Earliest Jurassic patellogastropod, vetigastropod, and neritimorph gastropods from Luxembourg with considerations on the Triassic–Jurassic faunal turnover

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The Hettangian to earliest Sinemurian Vetigastropoda, Patellogastropoda, and Neritimorpha housed in the National Museum of Natural History of Luxembourg are studied. Most of the species comes from the Luxembourg Sandstone Formation. This deposit formed along the southern margin of the London-Brabant-Ardennes Landmass, in a region that during the earliest Jurassic constituted a seaway connecting the Paris Basin with the epicontinental seas of the Netherlands and northern Germany. The systematic analysis revealed high diversity of the studied fauna; we identified twenty-two species, eleven genera, nine families, and six superfamilies. A new genus, *Meiersia* gen. nov., and three new species, *Anodomaria schroederi* sp. nov., *Meiersia disarmata* sp. nov., and *Spirocirrus weisi* sp. nov. are described. The fauna is dominated by pleurotomarioideans representing the genera *Ptychomphalus*, *Pleurotomaria*, and *Trochotoma*, and by the patellogastropod genus *Scurriopsis* both in number of species and specimens. The neritimorph genus *Neridomus* is also well represented. Among the accessory taxa, *Anodomaria* and *Spirocirrus* first appeared in the Late Hettangian of the Luxembourg area. Most of these genera show a species radiation in the Early Jurassic and are distributed over the western European epicontinental shelf, probably favoured by an east to west marine transgression which influenced wide areas from the basins of the northern Germany to the Paris Basin through the Luxembourg seaway. The evolutionary and palaeobiogeographical data demonstrate that this radiation was already considerably advanced in the Late Hettangian. This suggests that the recovery of the gastropod diversity after the end-Triassic crisis was relatively fast in western Europe.

Key words: Gastropoda, end-Triassic crisis, palaeobiogeography, Early Jurassic, Hettangian, Luxembourg Sandstone Formation, Paris Basin.

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Introduction

The Triassic–Jurassic boundary is marked by a mass extinction event deemed to be related to organic carbon anomalies and an important crisis of the biotic carbonate production (e.g., Hesselbo et al. 2002; Hautmann 2004; Galli et al. 2005; van de Schootbrugge et al. 2007; Hautmann et al. 2008). As underlined by Seuss et al. (2005), its timing and effects on the benthic communities are still controversial. In this context, the study of the earliest Jurassic reef-building corals is particularly promising (for a synthesis see Seuss et al. 2005; Kiessling et al. 2007, 2009 and references therein) owing to the high sensitivity of these organisms to the changes of the chemical environmental conditions. However, the studies of other benthic groups, particularly those of Hettangian age are needed to better understand the evolutionary effects of the end-Triassic crisis.

Hettangian gastropods of Europe were the subject of numerous papers (Dunker 1847, 1848; Chapuis and Dewalque 1853; Terquem 1855; Martin 1863; Dumortier 1864; Terquem and Piette 1865; Tawney 1866; Moore 1867; Henry 1876; Ammon 1893; Böhm 1901; Chartron and Cossmann 1902; Bistram 1903; Joly 1907, 1908, 1936; Brösamlen 1909; Dareste de la Chavanne 1912; Kuhn 1934; Berini 1957; Gaetani 1970; Meier and Meiers 1988; Szente 1992; Gründel 2003). During the last decades several studies (see Bouchet and Rocroi 2005 for references) greatly improved the knowledge on the systematics and phylogeny of the Recent and fossil gastropods. Thus, generic and higher level assignments of the older literature need a systematic revision. This would facilitate palaeobiogeographical and diversity comparisons across the Triassic–Jurassic boundary.

The National Museum of Natural History of Luxembourg houses outstanding collections of gastropods from the Het-

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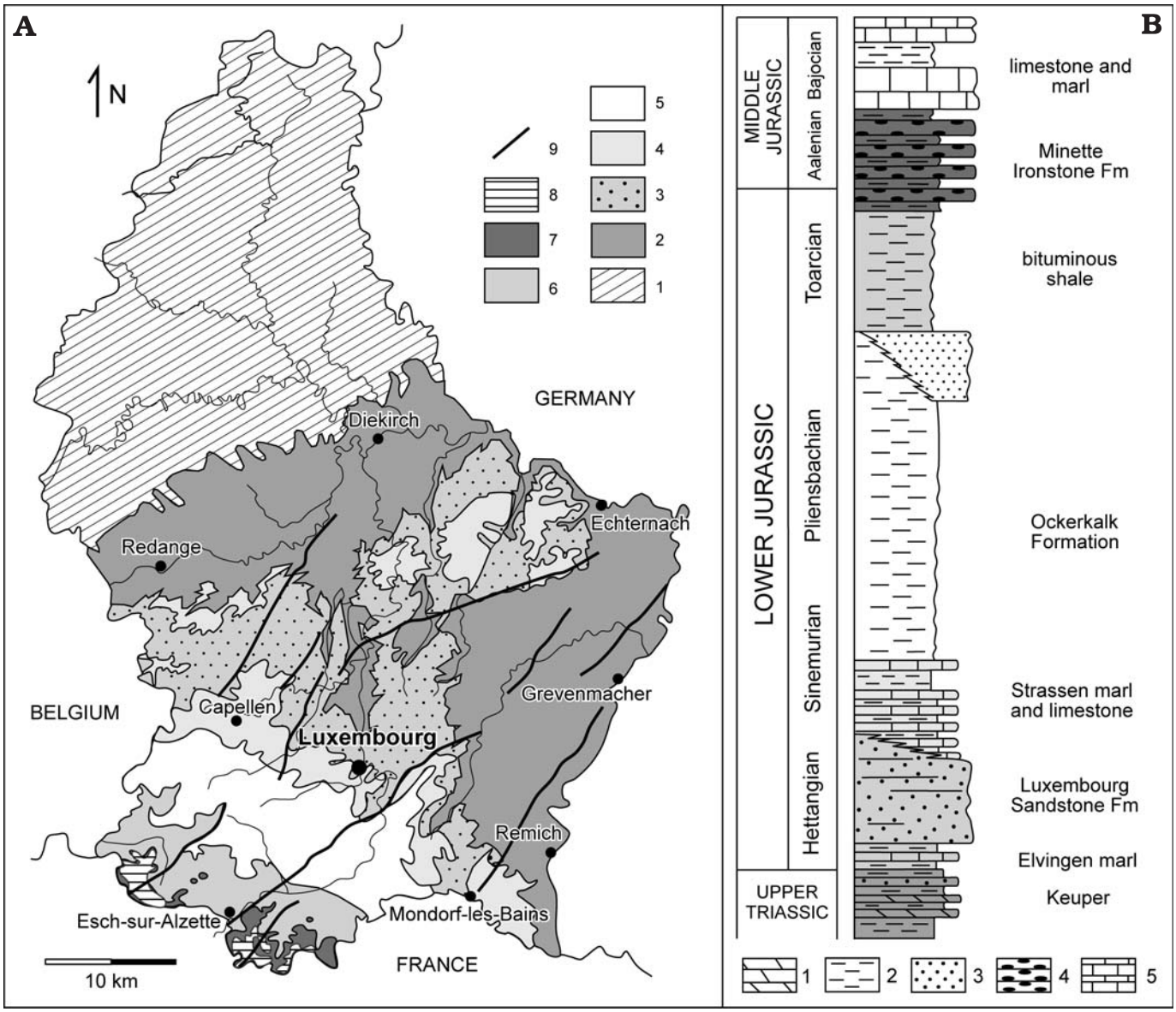

Fig. 1. Jurassic geology of Luxembourg. **A**. Schematic geological map of the Mesozoic units. 1, Palaeozoic basement; 2, Triassic sediments; 3, Luxembourg Sandstone Formation including the Elvingen marl at its base (Hettangian to lowermost Sinemurian); 4, Strassen marl and limestone (Lower Sinemurian to Upper Sinemurian); 5, Ockerkalk Formation (Upper Sinemurian to Pliensbachian); 6, bituminous shale (uppermost Pliensbachian to Toarcian); 7, Minette Irostone Formation (Toarcian–Aalenian); 8, limestone and marl (Lower Bajocian); 9, major fault lines. **B**. Stratigraphical sketch of the Jurassic succession. 1, dolostone; 2, clay and marl; 3, sandstone; 4, oolitic ironstone; 5, limestone. Map and stratigraphical column redrawn from Service Géologique de Luxembourg (1998). Other data from Boulvain et al. (2000, 2001) and Van den Bril and Swennen (2008).

tangian to early Sinemurian sediments of the Grand-Duchy of Luxembourg, which include five hundred specimens representing about fifty species (see Thuy et al. 2005 and Valentini 2007 for a preliminary account). Their importance is evident if one considers that Terquem's (1855) monograph, which is a major contribution to the study of the Hettangian European macrofossils, reported sixty-nine gastropod species. The present paper deals with the systematic study of the patellogastropod, neritimorph, and vetigastropod groups. Higher prosobranch, heterobranch, and opisthobranch gastropods are currently under study. They will be the subject of a subsequent paper. The Early Jurassic evolutionary and palaeogeographical histories of the taxa analysed here are traced in order to elucidate their role in the Triassic–Jurassic faunal turnover.

Institutional abbreviations.—MNHNL, National Museum of Natural History, City of Luxembourg, Grand-Duchy of Luxembourg; UCBL, University Claude Bernard, Lyon 1 (Villeurbanne, France), collections of the Ecole des Mines.

Geological setting

The Mesozoic sedimentary succession of Grand-Duchy of Luxembourg crops out extensively in the central and southern

part of the country. The Mesozoic sediments are underlain by a Devonian basement which belongs to the southern belt of the Ardennes Massif (Fig. 1A). The Jurassic sequence, represented by Hettangian to Lower Bajocian units, directly overlies Triassic deposits of the German facies (Fig. 1B). It covers a SW to NE extending area. Its units become progressively younger south-westward and continue to equivalent units in Gaume (Belgium) as well as in the Belgian and French Lorraine, which form the eastern boundary of the Paris Basin. During the Early Jurassic the southern area of the Grand-Duchy of Luxembourg was part of a seaway insinuated between the London-Brabant-Ardennes Landmass and the Rhenish Massif, that connected the Paris Basin with the epicontinental seas of the Netherlands and northern Germany (De Graciansky et al. 1998; Van den Bril and Swennen 2008) (Fig. 2).

The Hettangian to Sinemurian succession of Grand-Duchy of Luxembourg consists of three lithostratigraphical units, namely the Elvingen marl (lowermost Hettangian), an informal unit roughly corresponding to the Jamoigne Marl Formation in southern Belgium, the Luxembourg Sandstone Formation (Hettangian to lowermost Sinemurian), and the Strassen marl and limestone (Lower to Upper Sinemurian) (Bintz and Maquil 1992; Van den Bril and Swennen 2008) (Fig. 1B). The latter is an informal unit in Luxembourg, whereas it is a formal member of the Arlon Formation in southern Belgium (Boulvain et al. 2000, 2001).

The great majority of the material considered in this study comes from the Luxembourg Sandstone Formation. That unit consists of a yellowish, poorly cemented sandstone and grey to whitish, well-cemented sandy limestone originating from the deposition of well-sorted, fine to medium sized sands (Colbach 2005). In the Grand-Duchy of Luxembourg, it is 110 m thick in the centre of the country (Faber and Weis 2005). It encompasses most of the Hettangian stage and its top has an Early Sinemurian age in the westernmost area (Guérin-Franiatte and Muller 1986, 2005; Guérin-Franiatte et al. 1991).

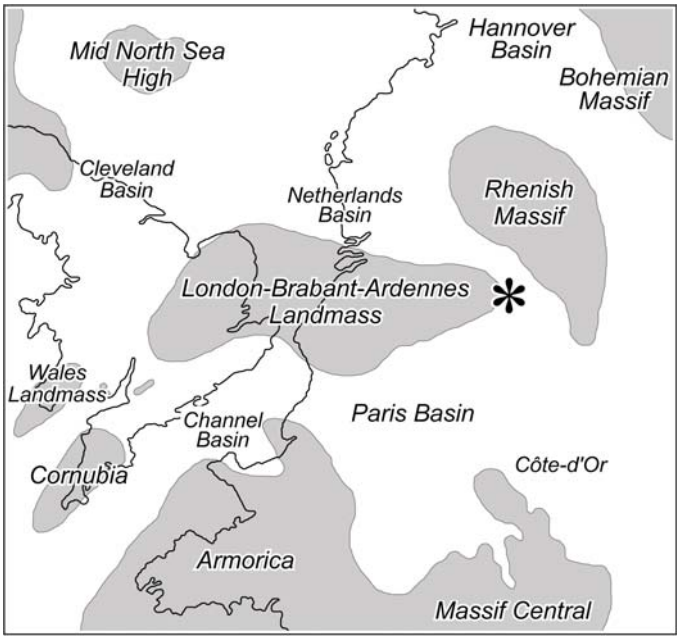

Fig. 2. Palaeogeographical reconstruction of western Europe during the earliest Jurassic times. Exposed lands are in grey. The position of Luxembourg area is indicated by an asterisk (*). Map redrawn and simplified from Bradshaw et al. (1992), De Graciansky et al. (1998), and Dercourt et al. (2000).

The Luxembourg Sandstone Formation mainly represents a complex of sand waves and bars deposited diachronically, east to west, on a shallow marine shelf under tidal-deltaic environmental conditions (Colbach 2005; Van den Bril et al. 2007; Van den Bril and Swennen 2008 and references therein). The facies organisation and their palaeoenvironmental interpretation were recently treated in detail by Van den Bril and Swennen (2008) who recognised a set of sequences mainly composed of fine and laminated sands followed by large scale sand bars with foresets.

The fossil content of the Luxembourg Sandstone Formation is rather poor if one considers the thickness of the unit. It consists of sponges, corals, bryozoans, bivalves, gastropods, cephalopods, and echinoderms which are mainly concentrated in few coarse grained layers where they frequently form coquinas. According to Van den Bril and Swennen (2008) these sediments were deposited under high energy conditions in a shallow marine environment. The substrate was reworked and winnowed partly under storm event conditions during which finer grains were washed out.

