 1974; Jablonski & Lutz 1983). The data concerning the change of the degree of endemism during time also contrast with this paradigm. On the whole, our data suggest that the degree of endemism is positively correlated with the species richness, which would indicate that the taxonomic diversity increased mainly due to the appearance of endemic species. The species richness in the late Sinemurian – Pliensbachian interval is *c.* 10% higher than in the Hettangian – early Sinemurian, and the faunas of the European shelf contributed in large measure (*c.* 30%) to this increase. In this region, the Vetigastropoda show a distinct increase in richness (54%) but a very low increase in endemism (2%). In contrast, the increase in richness is limited in the Caenogastropoda (5%) but it is paralleled by an increase in endemism (11%) much higher than in the Vetigastropoda. In the Heterobranchia both the species richness and the endemism rise much more than in the other subclasses (91% and 23%, respectively). This indicates that the increase in richness of groups with lecitotrophic larval development (vetigastropods) is mainly due to the appearance of widely distributed (two or more OGUs) species, whereas in the planktotrophic groups (caenogastropods and heterobranchs) the increase in species richness is mainly determined by the appearance of endemic species. However, as reported in a vast literature dealing with cases deviating from the paradigm (see Barroso *et al.* 2022 for an excursus), the geographic distribution of a marine benthic taxon is not only determined by the larval development but also by other numerous biotic and abiotic factors, among which the adaptive capabilities, the environmental heterogeneity and the continuity and stability in space and time of the ecological parameters are the most prominent (e.g. Hansen 1980; Bhaud 1993). Clearly, further investigation is necessary to disentangle these many variables.

Other data listed in Table 4 are probably not significant and possibly misleading. For example, the Neritimorpha are represented by few species and this makes comparisons with the other subclasses unreliable. However, considering that this group was one of the most characteristic clades among the gastropods of the Triassic carbonate platforms, the generalized loss of species richness reflects well its decline in the Jurassic. Furthermore, the constraints on the analysis mentioned above concerning the faunas of intra-Tethyan carbonate platforms also affect the assessment of their species richness. Its drastic decrease, both overall and in the single subclasses, is unrealistic and surely overestimated by the scarcity or absence of information on the communities inhabiting several late Sinemurian – Pliensbachian persistent platforms (e.g. Latium-Abruzzo, Apulia, Friuli). However, it is reasonable to suppose that the drowning and consequent disappearance of vast areas of carbonate platforms contributed in part to this decrease. The overall loss of taxonomic diversity was partly compensated for by the appearance of the faunas of the pelagic deposits, which, however, have a much lower species richness and a lower endemic character than those of the European shelf. Their taxonomic composition is also peculiar given that the Vetigastropoda account for a little more than 80% of these associations. The other subclasses are almost accessory and this is reflected by the overall strong decrease (21%) of richness of the Caenogastropoda. This particular taxonomic structure, characterized by a poor diversification at higher taxonomic ranks, the low species richness and the weak differentiation between the faunas of these areas (low endemism) are probably related to the relatively uniform and continuous open sea environment.

In summary, the rise of diversity of the western Tethyan gastropods, especially in the European shelf, appears to have the general character of an intense local speciation in scattered areas where immigration and faunal exchange were marginal processes. A similar palaeogeographic distribution and extremely high degree of endemism at species level have been recorded by Monari & Dellantonio (2024) for the late Anisian Pleurotomariida, which characterized the Middle Triassic main phase of recovery after the end-Permian mass extinction. These authors interpreted the endemism of the Pleurotomariida as a result of the combined effect of the low dispersal ability and the patchy resurgence of the carbonate platforms. In the present case, at least for the European shelf, the causes could be related to eustatic sealevel changes. Detailed studies of sequence stratigraphy have shown that the Hettangian–Sinemurian general sealevel rise occurred in a complex way, producing transgressive–regressive cycles of variable duration and at different geographic scales, recognized throughout the Euro-Boreal sector from the basins of France and England to those of Germany and Poland, (Gély & Lorenz 1991; De Graciansky *et al.* 1998; Hallam 2001; Barth *et al.* 2018 and references therein). These frequent changes could have contributed to maintain an environmental heterogeneity in space and time that favoured high degrees of endemism. The essentially taxonomic character of our analysis and the low stratigraphic resolution of our data do not enable identification of possible correlations between the endemism variation and the sealevel changes, which should be more correctly investigated using a different approach (e.g. Patzkowsky & Holland 2012; Danise & Holland 2017 and references therein).