Material and methods

All specimens belong to the collections housed in the National Natural History Museum of Luxembourg. Most of them were collected in a large quarry opened by the Feidt Company in the Luxembourg Sandstone Formation at Reckinger Wald, near Brouch (Mersch), about twenty kilometres north of the city of Luxembourg (Fig. 3A). Therein, two well-defined levels yielded fossils: a Lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras* beds) level and an Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone) level (see Guérin-Franiatte and Weis 2010 for further details). Almost all the material comes from the latter level and, in particular, from a couple of beds about ten metres below the transition to the Strassen marl and limestone. The study also includes the revision of the material published by Meier and Meiers (1988), from the Upper Hettangian beds of the Brouch quarry. That material was originally part of Kurt Meiers's private collection who subsequently donated it to the National Natural History Museum of Luxembourg.

The remaining specimens from the Luxembourg Sandstone Formation, have a less precise stratigraphical position and come from the following localities: Mamer (Kaatzefiels), Hespérange, Burmerange, Steinfort, Kopstal (Biremdall), and Bridel (Birgerkeiz) (Fig. 3B, C). The present study includes also some Hettangian to Early Sinemurian material from older collections. Although their exact geographical and/or stratigraphical position are uncertain, their analysis gave important insights into the variability and ontogeny of

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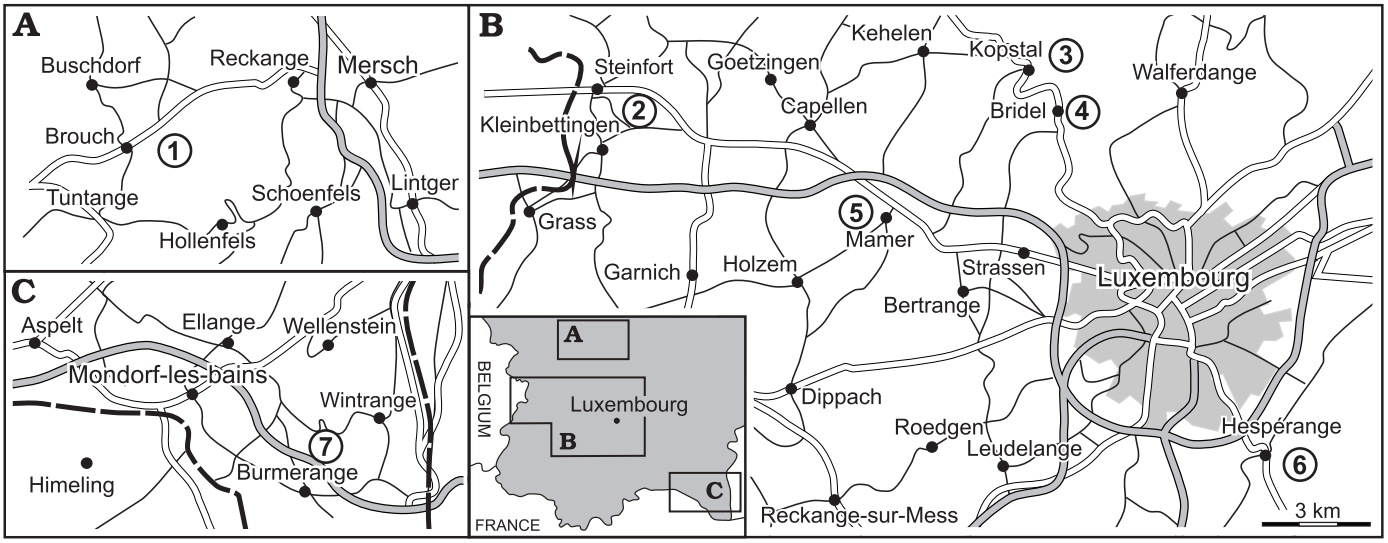

Fig. 3. Location of the outcrops yielding the material studied here. 1, Brouch (Mersch); 2, Steinfort; 3, Kopstal (Biremdall); 4, Bridel (Birgerkeiz); 5, Mamer (Kaatzefiels); 6, Hespérange; 7, Burmerange. Grey lines, motorways and link motorways; double lines, national roads; single lines, byroads; dashed lines, state boundary.

the species concerned. In some cases, it also allowed identification of species rarely quoted by past authors or described here for the first time in Lower Jurassic sediments of the eastern Paris Basin.

The higher classification of the class Gastropoda Cuvier, 1797 adopted here is basically that reported in Gatto and Monari (2010) to which paper reference may be made for further details.

A number of species determinations was supported by direct comparison with the material of Terquem's (1855) collection, from the Hettangian of Hettange-Grande (Lorraine, France) housed in the University Claude Bernard, Lyon 1, collection of the Ecole des Mines (Villeurbanne, France). The most representative specimens were figured and measured (Tables 1 and 2). The abbreviations for the dimensions are illustrated in Fig. 4.

Systematic palaeontology

Subclass Eogastropoda Ponder and Lindberg, 1996

Order Patellogastropoda Lindberg, 1986

Suborder Patellina von Ihering, 1876

?Superfamily Lottioidea Gray, 1840

?Family Acmaeidae Forbes, 1850

Genus *Scurriopsis* Gemmellaro, 1879

Type species: *Scurriopsis neumayri* Gemmellaro, 1879. Sinemurian, north-western Sicily, Italy.

Subgenus *Scurriopsis* Gemmellaro, 1879

Type species: as for the genus.

Remarks.—The genus *Scurriopsis* Gemmellaro, 1879 is assigned here to the suborder Patellina von Ihering, 1876 because of the presence of an horseshoe-shaped muscle scar in the type species, *Scurriopsis neumayri* Gemmellaro, 1879 (Gemmellaro 1879: 381, pl. 29: 5, 6; Cox and Keen 1960). The same character was described by Terquem (1855: 281, pl. 18: 2) for *Scurriopsis* (*Hennocquia*) *hettangiensis* (Terquem 1855). The lack of information on the protoconch and microstructure of the shell, which are fundamental aspects for the systematic placement of the limpet-shaped gastropods (see Hedegaard et al. 1997; Fuchigami and Sasaki 2005 and references therein) leaves the superfamily and family position uncertain.

Scurriopsis (*Scurriopsis*) *schmidti* (Dunker, 1844)

Fig. 5A–C.

1844 *Patella schmidtii* sp. nov.; Dunker 1844: 187.
1847 *Patella schmidtii* Dunker; Dunker 1847: 113, pl. 13: 17a–c.
1855 *Patella schmidtii* Dunker; Terquem 1855: 281–282, pl. 18: 4, 4a, 4b.
1884 *Patella schmidtii* Dunker; Quenstedt 1884: 756, pl. 215: 35.
?1901 *Patella delgadoi* sp. nov.; Böhm 1901: 213, pl. 8: 1, 2.
1902 *Patella schmidti* Dunker; Cossmann in Chartron and Cossmann 1902: 201, pl. 3: 34, 35.
1932 *Acmaea schmidti* (Dunker); Haber 1932: 164–166.
1988 *Scurriopsis schmidtii* (Dunker); Meier and Meiers 1988: 25, pl. 2: 4a, b.

Material.—Fourteen specimens: MNHNL BR109, MNHNL BR180, MNHNL BR190, MNHNL BR222, MNHNL BR360, MNHNL BR493, MNHNL BR495 (three specimens), MNHNL BR501, MNHNL BR502, MNHNL BR506, MNHNL BR580, MNHNL BR672, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Two specimens: MNHNL HE138, MNHNL HE149, Brouch, Hettangian, exact stratigraphical level unknown.

Dimensions.—See Table 1.

Description.—Limpet-shaped shell. Peristome moderately elliptical, tending to subrectangular, slightly wider in the posterior region. Width of peristome 77–93% of its length. Shell moderately to rather high, with height varying 37–52% of the shell length. Apical shell slightly coeloconical and rather high. Apex weakly pointing anteriorward and placed anteriorly at 57–67% of the shell length. Posterior outline of shell in lateral view convex. Anterior outline from convex to moderately concave. Sculpture made of sharp and rounded radial ribs on the entire surface. Juvenile shell bearing 20 to 25 radial ribs. Adult shell ornamented with 40 to 60 radial ribs consisting of two orders of alternating ribs which make the peristomal edge slightly undulated. Ribs are commonly denser on the lateral regions of the shell where they are separated by thinner intervals. Primary ribs appear at a short distance from the apex. Secondary ribs rapidly reach the same size of the primary ribs during the growth. Intercalation of primary and secondary ribs well visible on the posterior area where the intervals between the primary ribs are wider. Radial ribs strongly roughed by intersection with marked and dense growth striae.

Remarks.—The original name given by Dunker (1844) to this species, *Patella schmidtii*, was corrected by Cossmann (in Chartron and Cossmann 1902) to *Patella schmidti*. This correction was confirmed by Haber (1932) in his revision of Dunker's (1844) species.

Dunker (1847) described small shells of *Scurriopsis* (*Scurriopsis*) *schmidti* (Dunker, 1844) corresponding well to the juvenile specimens described here. In Dunker's specimens the shape of the shell is rather high and the ornament is made of about twenty radial ribs. The juvenile part of the shell of the specimens from Luxembourg have the same shape and ornament.

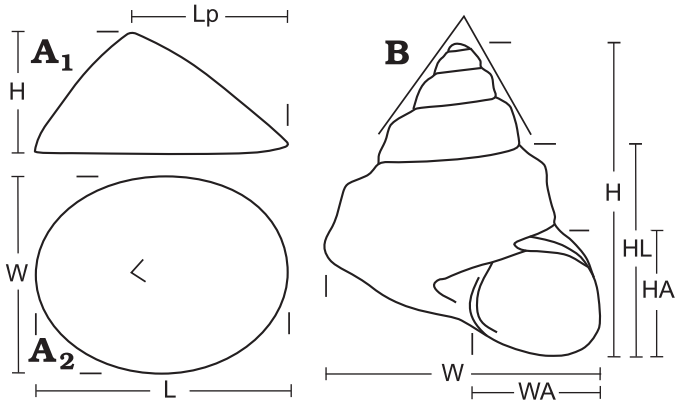

Fig. 4. Explanatory drawings of gastropod shells morphology. **A**. Limpet-shaped shells, in lateral (A_1) and apical (A_2) views. **B**. Trochospiral shells. Abbreviations: H, height of the shell; HA, height of the peristome; HL, height of the last whorl; L, length of the peristome; Lp, distance of the apex from the posterior margin of the peristome; W, width of the base; WA, width of the peristome; α, mean spiral angle.

The material shows a relatively high intraspecific variation. It includes specimens of two different adult shapes which are clearly in morphological continuity. A first morphology consists of moderately high shells with slightly concave anterior slope. These specimens are the most similar to the shells ascribed by Terquem (1855) and Cossmann (in Chartron and Cossmann, 1902) to *S*. (*S*.) *schmidti*. The other morphology is more globose due to the convex anterior slope. The ornament of the adult shell is rather variable as well, the number of primary and secondary ribs ranging from about 40 to 60. Finally, the anterior position of the apex is also variable.

Patella delgadoi Böhm, 1901 from the earliest Jurassic of

Table 1. Measurements of the specimens belonging to the patellogastropod species. The linear measurements are in millimetres. Abbreviations: H, height of the shell; L, length of the peristome; Lp, distance of the apex from the posterior margin of the peristome; W, width of the base.

Specimen	L	Lp	H	W	Specimen	L	Lp	H	W
Scurriopsis (*Scurriopsis*) *schmidti* (Dunker, 1844)									
MNHNL BR109	21.8	14.5	19.8	9.6	MNHNL BR501	16.6	11.2	13.3	8.7
MNHNL BR180	18.4	11.5	14.7	7.2	MNHNL BR502	17.0	10.7	13.2	6.7
MNHNL BR190	16.9	11.2	13.4	6.4	MNHNL BR506	23.2	14.1	18.8	10.5
MNHNL BR360	20.3	11.5	17.3	9.9	MNHNL BR580	12.7	8.3	11.1	6.2
MNHNL BR495-1	18.5	10.9	17.2	8.8	MNHNL BR672	19.2	12.7	14.8	7.4
MNHNL BR495-2	16.6	–	13.8	5.6P	MNHNL HE149	17.0	11.2	13.6	8.7
MNHNL BR495-3	15.9	10.2	12.6	6.6					
Scurriopsis (*Hennocquia*) *hettangiensis* (Terquem, 1855)									
MNHNL BR159	30.6	17.3	23.4	13.9	MNHNL BR497	36.8	25.7	33.0	19.6
MNHNL BR260	20.5	11.7	16.8	6.9	MNHNL BR503	27.4	17.8	22.5	9.8
MNHNL BR363	28.8	17.0	23.9	12.0	MNHNL BR650	26.8	15.3	22.5	13.6
MNHNL BR366	35.8	21.2	29.7	20.5	MNHNL BR669	27.5	17.9	22.0	9.3
MNHNL BR487	36.8	20.7	29.6	14.9	MNHNL BR673	37.3	22.6	30.9	19.5
MNHNL BR489	39.6	23.2	31.0	22.0	MNHNL GL154	29.0P	20.1	24.0	14.6
MNHNL BR491	13.9	8.0	10.9	7.8	MNHNL GL222-1	28.4	18.5	23.3	17.6
MNHNL BR492-1	14.1	10.3	10.9	8.6					

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Table 2. Measurements of the specimens belonging to the neritimorph and vetigastropod species. The linear measurements are in millimetres. Abbreviations: H, height of the shell; HA, height of the peristome; HL, height of the last whorl; W, width of the base; WA, width of the peristome; α, mean spiral angle. The symbol P accompanies partial measurements on incomplete specimens.

Specimen	H	HL	HA	W	WA	α	Specimen	H	HL	HA	W	WA	α
Neridomus liasina (Dunker, 1844)													
MNHNL BR362	16.8	15.7	13	16.6	8.6	99°	MNHNL BR701-1	14.8	13.8	12.4	13.4	–	102°
MNHNL BR446	11.4	10.3	–	11.6	–	102°	MNHNL BR701-2	14.5	14.2	13.5	14.2	–	104°
MNHNL BR693	13.9	13.0	–	14.8	–	106°	MNHNL BR702	10.7P	–	–	13.6	–	110°
MNHNL BR696	12.4P	11.3P	–	14.5	–	101°	MNHNL BR877	14.0	12.9	11.2	12.0	8.2	104°
Neridomus cannabis (Terquem, 1855)													
MNHNL BR365	10.6	9.8	8.9	11.4	–	124°	MNHNL BR879	6.3	6.1	5.7	6.9	–	123°
MNHNL BR878	10.4	10.0	9.2	11.4	6.4	121°							
Bandelopsis? cf. *exigua* (Terquem, 1855)													
MNHNL BR300	12.1	11.7	10.4	13.4	–	113°	MNHNL BR880	13.4	12.9	11.7	15.2	–	110°
MNHNL BR700	11.2	10.4	–	12.1	–	109°							
Bandelopsis? sp.													
MNHNL BR367	7.3	7.2	–	8.9	–	126°							
Pleurotomaria wanderbachi Terquem, 1855													
MNHNL BR306-2	68.7	41.7	25.2	–	–	63°	MNHNL BR432-1	60.2	38.1	–	55.8	–	64°
MNHNL BR308	66.8	40.0	29.1	59.6	33.4	62°	MNHNL BR677	46.2	33.3	–	48.0	–	67°
MNHNL BR359	26.5	18.2	10.9	24.8	12.7	70°	MNHNL GL121	78.2	53.5	36.6	75.3	42.6	64°
Pleurotomaria hettangiensis Terquem, 1855													
MNHNL BR294	58.2	35.5	–	56.2	–	64°	MNHNL BR443	44.2P	29.2P	–	43.1	–	64°
MNHNL BR304	31.5	21.2	–	31.4P	–	67°	MNHNL BR676	38.1P	22.9P	–	40.9	–	67°
MNHNL BR375-1	49.1	30.0	19.2	47.0P	–	68°							
Pleurotomaria cf. *hettangiensis* Terquem, 1855													
MNHNL BR432-2	58.0	34.5	–	49.5	–	60°							
Pleurotomaria hennocquii Terquem, 1855													
MNHNL BR881	22.7	15.5	–	24.2	–	70°							
Pleurotomaria cognata Chapuis and Dewalque, 1853													
MNHNL HE197-1	26.6	18.2	11.4	29.4	–	74°	MNHNL LI113	34.0	24.9	18.0	39.9	20.0	75°
MNHNL HE197-2	22.9	–	–	25.9	–	77°							
Pleurotomaria sp.													
MNHNL GL344	58.1P	41.2P	–	61.4	–	74°							
Anodomaria schroederi sp. nov.													
MNHNL BR342	21.3	16.9	11.5	29.1	–	79°	MNHNL BR871	10.8	9.0	6.7	17.3	–	98°
Ptychomphalus rotellaeformis (Dunker, 1847)													
MNHNL BR364	13.1	12.2	–	22.3	–	134°	MNHNL BR703	11.3	–	–	19.8	–	131°
Ptychomphalus caepa (Eudes-Deslongchamps, 1849)													
MNHNL BR810-1	15.2	14.0	11.5	21.8	12.2	112°	MNHNL GL213-2	21.2	18.5	14.8	28.9P	–	105°
MNHNL BR826-1	27.1	22.9	–	38.6	–	100°	MNHNL GL213-3	21.0	19.0	–	31.3	–	109°
MNHNL BR826-2	25.7	22.5	–	33.1	–	110°	MNHNL GL271-1	18.9	17.1	15.6	31.3	–	116°
MNHNL BR830-1	23.6	20.1	–	31.6	–	102°	MNHNL GL271-2	24.5	22.5	–	30.9	–	108°
MNHNL BR830-2	16.4	14.6	13.2	22.8	14.5	113°	MNHNL GL449	24.3	21.1	–	34.5	–	108°
MNHNL GL213-1	24.5	20.8	16.0	31.2	–	97°							
Ptychomphalus wehenkeli (Terquem and Piette, 1865)													
MNHNL BR123	9.0P	–	–	18.4	–	121°	MNHNL BR368	12.8	11.5	9.9	20.7	7.9	125°
MNHNL BR161	13.5	–	–	24.9	–	110°	MNHNL BR456	11.0P	–	–	24.4	–	123°
MNHNL BR206	13.1	10.8	–	20.1	–	108°°	MNHNL BR470	13.5	–	–	20.4	–	107°
MNHNL BR225	12.4	–	–	20.6	–	120°	MNHNL BR545	16.5P	–	–	30.4	–	122°
MNHNL BR259	16.3	14.0	11.7	25.0	–	123°	MNHNL BR717	16.7	13.9	–	28.2	–	122°
MNHNL BR341-1	16.0	14.1	13.5	25.7	–	124°	MNHNL BR305-2	12.5	11.6	–	20.0	–	115°
MNHNL BR341-2	10.0	9.0	7.0	16.1	6.9	122°							

Specimen	H	HL	HA	W	WA	α	Specimen	H	HL	HA	W	WA	α
Trochotoma vetusta Terquem, 1855													
MNHNL BR221-2	18.4	13.9	–	16.4	–	93°	MNHNL BR698-2	20.9	17.8	12.7	34.3	–	94°
MNHNL BR361	15.1	11.8	8.6	24.3	10.1	98°	MNHNL BR704	22.1P	17.6P	–	33.4P	–	95°
MNHNL BR375-2	16.5P	–	–	29.8	–	97°	MNHNL BR705	26.5	19.7	–	40.8	–	94°
MNHNL BR455-2	21.4	15.0	–	31.1	–	95°	MNHNL BR708	12.6	10.5	8.0	20.5	–	102°
MNHNL BR466	22.0P	18.9	–	35.5	–	99°	MNHNL BR710	21.9	15.6	11.0	27.0	–	89°
MNHNL BR685	19.0P	14.7	–	36.2	–	91°	MNHNL BR754	20.9P	16.7P	–	26.5	–	92°
MNHNL BR698-1	21.5	15.0	–	26.1	–	93°	MNHNL HE133-1	16.0	14.7	–	29.5	–	90°
Trochotoma clypeus Terquem, 1855													
MNHNL BR124	10.4P	–	–	15.7	–	116°	MNHNL BR305-1	15.6	13.4	–	23.9	–	118°
Meiersia disarmata sp. nov.													
MNHNL BR358	12.4	–	10.4	29.6	13.4	156°	MNHNL BR873	8,8	7.9	6.4	19.2	8.6	150°
MNHNL BR758	11.6	–	11.0	27.2	13.5	–	MNHNL BR874	9.5	–	7.8	23.32	–	–
MNHNL BR872	14.4	–	11.1	35.4	15.2	157°							
Eucyclus sp.													
MNHNL GL205	–	33.2	22.3	36.9	19.7	60°							
Spirocirrus weisi sp. nov.													
MNHNL BR299	23.3	15.7	–	19.5	–	56°	MNHNL BR374	35.3	21.8	15.4	25.5P	–	54°
Platyacra aff. *sinistrorsa* (Terquem, 1855)													
MNHNL BR373	32.4P	24.6P	–	36.2	–	67°	MNHNL BR876	16.1P	11.9P	–	14.5P	–	65°

the Lusitanian Basin (Portugal), differs from *S*. (*S*.) *schmidti* only in its higher shell. The other differences mentioned by Böhm (1901), such as the larger size and the stronger ornament fall within the field of variability of *S*. (*S*.) *schmidti* as here described. This leaves open the possibility that *P. delgadoi* is a synonym of Dunker's (1844) species.

Helcion discrepans de Ryckholt, 1852 (Ryckholt 1852: 61, pl. 2: 24, 25; Chapuis and Dewalque 1853: 109, pl. 14: 7; Haber 1932: 155), from the Luxembourg Sandstone Formation, differs from *S.* (*S.*) *schmidti* in having an almost circular peristome, and a radial ornament composed of much stronger radial ribs which make the peristomal rim strongly crenulated.

Stratigraphic and geographic range.—Early Hettangian (*Psiloceras planorbis* Zone), Halberstadt (Saxony-Anhalt, Germany); Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); Hettangian, Le Simon-la-Vineuse (Vendée, France); ?Early Sinemurian, Coimbra (Lusitanian Basin, Portugal).

Subgenus *Hennocquia* Wenz, 1938

Type species: *Patella hennocquii* Terquem, 1855. Hettangian, Hettange-Grande (Lorraine, France).

Scurriopsis (*Hennocquia*) *hettangiensis* (Terquem, 1855)

Fig. 5D–I.

?1844 *Patella subquadrata* sp. nov.; Dunker 1844: 188.
?1847 *Patella subquadrata* Dunker; Dunker 1847: 113, pl. 13: 18a, b.
?1850 *Helcion dunkeri* nom. nov.; Orbigny 1850: 215 (pro *Patella subquadrata* Dunker, 1844 non York, 1837).
1855 *Patella hettangiensis* sp. nov.; Terquem 1855: 281, pl. 18: 2, 2a.
1855 *Patella dunkeri* Dunker [sic]; Terquem 1855: 280, pl. 18: 3, 3a, 3b.
1866 *Patella suttonensis* sp. nov.; Tawney 1866: 88, pl. 4: 9a, b.
1884 *Patella hettangiensis* Terquem; Quenstedt 1884: 755, pl. 215: 29.
1932 *Scurria hettangiensis* (Terquem); Haber 1932: 190–192.
1988 *Scurriopsis dunkeri* (Orbigny); Meier and Meiers 1988: 23, pl. 1: 1a, b.
1988 *Scurriopsis* (*Hennocquia*) *hennocquii* (Terquem); Meier and Meiers 1988: 23–24, pl. 1: 2a, b.
1988 *Scurriopsis hettangiensis* (Terquem); Meier and Meiers 1988: 24, pl. 1: 3a, b.

Material.—Thirty-three specimens: MNHNL BR153, MNHNL BR159, MNHNL BR239, MNHNL BR260, MNHNL BR363, MNHNL BR366, MNHNL BR377, MNHNL BR487, MNHNL BR488, MNHNL BR489, MNHNL BR490, MNHNL BR491, MNHNL BR492, MNHNL BR496, MNHNL BR497, MNHNL BR498, MNHNL BR499, MNHNL BR500, MNHNL BR503, MNHNL BR504, MNHNL BR505, MNHNL BR551, MNHNL BR650, MNHNL BR668, MNHNL BR669, MNHNL BR670, MNHNL BR671, MNHNL BR673, MNHNL BR674, MNHNL BR675, MNHNL BR756, MNHNL BR764, MNHNL BR767, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). Three specimens: MNHNL HE112, MNHNL HE122, MNHNL HE164, Brouch, Hettangian exact stratigraphical level unknown. Eight specimens: MNHNL GL154, MNHNL GL222 (four specimens), MNHNL GL250 (two specimens), MNHNL LI147, Luxembourg Sandstone Formation, locality and stratigraphical level unknown.

Dimensions.—See Table 1.

Description.—Medium-sized, limpet-shaped to cap-shaped shell with mamillated, moderately to strongly anterior apex. Shell wall somewhat thick. Peristome elliptical to subrectan-

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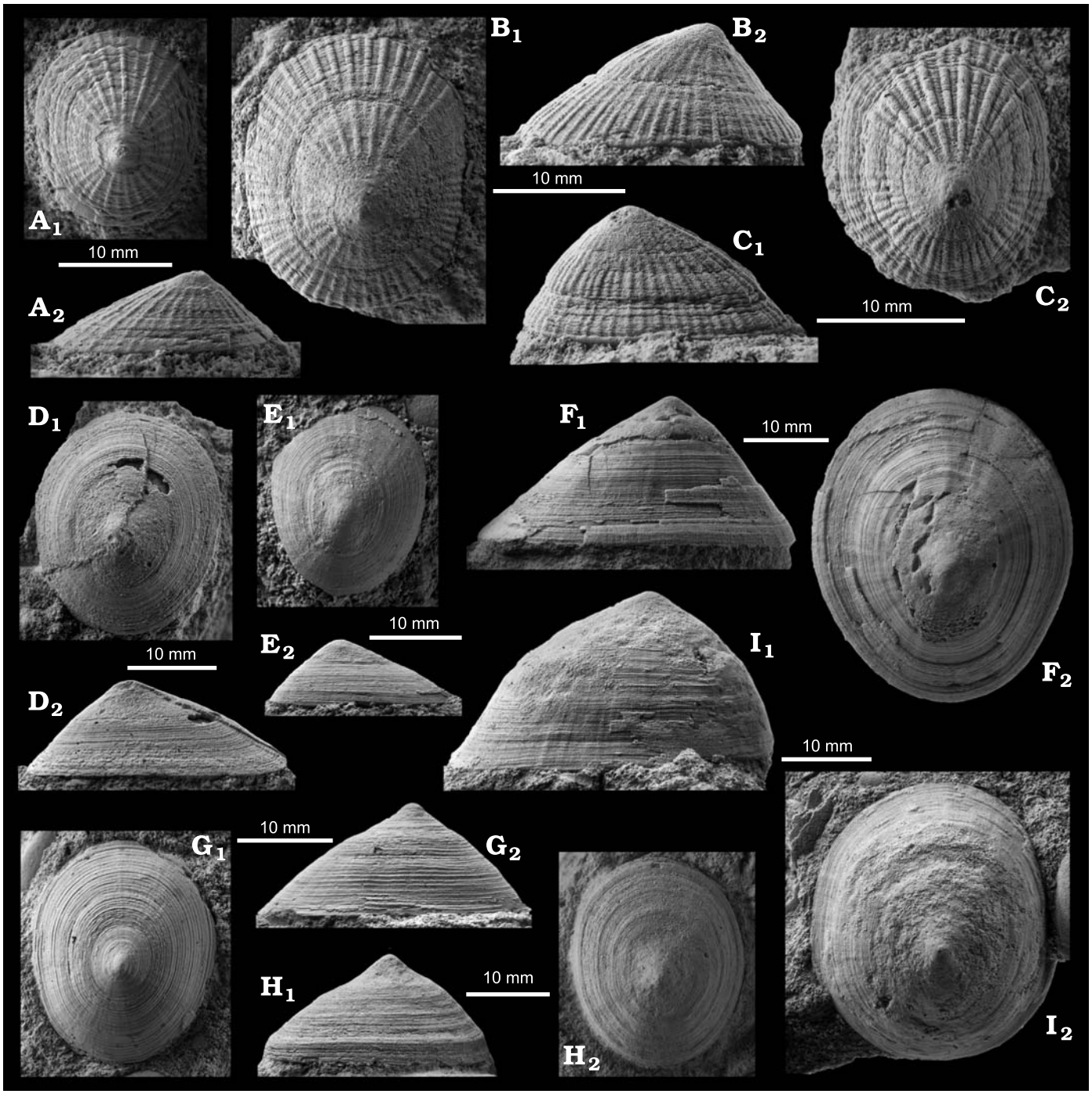

Fig. 5. Patellogastropods from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**–**C**. *Scurriopsis* (*Scurriopsis*) *schmidti* (Dunker, 1844). **A**. MNHNL BR180, apical (A_1) and lateral (A_2) views. **B**. MNHNL BR109, apical (B_1) and lateral (B_2) views. **C**. MNHNL BR360, lateral (C_1) and apical (C_2) views. **D**–**I**. *Scurriopsis* (*Hennocquia*) *hettangiensis* (Terquem, 1855). **D**. MNHNL BR503, apical (D_1) and lateral (D_2) views. **E**. MNHNL BR260, apical (E_1) and lateral (E_2) views. **F**. MNHNL BR673, lateral (F_1) and apical (F_2) views. **G**. MNHNL BR363, apical (G_1) and lateral (G_2) views. **H**. MNHNL BR650, lateral (H_1) and apical (H_2) views. **I**. MNHNL BR497, lateral (I_1) and apical (I_2) views.

gular and slightly narrower anteriorly. Width of peristome ranging 76–90% of its length. Height of the shell rather variable, 34–61% of its length. Posterior slope almost straight to definitely convex. Anterior slope slightly to strongly convex. Apex in anterior position at 56–73% of the total length of the shell. Surface of the shell covered with strong and sharp growth striae roughly forming threads. Obscure radial lines and riblets commonly present.