The differentiation of the facies in the intra-Tethyan region, and consequent appearance of the Alpine stock, played an important role in the further diversification of the early Jurassic gastropods. The origin of this stock from the pre-existing faunas is an intriguing question. Intuitively, the faunas of intra-Tethyan carbonate platforms should have contributed more to the emergence of the Alpine stock than those of the European shelf, but establishing how many and which groups derived from one or the other fauna requires a phylogenetic approach and palaeobiogeographical analyses at the supraspecies level. Whatever its origin, a peculiarity of the Alpine stock is the sudden appearance in the fossil record of already diversified faunas. This is a further clue to the high diversity achieved by the faunas from which it derived and, consequently, the appearance of this stock can be considered a late event of the main phase of recovery.

CONCLUSION

Systematic study of the Caenogastropoda and Heterobranchia from the *Psiloceras planorbis* Zone and the *Schlotheimia angulata* Zone of the Luxembourg Sandstone Formation identified 33 species, including 11 new species, representing 13 families and at least eight superfamilies. Together with the Patellogastropoda, Neritimorpha and Vetigastropoda recognized in a previous study, this Hettangian fauna consists of 55 species belonging to 22 families and 14 superfamilies. Considering also the species from the Hettangian type locality, the gastropod faunas of the eastern Paris Basin are the most diverse of those inhabiting the European epicontinental shelf in the earliest Jurassic. Analysis of the palaeobiogeographic relationships among these and other western Tethyan faunas through the first stages of the Lower Jurassic can be summarized as follows:

1. The overall taxonomic structure of the gastropod faunas became more complex from the *Psiloceras planorbis* Zone to the *Schlotheimia angulata* Zone and stabilized in the early Sinemurian. This trend indicates a rapid rediversification after the end-Triassic crisis and supports, together with the absence of homogeneous and low-diversified associations and of true cosmopolitan taxa, the lack of an initial delay phase of the recovery.
2. During the Hettangian and early Sinemurian, the faunas inhabiting the European epicontinental shelf, where a mixed siliciclastic–carbonate sedimentation prevailed, and those of the intra-Tethyan region, characterized by a system of carbonate platforms, were clearly different. This distinction reflects the strong facies control on gastropod distribution that is evident also at a smaller scale in the interrelationships between the faunas of the intra-Tethyan carbonate platforms and those of the north African margin.
3. During the late Sinemurian and Pliensbachian, a new faunal complex (Alpine stock) appeared in the intra-Tethyan areas where pelagic sedimentation took place as an effect of the drowning of vast sectors of carbonate platforms. Moreover, the areas of endemism in the European shelf became more distinct. The distribution of faunas, especially in the intra-Tethyan region, appears to also be under latitudinal control.
4. Although probably biased in part by the strict criteria used in data compilation, the analysis indicates a gradual increase in endemism over time, particularly in the European epicontinental shelf. This increase is positively correlated with the rise in species richness and this suggests that the taxonomic diversity increased mainly through the appearance of endemic species in a scenario in which local speciation prevailed over faunal exchange.
5. The faunas of the Alpine stock were dominated by Vetigastropoda and characterized by a proportionally low degree of endemism, probably as a consequence of the continuity and homogeneity of the pelagic environment.
6. The major gastropod clades exhibited contrasting pattern of diversification during the recovery. Contrary to the paradigm assigning higher dispersal potential and lower speciation rates to the groups with planktotrophic larval development, caenogastropods and heterobranch gastropods show a higher number of endemic species than vetigastropods. Biotic and abiotic factors (such as differential adaptive capabilities and the continuity and stability in space and time of the ecological parameters), may have played a role in modelling the evolutionary trajectories of each clade, but the large scale, species-based approach of the present research is not suitable to analyse these patterns. However, at least in the European shelf, eustatic sealevel fluctuation may have been the driver behind the establishment of the areas of endemism.

The gastropods have an eventful evolutionary history, ecologic diversity and adaptive plasticity that make them a useful proxy to evaluate the response of the biota to macroevolutionary events, but their potential appears to have been underexploited so far. In order to unlock this wealth of information, future research should be focused on improving global databases at the species level (in our research at least 15% of citations in each database have been left out due to poor documentation), but also on refining supraspecies systematics and phylogenetic relationships.

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DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains have been registered in ZooBank: https://zoobank.org/References/4081b438-4c75-4dd5-b9b2-8bccb6bf29e0

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1002/spp2.70062):

Appendix S1. Presence/absence gastropod species matrices used to perform the palaeobiogeographical analysis.
Figure S1. Results of the CA and PCoA using the Ochiai coefficient based on the Hettangian – early Sinemurian and late Sinemurian – Pliensbachian databases including singletons.

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