Remarks.—A comparison with *Scurriopsis* (*Hennocquia*) *hennocquii* Terquem, 1855, type species of *Scurriopsis* (*Hennocquia*) Wenz, 1938 facilitates the subgenus attribution of the species described here. *Scurriopsis* (*Hennocquia*)

hettangiensis (Terquem, 1855) shows strong similarities with *S.* (*H.*) *hennocquii* in the elliptical shape of the peristome, which is narrower in the anterior part, and in the shape of the lateral profile. *S.* (*H.*) *hennocquii* is characterised by a thin, light radial ornament of the posterior slope which Wenz (1938) and Cox and Keen (1960) considered to be significant at supraspecific level. However, in *S.* (*H.*) *hettangiensis* the surface of the shell is frequently crossed by variably obscure radial lines occurring on the whole surface of the shell or only on some parts of it. The characters differentiating *S.* (*H.*) *hennocquii* from S. (*H.*) *hettangiensis* are interpreted here as distinctive only at specific level. In addition to the slightly more marked radial ornament and its exclusively posterior location, *S.* (*H.*) *hennocquii* differs from S. (*H.*) *hettangiensis* in having a narrower outline of the peristome and a lower profile with slightly concave anterior slope.

As pointed out by Terquem (1855), *S.* (*H.*) *hettangiensis* displays a high variability in the general shape of the shell. The shell is moderately to rather high. The slopes are slightly to strongly convex. In most of the specimens the apex is moderately anterior but in some specimens it shifts to a strongly anterior position during growth. The early juvenile shell is commonly rather high. During the juvenile growth the shape of the shell becomes more depressed. However, in some specimens the inflation of the shell increases again during the adult growth. Constant characters consist of a mamillated shape of the apical shell, and an elliptical-subrectangular, posteriorly larger outline of the peristomal edge. The growth striae are always well-marked and form a variably rough pattern of commarginal threads.

In the light of the strong variability described above, *Patella suttonensis* Tawney, 1866 is here synonymised with *S.* (*H.*) *hettangiensis*, as was suggested by Haber (1932). *Patella dunkeri* d'Orbigny, 1850 (= *Patella subquadrata* Dunker, 1844, non York, 1837) is represented by very small specimens (Dunker 1847: 113, pl. 13: 18) which could represent the juvenile stage of *S.* (*H.*) *hettangiensis*. In that case, the name of Orbigny's (1850) species should have the priority (Haber 1932). The poor information about *P. dunkeri* prevents more detailed comparisons. The shell ascribed by Terquem (1855) to *P. dunkeri* is strongly reminishent of some of the specimens described here. For this reason, it is here included in the synonymy of *S.* (*H.*) *hettangiensis*.

Helcion infraliasina de Ryckholt, 1852 (Ryckholt 1852: 60, pl. 2: 26, 27; Chapuis and Dewalque 1853: 108, pl. 14: 6) from the Luxembourg Sandstone Formation differs from *S.* (*H.*) *hettangiensis* in having an evenly elliptical and less wide peristome, and in the surface of the shell which is ornamented with stronger radial striae.

Stratigraphic and geographic range.—Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); Late Hettangian to earliest Sinemurian, Sutton (South Wales, United Kingdom); ?Early Hettangian (*Psiloceras planorbis* Zone), Halberstadt (Saxony-Anhalt, Germany).

Subclass Neritimorpha Koken, 1896
Superorder Cycloneritimorpha Frýda, 1998
Order Neritoina Rafinesque, 1815
Superfamily Neritoidea Rafinesque, 1815
Family Neridomidae Bandel, 2008
Genus *Neridomus* Morris and Lycett, 1851

Type species: *Neridomus anglica* Cox and Arkell, 1950 (new name pro *Nerita hemisphaerica* Morris and Lycett, 1851, non Roemer, 1836). Bathonian, Minchinhampton (England).

Remarks.—The species described below are assigned to the genus *Neridomus* Morris and Lycett, 1851 for the presence of a broad, thick and smooth callus on the inner lip. According to Bandel (2008) this is one of the main characters of the family Neridomidae Bandel, 2008. *Neritaria* Koken, 1892 has a shell similar to that of *Neridomus.* It differs in having a tooth on the inner lip (Bandel 2007, 2008).

In some specimens (e.g., Figs. $6D_1$, $7A_3$, A_4) the callous pad shows a rounded swelling on the axial region of the base which could be interpreted as a tooth-like structure. However, this swelling is much shallower and more rounded than the tooth of *Neritaria*. Moreover, it is clearly an aspect of intraspecific variability and, most probably it is related to an occasional owergrowth of the callus.

Neridomus liasina (Dunker, 1844)

Fig. 6.

1844 *Neritina liasina* sp. nov; Dunker 1844: 188.
1847 *Neritina liasina* Dunker; Dunker 1847: 110–111, pl. 13: 13–16.
1855 *Neritina hettangiensis* sp. nov.; Terquem 1855: 262, pl. 15: 11.
1867 *Neritina hettangiensis* Terquem; Moore 1867: 564, pl. 15: 25, 26.
1901 *Neritina liasina* Dunker; Böhm 1901: 214–215, pl. 8: 3, 4.
1988 *Neritoma* (*Neridomus*) *hettangiensis* (Terquem); Meier and Meiers 1988: 27, pl. 3: 8a, b.
1992 *Neritoma* (*Neridomus*) *liasina* (Dunker); Szente 1992: 334, pl. 2: 14.

Material.—Ten specimens: MNHNL BR362, MNHNL BR446, MNHNL BR693, MNHNL BR696, MNHNL BR701 (two specimens), MNHNL BR702, MNHNL BR772, MNHNL BR877, MNHNL BR882, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Globose, obliquely elongated shell composed of about four, quite strongly convex whorls. Inner wall of the shell dissolved. Spire clearly to moderately elevated, formed by evenly convex whorls with rounded ramp. Last whorl with downward asymmetrical, pendant profile, and with concave subsutural band. Suture moderately impressed, quite rapidly shifting downward during the growth. Base globose, anomphalous. Aperture semilunar to drop-shaped, with distinct, acute sutural corner. Peristome continuous on the parietal lip and strongly prosocline. Outer lip sharp and smoothly passing to the basal lip. Inner lip very short. Parietal lip long. A broad, thickened, smooth to slightly swollen callus covers the inner and parietal lips and extends greatly over the base. Outer rim

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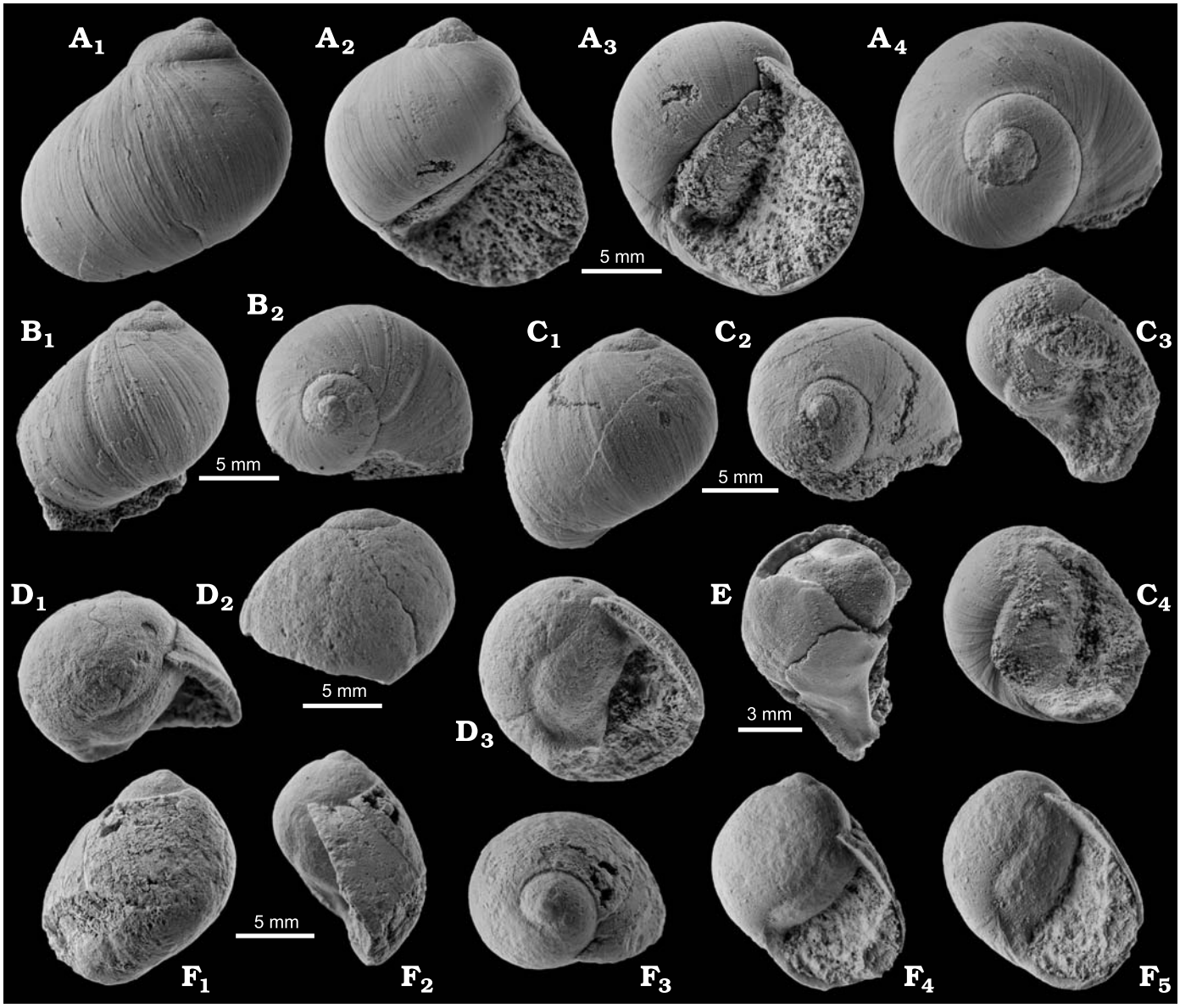

Fig. 6. Neritimorph gastropod *Neridomus liasina* (Dunker, 1844) from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. MNHNL BR362, dorsal (A_1), apertural (A_2), subapertural (A_3), and apical (A_4) views. **B**. MNHNL BR701-1, dorsal (B_1), and apical (B_2) views. **C**. MNHNL BR701-2, dorsal (C_1), apical (C_2), apertural (C_3), and subapertural (C_4) views. **D**. MNHNL BR702, apertural (D_1), dorsal (D_2), and subapertural (D_3) views. **E**. MNHNL BR882 showing the absence of the inner shell wall by dissolution. **F**. MNHNL BR877, dorsal (E_1), lateral (E_2), apical (E_3), apertural (E_4), and subapertural (E_5) views.

of callus distinct, evenly and widely arched in its lower part, slightly sinuous in its upper part. Apertural rim of callus slightly wavy. Shell smooth. Growth lines prosocline, straight to slightly prosocyrt.

Remarks.—Distinctive characters are the obliquely elongated shell, the asymmetrical, pendant profile of the whorls, which is slightly concave on the subsutural band of the last whorl, and the suture that distinctly shifts downward during the adult growth. These features permit us to ascribe the material to *Neridomus liasina* (Dunker, 1844).

Neridomus hettangiensis (Terquem, 1855) seemingly differs from *N. liasina* in having a more impressed suture resulting in a more turbiniform shape of the spire. However, Dunker (1847) described a rather high variability in *N. liasina*. A relatively high variability has been observed in the specimens from Luxembourg as well. This mainly concerns the height of the spire and the convexity of the whorls. Thus, there is a morphological continuity between *N. liasina* and *N. hettangiensis* and both the species probably represent synonyms.

Stratigraphic and geographic range.—Early Hettangian (*Psiloceras planorbis* Zone), Halberstadt (Saxony-Anhalt, Germany); Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); Hettangian, Mecsek Mountains (southern Hungary); Late Hettangian to Early Sinemurian, Coimbra and Algarve (Lusitanian Basin,

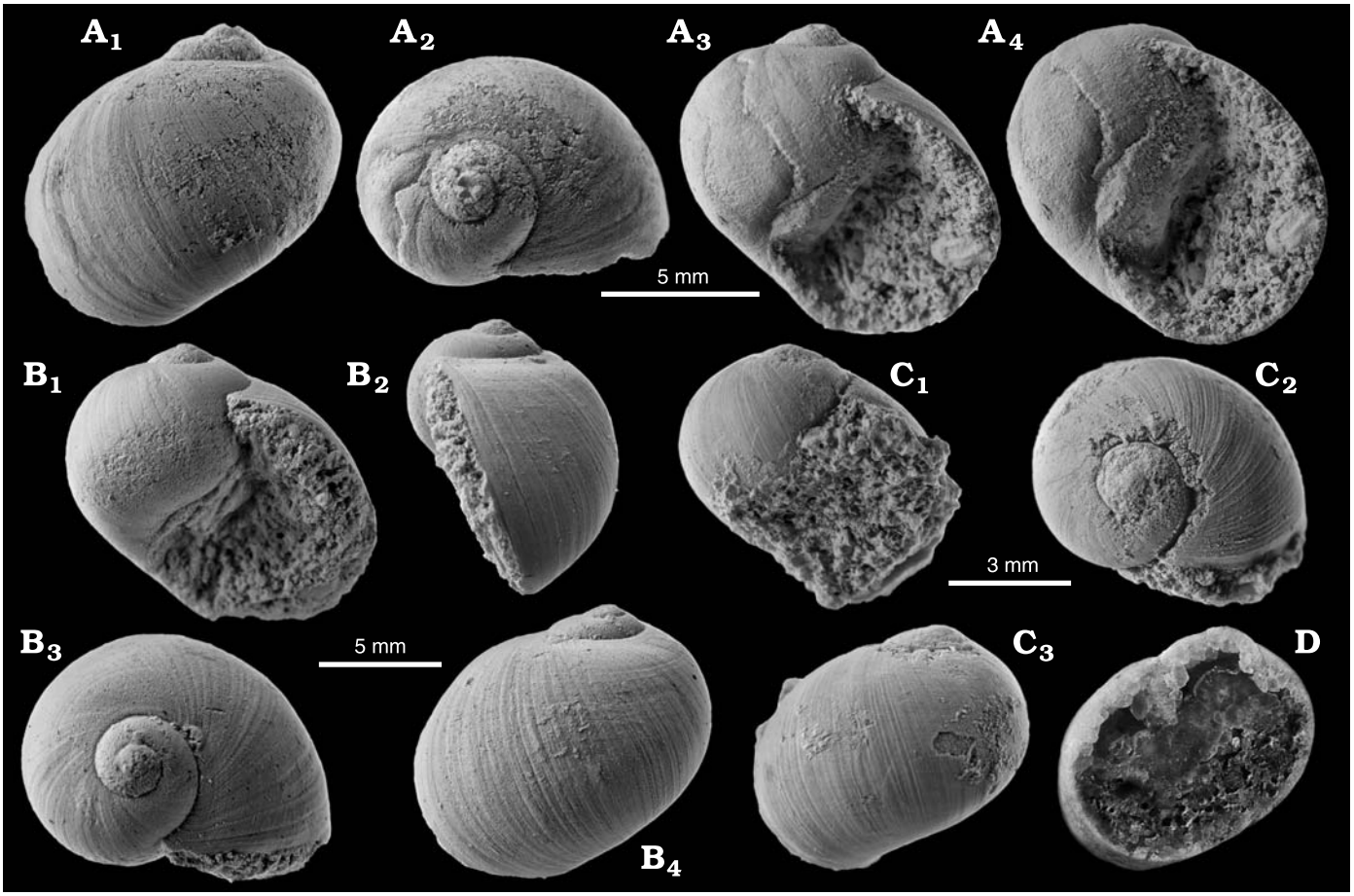

Fig. 7. Neritimorph gastropod *Neridomus cannabis* (Terquem, 1855) from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. MNHNL BR365, dorsal (A_1), apical (A_2), apertural (A_3), and subapertural (A_4) views. **B**. MNHNL BR878, apertural (B_1), lateral (B_2), apical (B_3), and dorsal (B_4) views. **C**. MNHNL BR879, apertural (C_1), dorsal (C_2), and apical (C_3) views. **D**. MNHNL BR883, subaxial section showing the absence of the inner shell wall by dissolution.

Portugal); earliest Sinemurian (*Coroniceras* [*Arietites*] *bucklandi* Zone), Southerndown (South Wales, United Kingdom).

Neridomus cannabis (Terquem, 1855)

Fig. 7.

1855 *Neritina cannabis* sp. nov.; Terquem 1855: 262, pl. 15: 12a, b.
?1855 *Neritina arenacea* sp. nov.; Terquem 1855: 263, pl. 15: 10a, b.
1867 *Neritina canalis* [sic] Terquem; Moore 1867: 564, pl. 15: 21, 22.
1902 *Neritina cannabis* Terquem; Cossmann in Chartron and Cossmann 1902: 193–194, pl. 4: 18, 19.
1988 *Neritoma* (*Neridomus*) *arenacea* (Terquem); Meier and Meiers 1988: 27, pl. 2: 7a, b.

Material.—Five specimens: MNHNL BR305, MNHNL BR365, MNHNL BR878, MNHNL BR879, MNHNL BR883, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Neritiform, globose shell consisting of four, strongly convex whorls. Inner wall of the shell dissolved. Spire moderately prominent. Whorls profile evenly convex in the juvenile and adult spire, slightly downward asymmetrical in the last whorl. Whorls provided with a convex ramp smoothly passing to the outer whorl face and becoming indistinct during the last growth. Suture slightly impressed and shifting downward only in the final half of the last whorl. Periphery well rounded and not exposed on the spire. Base globose and anomphalous. Aperture drop-shaped, with acute sutural corner. Peristome prosocline and continuous on the parietal lip. Outer lip evenly convex, increasing its convexity in the basal part. Parietal region strengthened by a strong and broad callus covering the axial depression of the base where it can form a slightly swollen pad. Outer rim of callus distinct, forming a semicircular line around the axial region of the base. Apertural rim of callus sharp, slightly concave along the middle part of parietal lip. Shell smooth. Growth lines prosocline, almost straight on the spire, feebly prosocyrt on the base.

Remarks.—The smallest specimens (MNHNL BR305, MNHNL BR365) correspond to the original description and illustration of *Neridomus cannabis* (Terquem, 1855), a species erected by Terquem (1855) based on shells with a size of few millimetres. However, some of the largest specimens tend to resemble *Neridomus arenacea* (Terquem, 1855). One cannot exclude that a detailed study of more material would

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reveal that *N. arenacea* represents the fully adult stage of *N. cannabis*.

Neridomus cannabis clearly differs from *Neridomus liasina* (Dunker, 1844) in its smaller size, a more globose shape of the shell, and more evenly convex whorls. Moreover, in *N. cannabis* the suture is more impressed and it shifts downward only during the last growth stage.

The specimen ascribed by Bourrouilh (1966: 34, fig. 6) to *N. cannabis*, from the Early Sinemurian (*Caenisites turneri* Zone to *Asteroceras obtusum* Zone) of Rosfet-er-Rjem (Eastern High Atlas, Morocco) (Bourrouilh 1966; Dresnay 1966) has a much more depressed spire, and the whorls lack a ramp. This assignment to Terquem's (1855) species is highly questionable.

Stratigraphic and geographic range.—Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); Hettangian, Le Simon-la-Vineuse (Vendée, France); earliest Sinemurian (*Coroniceras* [*Arietites*] *bucklandi* Zone), Brocastle (South Wales, United Kingdom).

Superfamily Neritopsoidea Gray, 1847

Family uncertain

Genus *Bandelopsis* Frýda, Blodgett, and Stanley, 2003

Type species: *Bandelopsis oregonensis* Frýda, Blodgett, and Stanley, 2003. Late Carnian–Early Norian, Wallowa Mountains (Oregon, USA).

Remarks.—The following species are here tentatively ascribed to the genus *Bandelopsis* Frýda, Blodgett, and Stanley, 2003 on the basis of the general shape of the shell and ornament. Moreover in the specimen here assigned to *Bandelopsis*? sp. the peristome, though partly preserved, is very similar to that of the type species, *B. oregonensis* Frýda, Blodgett, and Stanley, 2003, i.e., thickened, slightly trumpet-shaped and with inner lip seemingly smooth and simple.

The species described below differ from *B. oregonensis* in having a larger number of spiral cords, and a slightly convex and inclined ramp. They differ from *Nuetzelopsis* Frýda, Blodgett, and Stanley, 2003 in having the ramp delimited by a distinct outer angulation and in the presence of granules or nodes at the intersection of the collabral ribs wih the spiral cords. The poor preservation of the material and the few available specimens suggest to leave open their generic assignment.

According to Bandel (2007), a simple inner lip distinguishes *Bandelopsis* from *Fossariopsis* Laube, 1869. The latter has the inner lip with two teeth separated by a median depression which is a diagnostic character of the family Neritopsidae Gray, 1847 (Bandel 2007, 2008). For this reason, Bandel (2007) excluded *Bandelopsis* from the Neritipsidae, but he did not suggest an alternative systematic placement for Frýda et al.'s (2003) genus. In fact, none of the combinations of characters established by him for identifying the neritimorph families corresponds to that exhibited by *Bandelopsis*.

Bandelopsis? cf. *exigua* (Terquem, 1855)

Fig. 8A, B.

cf. 1855 *Neritopsis exigua* sp. nov.; Terquem 1855: 279, pl. 17: 11a, b.
?1861 *Neritopsis compressula* sp. nov.; Gümbel 1861: 861.
?1867 *Neritopsis exigua* Terquem; Moore 1867: 547–548, pl. 15: 19.
?1893 *Neritopsis compressula* Gümbel; Ammon 1893: 174–175, fig. 12.
1988 *Neritopsis exigua* Terquem; Meier and Meiers 1988: 25–26, pl. 2: 5a, b.

Material.—Four specimens: MNHNL BR300, MNHNL BR357, MNHNL BR700, MNHNL BR880, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Globose, relatively small-sized shell with prominent spire. Spire formed by about four rapidly expanding whorls with inner shell wall not dissolved. Early spire with relatively high, convex whorls. Last whorls bearing a spiral angulation which delimits a somewhat wide ramp. Ramp shallow, inclined and feebly convex. Suture impressed and downward shifting on the last whorl. Outer whorl face convex, with lower rim corresponding to a rounded, feeble angulation which becomes slightly exposed on the spire during the last whorl growth. Base well rounded and swollen, seemingly anomphalous or with a very narrow axial fessure. Ornament consists of collabral ribs crossed by spiral threads. Collabral ribs prosocline, strong, evenly sized and widely spaced. They tend to vanish on the ramp where they disappear before reaching the adapical suture. About ten collabral ribs on the last whorl which smoothly pass onto the base. Spiral threads of two alternating orders in the juvenile spire. They become almost equally strong on the last whorl. Last whorl sculptured with about fifteen spiral threads on the base and about ten on the ramp. The spiral threads limiting the outer whorl face are more marked than the others. Intersection between spiral threads and collabral ribs marked by granulae and by low nodes on the outer angulation of the ramp. Growth lines prosocline, prosocyrt on the spire and slightly opisthocyrt on the base.

Remarks.—The material shows similarities to *Bandelopsis*? *exigua* (Terquem, 1855), from the Hettangian of Hettange-Grande (Lorraine, France) in the growth rate, in the height of the spire, and in the sculpture of the ramp. However, Terquem (1855) erected the species on the basis of a single specimen partly embedded in the sediment, whose characters are hardly noticeable. This forced us to leave open the species attribution.

The specimen from the Hettangian of the Vendée (western France) ascribed by Cossmann (in Chartron and Cossmann 1902: 193, pl. 4: 29, 30) to *Neritopsis exigua* Terquem, 1855 shows a much more laterally compressed shell. The ornament consists of collabral riblets which are nearly as strong as the spiral threads, thus producing an evenly reticulated pattern. The specimen from the Early Sinemurian of the Peloritani Mountains (eastern Sicily, Italy) described by Lentini (1973: 61, pl. 18: 10) as *N.* aff. *exigua* has a clearly less globose shell and a much more acute and prominent

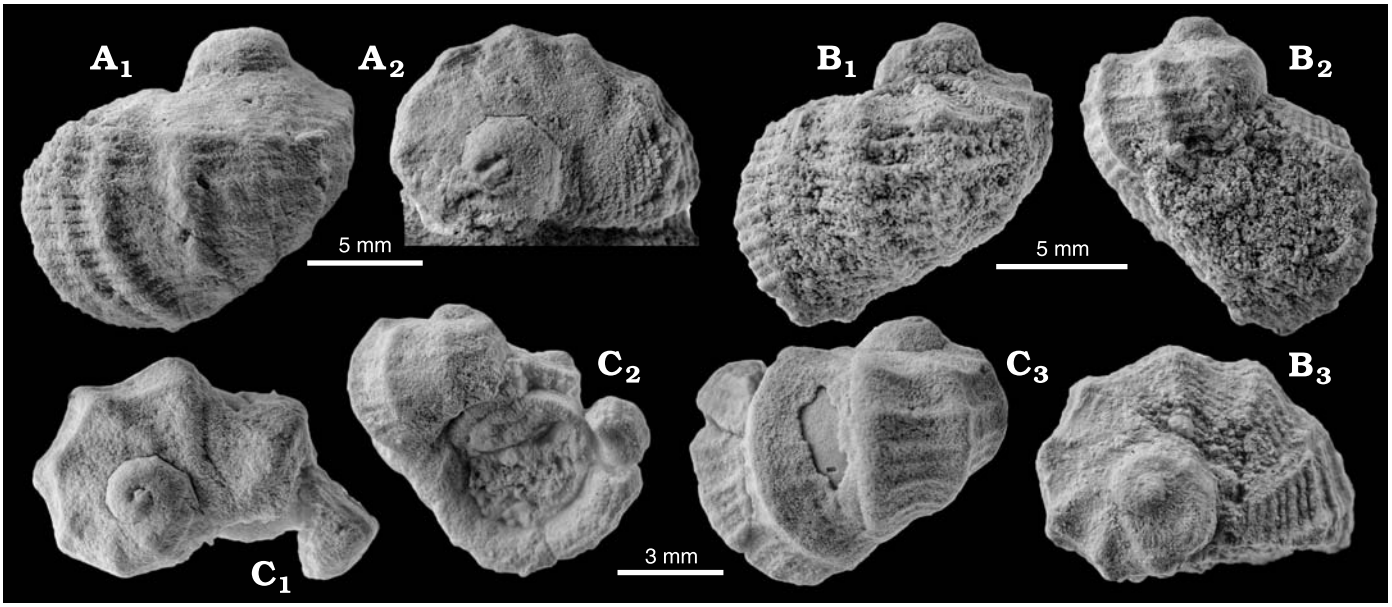

Fig. 8. Neritopsoideans from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**, **B**. *Bandelopsis*? cf. *exigua* (Terquem, 1855). **A**. MNHNL BR880, dorsal (A_1), and apical (A_2) views. **B**. MNHNL BR700, dorsal (B_1), apertural (B_2), and apical (B_3) views. **C**. *Bandelopsis*? sp., MNHNL BR367, apical (C_1), apertural (C_2), and dorsal (C_3) views.

spire. Moore (1867) quoted *N. exigua* in the lowermost Sinemurian sediments of Brocastle (Glamorganshire, United Kingdom). However, the poor illustration and description made by that author prevent more detailed comparisons.

The specimens described here are also strongly reminiscent of *Neritopsis compressula* Gümbel, 1861, a species known from the Early Jurassic sediments of the Hochfelln Mountain (Northern Calcareous Alps, Austria). They differ in the presence of a more inclined and wider ramp on the adult shell. Moreover the ramp is sculptured with a marked spiral ornament.

Stratigraphic and geographic range.—Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); ?Hettangian, Hettange-Grande (Lorraine, France); ?Hettangian–earliest Sinemurian, South Wales (United Kingdom); ?Early Jurassic, Hochfelln Mountain (Northern Calcareous Alps, Austria).

Bandelopsis? sp.

Fig. 8C.

1988. *Neritopsis* cf. *hebertan* [sic] d'Orbigny; Meier and Meiers 1988: 26, pl. 2: 6a, b.

Material.—One specimen: MNHNL BR367, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Neritiform, globose, moderately small-sized shell. Spire composed of about four rapidly expanding whorls. Early spire with relatively high and convex whorls. Last whorls exhibiting a spiral angulation which delimits a wide ramp. Ramp almost flat, slightly inclined, becoming feebly convex on the last whorl. Base globose. Umbilicus absent or reduced to a narrow axial fissure. Aperture subcircular and slightly elongated at the junction of the inner lip with the basal lip. Peristome continuous, with a rather thick parietal lip. Outer lip strengthened by an outer varix and smoothly passing to the inner lip. Inner lip strong, seemingly simple and smooth. Ornament composed of collabral ribs crossed by spiral threads. Collabral ribs originating from peristomal varices. They are prosocline, quite strong, evenly sized and spaced, and tend to fade out towards the upper suture. About ten collabral ribs on the last whorl. Spiral ornament composed of primary spiral threads alternating with secondary spiral threads. During the growth the secondary spiral threads appear into the interspaces between the primary spiral threads. Outer angulation of the ramp bearing a row of nodes. Growth lines prosocline, prosocyrt on the ramp, almost straight on the whorl side, straight to slightly opisthocyrt on the base.

Remarks.—The specimen differs from those ascribed here to *Bandelopsis*? cf. *exigua* (Terquem, 1855) in having a smaller size, a higher W/H ratio, and a less prominent spire. Moreover, the ramp is narrower and less sloping, and it lacks a spiral ornament. Finally, the collabral ribs are stronger. The presence in the material of a single specimen prevents further comparisons and the determination of the species variability.

Subclass Archaeogastropoda Thiele, 1925

Order Vetigastropoda Salvini-Plawen, 1980

Suborder Pleurotomariina Cox and Knight, 1960

Superfamily Pleurotomarioidea Swainson, 1840

Family Pleurotomariidae Swainson, 1840

Genus *Pleurotomaria* Defrance, 1826

Type species: *Trochus anglicus* Sowerby, 1815. Early Jurassic, Somerset (England).

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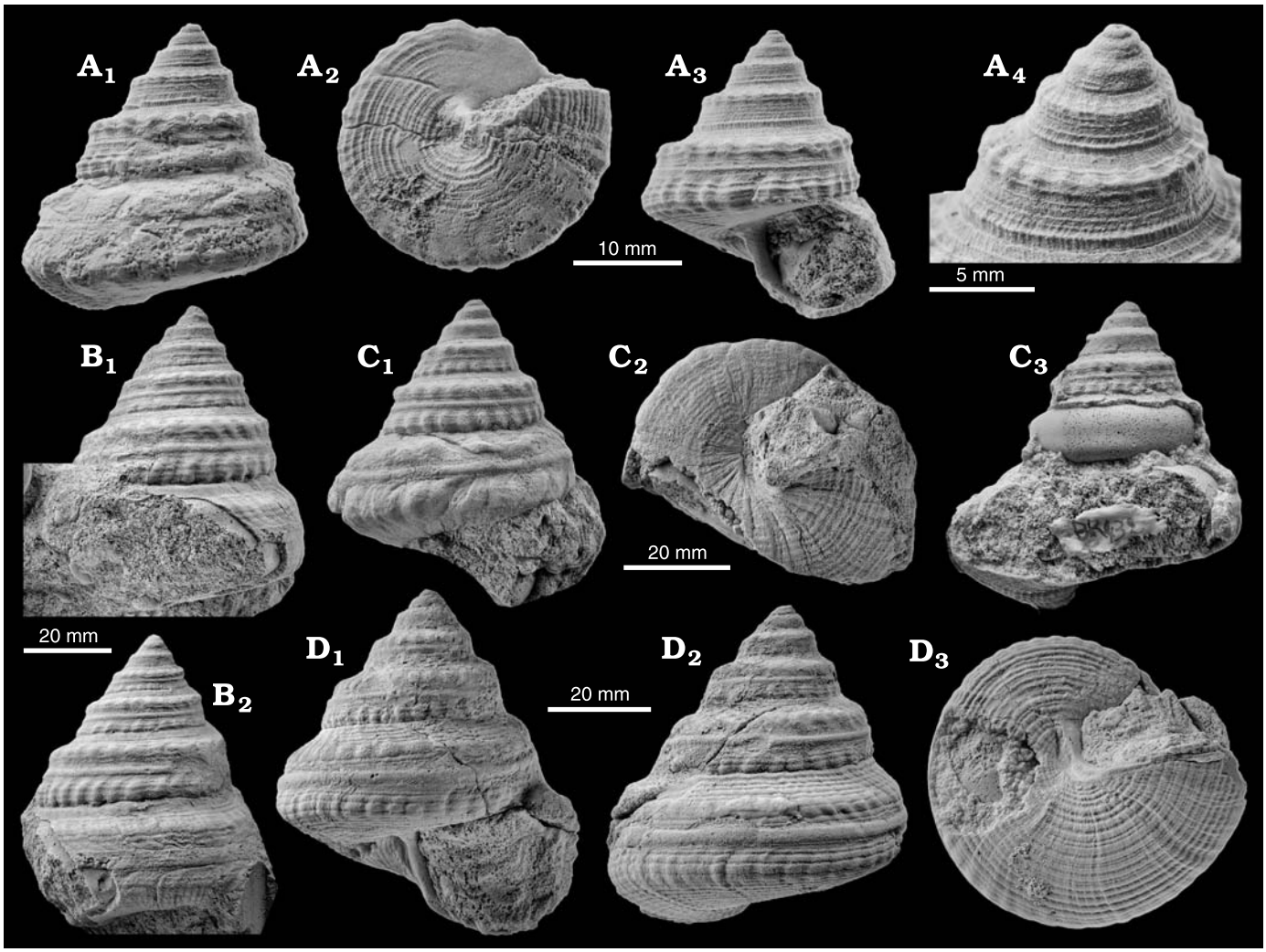

Fig. 9. Pleurotomariid gastropod *Pleurotomaria wanderbachi* Terquem, 1855 from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. MNHNL BR359, dorsal (A_1), basal (A_2), apertural (A_3) views, and detail of the apical spire (A_4). **B**. MNHNL BR306-2, lateral (B_1) and sublateral (B_2) views. **C**. MNHNL BR432-1, apertural (C_1), basal (C_2), and dorsal (C_3) views. **D**. MNHNL BR308, apertural (D_1), dorsal (D_2), and basal (D_3) views.

Pleurotomaria wanderbachi Terquem, 1855

Fig. 9.

1855 *Pleurotomaria wanderbachi* sp. nov.; Terquem 1855: 270, pl. 16: 13, 13a.

1855 *Pleurotomaria mosellana* sp. nov.; Terquem 1855: 274, pl. 16: 14, 14a.

1855 *Pleurotomaria densa* sp. nov.; Terquem 1855: 274, pl. 17: 1a, b.

1988 *Pleurotomaria mosellana* Terquem; Meier and Meiers 1988: 30–31, pl. 6: 12a, b.

Material.—Five specimens: MNHNL BR306-2, MNHNL BR308, MNHNL BR359, MNHNL BR432-1, MNHNL BR677, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). One specimen: MNHNL GL121, Mamer (Kaatzefiels), Luxembourg Sandstone Formation, stratigraphical level unknown.

Dimensions.—See Table 2.

Description.—Shell trochiform, gradate. Whorls rather high, angulated and with trapezoidal cross-section. Juvenile shell feebly cyrtoconical, adult shell almost conical. Ramp oblique, moderately wide and significantly narrower than the outer whorl face. During the adult growth, the ramp becomes slightly convex and the angulation of the whorls tends to fade out. Sutures impressed. Selenizone running on or slightly above the middle of the outer whorl face. It is flat on the juvenile spire and becomes convex and rather wide on the adult shell. In some specimens the selenizone tends to become flat again on the last growth stage. Periphery subangulated, not exposed on the juvenile spire, becoming exposed on the last whorls. Base flattened with feebly convex surface. Umbilicus absent to very narrow. Aperture subtrapezoidal, slightly larger than high. Peristome discontinuous on the parietal lip. Inner lip robust, reinforced by a callus, slightly prosocline and passing to the basal lip through an evenly rounded curve. Umbilical cavity partly closed by the outward reflection of the callus of inner lip. Parietal lip orthogonal to the columellar lip and covered by a very thin shelly coating. Collabral ornament consists of densely and regularly spaced threads. These are clearly

visible especially on the ramp and on the part of the outer whorl face below the selenizone of the juvenile whorls. Angulation of the whorls and peripheral angulation bearing marked nodes. Nodes on the peribasal angulation slightly more numerous and smaller than those on the angulation of the whorls. The angulation of the whorls bears about twenty-five nodes per whorl on the adult shell. On the last whorls, the nodes of the peripheral angulation tend to fade out. Spiral ornament consists of about four to six, relatively strong, widely spaced spiral threads on the ramp and on the part of the outer whorl face above the selenizone. Two to three widely spaced spiral threads run below the selenizone. Selenizone delimited by thin marginal spiral threads. On the juvenile spire, a sharp lira appears along the mid-line of the selenizone which becomes more and more prominent and wide during the adult growth so that the selenizone becomes bulge-shaped. Strong, dense, evenly spaced spiral threads ornament the base. Growth striae feebly prosocline and prosocyrt above the selenizone, slightly opisthocline to orthocline and prosocyrt below the selenizone, widely opisthocyrt on the base.

Remarks.—The material consists of a juvenile and several adult specimens showing a relatively low variability in the shell proportions and sculpture. *Pleurotomaria wanderbachi* Terquem, 1855 is here synonymised with other two species erected by Terquem (1855) in the same paper, namely *Pleurotomaria mosellana* Terquem, 1855 and *Pleurotomaria densa* Terquem, 1855. The holotype of *P. mosellana* differs from *P. wanderbachi* only in having stronger and less numerous nodes, a difference considered here to be included in the intraspecific variability. The holotype of *P. densa* differs from *P. wanderbachi* in a more rounded last whorl which tends to lose the nodes. These changes frequently appear during the latest growth of the pleurotomariid species. As a matter of fact, the sequence represented by *P. mosellana*, *P. wanderbachi* and *P. densa* corresponds to the transition from the juvenile to the adult shell of the same species, as also supported by the size of the specimens figured by Terquem (1855).

Pleurotomaria anglica Sowerby, 1815 (Sowerby 1815: 95, pl. 142) closely resembles *P. wanderbachi* in the general shape of the shell, in the main elements of the ornament and in the position of the selenizone. However, *P. anglica* has the outer whorl face and the nodes of the basal angulation ornamented by a pattern of thin and dense spiral lines whereas in *P. warderbachi* these parts of the shell are sculptured with few and marked spiral threads. Moreover, in *P. anglica* the selenizone is less prominent.

Stratigraphic and geographic range.—Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg).

Pleurotomaria hettangiensis Terquem, 1855

Fig. 10A–D.

1855 *Pleurotomaria hettangiensis* sp. nov.; Terquem 1855: 273, pl. 17: 2a, b.

?1907 *Pleurotomaria princeps* (Koch and Dunker); Sieberer 1907: 12–13, pl. 1: 2a, b.

1988 *Pleurotomaria hettangiensis* Terquem; Meier and Meiers 1988: 29–30, pl. 5: 11a, b.

Material.—Five specimens: MNHNL BR294, MNHNL BR304, MNHNL BR375-1, MNHNL BR443, MNHNL BR676, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). One specimen MNHNL GL281, Hespérange, Upper Hettangian.

Dimensions.—See Table 2.

Description.—Shell trochiform with a moderately gradate outline. Juvenile spire conical, composed of relatively high whorls. Ramp rather narrow and appearing from about the third whorl. Adult spire cyrtoconical, with an oblique and relatively narrow ramp delimited by an obtuse angulation. Ramp flat to slightly concave. Surface of the outer whorl face slightly inclined and flat. Sutures moderately impressed. Periphery angulated and slightly swollen. Base narrowly umbilicated and with a feebly convex surface. Selenizone rather wide, running at or slightly below the middle of the outer whorl face. It is convex and bulge-shaped in the adult shell. Aperture subtrapezoidal, wider than high, with discontinuous peristome on the parietal lip. Inner lip robust, inclined, and orthogonal to the basal lip. Inner lip callus relatively strong, outward reflected and partly closing the umbilical cavity. Parietal region covered by a very thin shelly coating. Ornament of the first observable whorls seemingly faint. Adult ornament consisting of spiral threads, collabral riblets and nodes at the angulation of the whorls and at the peripheral angulation. Spiral threads sharp and well spaced. Three spiral threads ornament the ramp. Two to three spiral threads run on the outer whorl face either above and below the selenizone. Collabral riblets feeble, prosocline on the ramp. They start from nodes on the angulation of the whorls and disappear before reaching the upper suture. The nodes at the angulation of the whorls are slightly prosocline and do not extend to the outer whorl face; those on the peripheral angulation are smaller, more elongated and opisthocline. Last whorls with about thirty nodes on the upper angulation. Selenizone almost smooth on the adult shell, delimited by sharp, marginal spiral lines. Base ornamented with dense spiral threads. Irregularly spaced and sized collabral ribs, made by strong and sinuous growth striae, arise from the peribasal nodes and tend to disappear during the last growth. Growth striae feebly prosocline and prosocyrt above the selenizone, slightly opisthocline to orthocline and prosocyrt below the selenizone, widely opisthocyrt on the base.

Remarks.—In Terquem's collection housed in the UCBL, the specimen indicated as the holotype of *Pleurotomaria hettangiensis* Terquem, 1855 is somewhat different from the original illustration given by the author (Terquem 1855: 273, pl. 17: 2) and from the specimens described herein. Indeed, it exhibits more numerous and smaller nodes and sharper collabral ribs. Moreover, during the growth of the last whorl the outer rim of the ramp becomes rounded and tends to lose the nodes. The analysis of the material from Luxembourg re-

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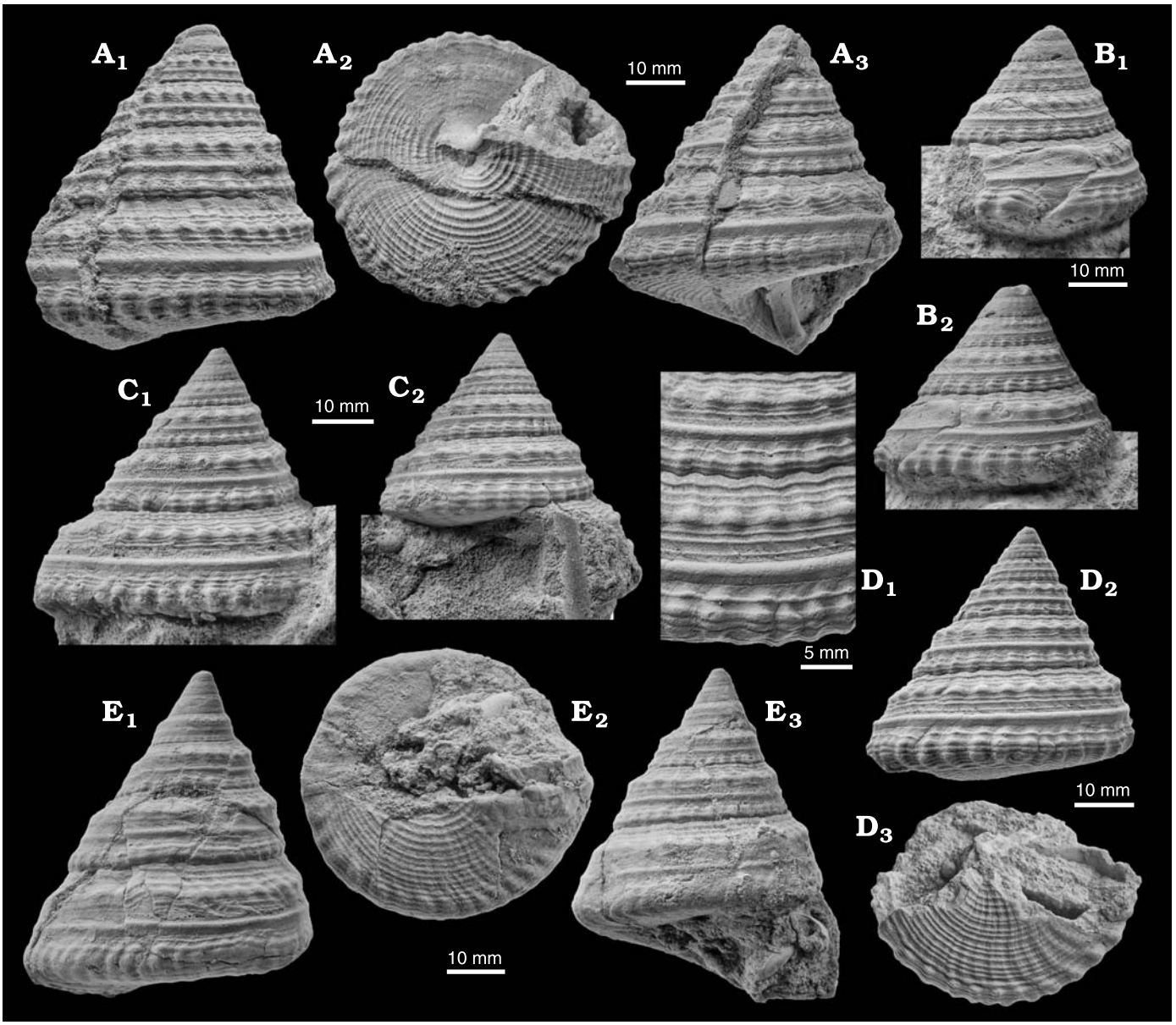

Fig. 10. Pleurotomariid gastropods from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**–**D**. *Pleurotomaria hettangiensis* Terquem, 1855. **A**. MNHNL BR294, dorsal (A_1), basal (A_2), and apertural (A_3) views. **B**. MNHNL BR676, lateral (B_1) and dorsal (B_2) views. **C**. MNHNL BR375-1, dorsal (C_1) and apertural (C_2) views. **D**. MNHNL BR443, detail of the ornament (D_1), dorsal (D_2), and basal (D_3) views. **E**. *Pleurotomaria* cf. *hettangiensis* Terquem, 1855, MNHNL BR432-2, dorsal (E_1), basal (E_2), and apertural (E_3) views.

veals that these differences are representative of the intraspecific variability and of the adult ontogenetic changes of *P. hettangiensis*, respectively.

Pleurotomaria hettangiensis Terquem, 1855 differs from most of the other Jurassic relatives in having a much less gradate shell owing to a narrower ramp. Consequently, the general shape of the shell tends to be conical. For this reason, it shows some similarities with *Pleurotomaria princeps* Koch and Dunker, 1837 (Koch and Dunker 1837: 26, pl. 1: 18). However, in *P. princeps*, the whorls lack a ramp and, consequently the shell is definitely conical. Moreover, the selenizone is lower on the whorl surface than in *P. hettangiensis*. In agreement with Fischer and Weber (1997: 156, 160, pl. 34: 10, 11), *P. princeps* should be assigned to the genus *Pyrgotrochus* Fischer, 1885.

Joly (1936: 75, pl. 1: 2) ascribed to *P. hettangiensis* some conical, not gradate shells that most probably should be assigned to *P. princeps*. In contrast, the specimen figured by Sieberer (1907) as *P. princeps* has a gradate shell and an ornament pattern similar to those of *P. hettangiensis*. It differs from the type material of Terquem's (1855) species and from the specimens described here in having a sharper ornament and a wider umbilicus. These differences could fall within the variability of *P. hettangiensis*.

Sacchi Vialli (1964: 5, pl. 1: 7–9) reviewed the gastropod fauna from the Sinemurian of Lombardy (northern Italy) pub-

lished by Parona (1893) and synonymised *Pleurotomaria oblita* Parona, 1893 (Parona 1893: 166, pl. 6: 4) and *Pleurotomaria granulatocincta* Parona, 1893 (Parona 1893: 166, pl. 6: 6), with *P. hettangiensis*. However, these species are clearly distinct from *P. hettangiensis* owing to their general shape of the shell and ornament details. Moreover, Parona (1893) described *P. oblita* and *P. granulatocincta* as anomphalous, whereas *P. hettangiensis* has a narrow umbilicus.

Pleurotomaria wanderbachi Terquem, 1855 differs from *P. hettangiensis* in having a more acute spiral angle, higher whorls, a wider ramp and a much less inclined outer whorl face. Moreover, the juvenile shell of *P. wanderbachi* is definitely gradate whereas in *P. hettangiensis* it tends to be conical. Finally, in *P. wanderbachi* the nodes on the outer edge of the ramp are slightly less numerous and more widely spaced.

Pleurotomaria anglica (Sowerby, 1815) differs from *P. hettangiensis* in the same characters listed above concerning the comparison between Sowerby's (1815) species and *P. wanderbachi*. Moreover, *P. hettangiensis* has a tendentially less high spire and a wider spiral angle.

Stratigraphic and geographic range.—Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); ?Late Hettangian (*Schlotheimia angulata* Zone), Ostdorf (Baden-Württemberg).

Pleurotomaria cf. *hettangiensis* Terquem, 1855

Fig. 10E.

Material.—One specimen: MNHNL BR432-2, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Remarks.—The specimen exhibits strong similarities with the material here assigned to *Pleurotomaria hettangiensis* Terquem, 1855. These concern the conical shape of the juvenile shell, the narrow ramp, the elements of the ornament, and the shape and position of the selenizone. It differs from the specimens ascribed here to *P. hettangiensis* in the narrower spiral angle and the slightly less prominent nodes. These differences are probably due to intraspecific variability. However, there are no intermediate morphs in the present material so that we leave species assignment of this specimen open.

The specimen differs from *Pleurotomaria wanderbachi* Terquem, 1855 in the shape of the juvenile shell. It is conical with flat whorls almost lacking a ramp, whereas in *P. wanderbachi* it is definitely gradate.

Pleurotomaria hennocquii Terquem, 1855

Fig. 11A.

1855 *Pleurotomaria hennocquii* sp. nov.; Terquem 1855: 275, pl. 16: 12, 12a.

Material.—One specimen: MNHNL BR881, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Trochiform, slightly cyrtoconical shell composed of about six whorls. Juvenile whorls moderately convex, with a weak, rounded angulation delimiting a slightly concave, relatively narrow ramp. Selenizone clearly raised on the whorl surface, running below the angulation and on the upper part of a convex outer whorl face. Convexity of the whorls increasing during the adult growth. Last whorls markedly and almost evenly convex, with feebly concave subsutural band. Suture impressed. Peripheral rim of the base subangulated. Selenizone of adult whorls relatively wide, running below the mid-line of the whorl surface and delimited by thin spiral lines. Spiral ornament composed of threads. They are thin, widely spaced and with slight variations in strength on the juvenile spire. The adult spire is ornamented with about six spiral threads of unequal strength running either above and below the selenizone. Thin, sharp and dense growth threads and spiral threads form a finely reticulate ornament with fine granules at the intersection. Peripheral angulation of the base bearing a row of low and small nodes which are exposed on the spire just above the suture. Small and dense nodes mark the angulation of the juvenile whorls, which attenuate during the adult growth. Selenizone seemingly smooth. Growth lines slightly prosocline above the selenizone, opisthocline below it.

Remarks.—This species belongs to the genus *Pleurotomaria* Defrance, 1826 as indicated by the morphology of the juvenile spire which bears a nodose angulation and by the selenizone running on the outer whorl face. It differs from the other congeneric species described here in having strongly and almost evenly convex mature whorls and in the weakness of the nodose ornament.

Stratigraphic and geographic range.—Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg).

Pleurotomaria cognata Chapuis and Dewalque, 1853

Fig. 11B, C.

1853 *Pleurotomaria cognata* sp. nov.; Chapuis and Dewalque 1853: 95–96, pl. 13: 1a, b.

?1936 *Pleurotomaria intermedia* Münster in Goldfuss; Joly 1936: 75, pl. 1: 1a–c.

Material.—Three specimens: MNHNL HE197-1, MNHNL HE197-2, MNHNL LI113, Burmerange, Hettangian–Lower Sinemurian (exact stratigraphical level uncertain).

Dimensions.—See Table 2.

Description.—Trochiform-gradate shell with slightly cyrtoconical outline. Early juvenile spire turbiniform and composed of strongly convex whorls. Post-juvenile spire gradate, with whorls having a well-marked and oblique ramp. Ramp flat to just slightly concave, narrower than the outer whorl face and delimited by an angulation which becomes progressively stronger during the adult growth. Outer whorl face feebly oblique and almost flat. Peripheral angulation swollen and relatively prominent, slightly exposed on the spire. Su-

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tures impressed. Selenizone moderately wide, running slightly above the middle of the outer whorl face. Surface of selenizone concave on the early teleoconch whorls, becoming flat and then slightly convex during the adult growth. Base flat, with slightly convex surface, phaneromphalous. Umbilicus moderately wide and deep. Aperture subtrapezoidal, with discontinuous peristome on the parietal lip. Ornament reticulate by intersection of sharp spiral and collabral threads. Collabral threads closely spaced and extending from suture to suture. Ramp with three to four spiral threads. Angulation of the whorls marked by a cord-like spiral thread. One spiral thread runs on the surface between the angulation and the selenizone, one to two spiral threads below the selenizone. Ramp crossed by shallow and wide prosocline collabral riblets. They originate from prominent nodes on the angulation of the whorls and disappear before reaching the upper suture. Nodes evenly spaced, about twenty on the last whorl. Peripheral angulation marked by a strong and sharp thread on the juvenile whorls, bearing nodes on the adult whorls. They are smaller than those of the angulation of the whorls and extend slightly on the peripheral band of the base. Selenizone delimited by thin spiral threads. A strong lira appears along the mid-line of the selenizone from about the third whorl onward, becoming progressively more prominent during the adult growth. Lunulae sharp, well separated from each other and equally sized in the juvenile spire, becoming closely packed and irregularly sized on the adult spire. Base ornamented with a dozen, relatively strong spiral threads. Dense collabral threads occur between the spiral threads. Growth striae prosocline and prosocyrt above the selenizone, slightly opisthocline and prosocyrt below the selenizone, widely opisthocyrt on the base, becoming slightly prosocyrt near the umbilicus.

Remarks.—The specimens are rather well preserved but their stratigraphical position is uncertain. The sediment infilling the shells consists of a grey marl similar to that of the Elvingen marl (lowermost Hettangian) and of the Strassen marl and limestone (Lower Sinemurian). The type material of *Pleurotomaria cognata* Chapuis and Dewalque, 1853 comes from the Jamoigne Marl Formation (Hettangian) of Belgium (Chapuis and Dewalque 1853). The specimens from Luxembourg differ from the type material only in having stronger and larger nodes.

The specimen figured by Joly (1936) as *Pleurotomaria intermedia* Münster in Goldfuss, 1844 differs from *P. cognata* in having stronger collabral riblets, less marked nodes, and the peripheral row of nodes ornamenting only the last whorl. The low number of available specimens prevents to establish whether or not these differences are due to intraspecific variation of *P. cognata*.

Pleurotomaria hettangiensis Terquem, 1855 differs from *P. cognata* in having a more prominent selenizone and in the presence of a much narrower umbilicus. Moreover, *P. cognata* is smaller and exhibits a more gradate spire due to the presence of a wider ramp. *Pleurotomaria wanderbachi* Terquem, 1855 differs from *P. cognata* in the larger size and in a more acute spire made by higher whorls. Moreover, the selenizone is more prominent and wider.

Stratigraphic and geographic range.—Early Hettangian, Chiny and Fontenoille (Belgium); earliest Hettangian or Early Sinemurian, Burmerange (Luxembourg).

Pleurotomaria sp.

Fig. 11D.

Material.—One specimen: MNHNL GL344, Burmerange, Hettangian–Lower Sinemurian, (exact stratigraphical level uncertain).

Dimensions.—See Table 2.

Description.—Trochiform, slightly coeloconical, gradate shell. Whorls with subtrapezoidal cross-section. Ramp moderately oblique and feebly convex, limited by a subrounded outer angulation. Outer whorl face subvertical, convex on the last whorl. Selenizone wide, flush, running slightly below the middle of the outer whorl face. Periphery marked by a rounded angulation. Base slightly convex. Apertural region not preserved. Ornament made of spiral and collabral threads. Five to six, widely spaced and sharp spiral threads ornament the ramp. Two to three relatively strong spiral threads run on the surface of the whorls between the selenizone and the periphery. Collabral threads densely spaced and of uneven size. Angulation of the whorl surface bearing small and numerous nodes which attenuate during the adult growth. Peripheral angulation ornamented with small nodes, slightly elongated and prosocline on the base surface and disappearing during the growth of the last whorl. Selenizone bordered by moderately thin, sharp marginal spiral threads. It bears a submedian lira which becomes relatively prominent on the last whorls. Base ornamented with strong, sharp and relatively widely spaced spiral threads. Growth lines prosocline and widely prosocyrt on the ramp, orthocline and prosocyrt on the whorls surface between the selenizone and the periphery, opisthocyrt on the base.

Remarks.—This specimen is poorly preserved. The shell wall is partly eroded and the apertural region is strongly incomplete. Its stratigraphical position is uncertain. As for the previous species, the sediment embedding the shell is a grey marl suggesting that the specimen comes from the Elvingen marl (lowermost Hettangian) or from the Strassen marl and limestone (Lower Sinemurian).

The specimen is reminiscent of that figured by Orbigny (1854: 396, pl. 346: 1–4) as *Pleurotomaria anglica* (Sowerby, 1815). It differs in the position of the selenizone, which runs slightly below the middle of the outer whorl face, whereas in Orbigny's (1854) specimen the selenizone is placed above it. Moreover, the nodes of the ornament are slightly less prominent.

Genus *Anodomaria* Szabó, 1980

Type species: *Pleurotomaria scacchii* Gemmellaro, 1874. Pliensbachian, Sicani Mountains (western Sicily, Italy).

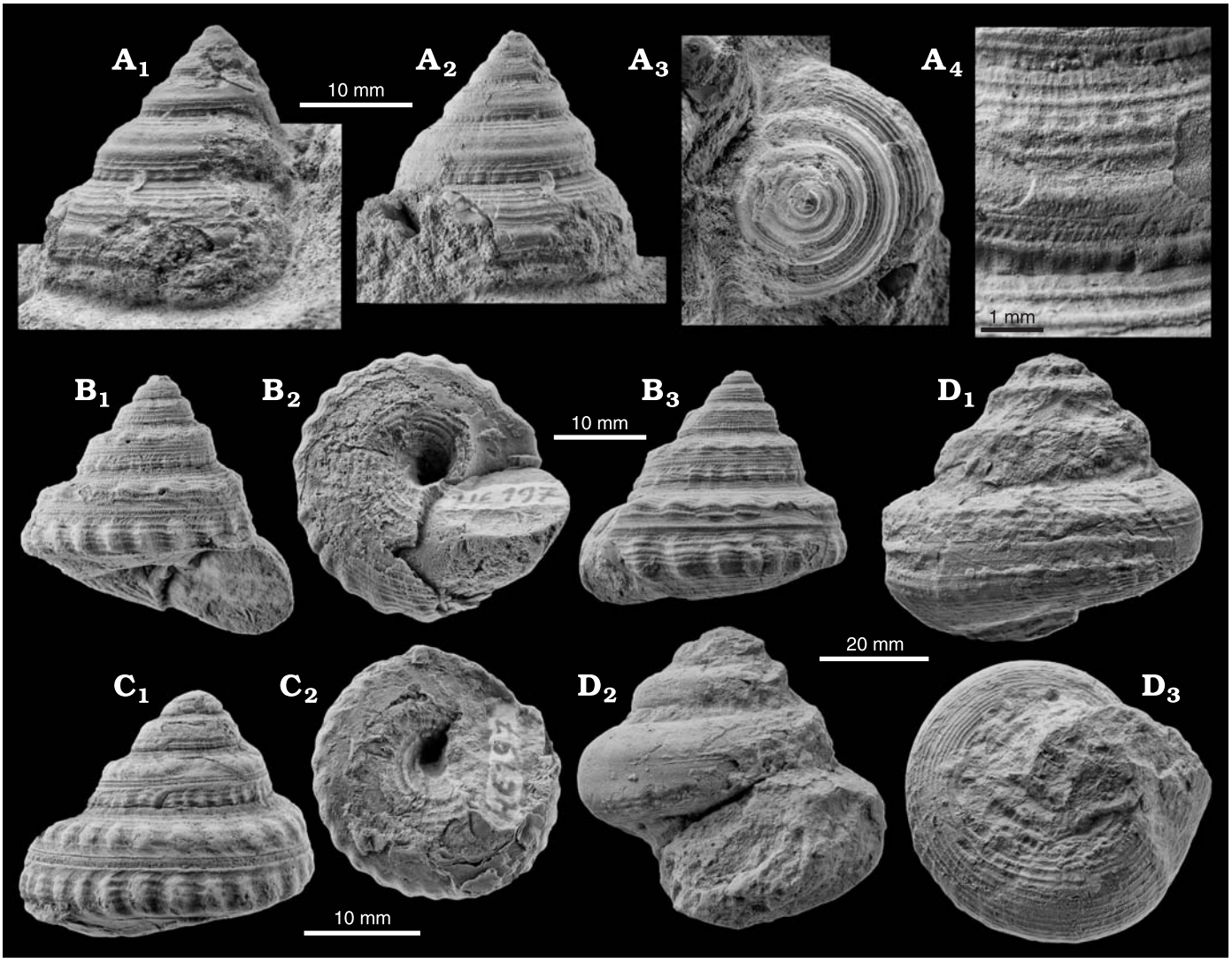

Fig. 11. Pleurotomariid gastropods from Hettangian–Early Sinemurian, Early Jurassic of Grand-Duchy of Luxembourg. **A**. *Pleurotomaria hennocquii* Terquem, 1855, MNHNL BR881, dorsal (A_1), lateral (A_2), apical (A_3) views, and detail of the ornament (A_4), Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). **B, C**. *Pleurotomaria cognata* Chapuis and Dewalque, 1853. B – MNHNL HE197-1, apertural (B_1), basal (B_2), and dorsal (B_3) views. C – MNHNL HE197-2, dorsal (C_1) and basal (C_3) views, Burmerange, exact stratigraphical level uncertain. **D**. *Pleurotomaria* sp., MNHNL GL344, dorsal (D_1), apertural (D_2), and basal (D_3) views, Burmerange, exact stratigraphical level uncertain.

Anodomaria schroederi sp. nov.

Fig. 12A, B.

v1988 *Trochotoma maubertense* Terquem and Piette; Meier and Meiers 1988: 33, pl. 7: 16a, b.

Etymology: The species is dedicated to Maggy Schroeder, a passionate collector of fossils who greatly contributed to enrich the palaeontological collections of the MNHNL.

Type material: Holotype: specimen MNHNL BR342 (Fig. 12A). Paratypes: one specimen, MNHNL BR871.

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

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

Dimensions.—See Table 2.

Diagnosis.—Shell distinctly gradate. Juvenile spire depressed. Early whorls provided with a relatively wide, convex ramp having the outer edge marked by a rounded angulation. Ornamentation roughly reticulate by intersection of evenly sized and spaced spiral threads with irregularly sized and dense collabral threads. Ramp sculptured with relatively strong, evenly distributed collabral riblets which fade out at the outer edge of the ramp. They tend to fade out during the last growth as well.

Description.—Trochiform, distinctly gradate shell consisting of about six whorls. Juvenile spire low. Early whorls well-rounded and separated by an impressed suture. Adult whorls angulated and with trapezoidal cross-section. Ramp slightly convex and weakly inclined. It enlarges and increases its inclination during the growth. Outer whorl face straight in juvenile whorls, slightly concave in adult whorls. Selenizone relatively wide, running slightly above the middle of the outer whorl face, weakly concave on the early

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whorls and becoming slightly convex on the last whorls. Periphery smoothly angulated, slightly prominent and swollen. Base relatively flat with feebly convex surface, and widely umbilicated. Aperture not preserved. Ornament composed of a network of spiral threads and collabral riblets and threads. Ramp ornamented with four to five, equally spaced and sized spiral threads intersected by marked, prosocline, and evenly spaced collabral riblets. Collabral riblets fading out at the edge of the ramp, intercalated to fine, irregularly sized and dense collabral threads. Other face with few spiral threads above and below the selenizone. These form a network with densely distributed collabral threads and bear small granulation at the intersection points. Angulation of the whorl surface and peripheral angulation marked by a spiral thread which is wider than the others. Selenizone with upper and lower rims marked by a fine spiral thread. Lunulae rather well defined. They are well spaced in the juvenile whorls and become thinner, densely spaced and unevenly sized on the adult spire. Base ornamented with regularly sized, somewhat densely spaced spiral threads roughed by intersection with growth threads. Growth lines moderately prosocline and prosocyrt on the ramp and above the selenizone, orthocline to slightly opisthocline and prosocyrt below the selenizone and on the peripheral band of the base. They are opisthocyrt on the base and become slightly prosocyrt on the periumbilical area.

Remarks.—This species belongs to the genus *Anodomaria* Szabó, 1980 as is indicated by the presence of an angulation of the whorl lacking nodes, a moderately wide, flat to concave selenizone running on the outer face of the whorls, a wide umbilicus, a slightly bulged peribasal angulation, and a reticulate ornament.

Meier and Meiers (1988) referred the material described here to *Trochotoma maubertense* Terquem and Piette, 1865 (Terquem and Piette 1865: 55, pl. 4: 20, 21). However, the species of the genus *Trochotoma* Eudes-Deslongchamps, 1843 are characterised by an exhalant hole and selenizone on the angulation of the whorls, and a funnel-like umbilicus. In contrast, in *Anodomaria schroederi* sp. nov., like in the other relatives, the exhalant hole is absent and the selenizone is located on the outer face of the whorls. Moreover, the umbilicus, although relatively wide, is not funnel-shaped.

Anodomaria schroederi is the oldest representative of the genus *Anodomaria*, a taxon previously known as ranging from the Late Sinemurian to Pliensbachian (Szabó 2009). It differs from the type species, *Anodomaria scacchii* (Gemmellaro, 1874) (Gemmellaro 1874: 92, pl. 12: 18; Szabó 1980: 58, pl. 2: 6, 7; Conti et al. 2007: pl. 12: 18; Szabó 2009: 37, fig. 31), and from *Anodomaria stojaspali* Szabó, 2008 (Szabó 2008: 171, fig. 3; 2009: 36, fig. 29), in the more gradate spire owing to a wider ramp, and in the presence of distinct collabral ribs on the ramp.

Stratigraphic and geographic range.—Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg).

Family Ptychomphalidae Wenz, 1938

Subfamily Ptychomphalinae Wenz, 1938

Genus *Ptychomphalus* Agassiz, 1839

Type species: *Helicina compressa* Sowerby, 1812. Leicestershire (United Kingdom), earliest Jurassic.

Ptychomphalus rotellaeformis (Dunker, 1847)

Fig. 12C.

1847 *Pleurotomaria rotellaeformis* sp. nov.; Dunker 1847: 111–113, pl. 13: 12a–e.

1855 *Pleurotomaria rotellaeformis* Dunker; Terquem 1855: 272–273, pl. 16: 11a, b.

1907 *Cryptaenia rotellaeformis* Dunker [sic]; Sieberer 1907: 24–25, pl. 2: 4.

1988 *Ptychomphalus rotellaeformis* (Dunker); Meier and Meiers 1988: 32–33, pl. 7: 15a, b.

Material.—Two specimens: MNHNL BR364, MNHNL BR703, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Shell low turbiniform, tending to lenticular, consisting of four moderately convex teleoconch whorls. Suture slightly impressed. Periphery formed by a somewhat rounded angulation, not exposed on the spire. Selenizone flush, moderately narrow, placed on the upper part of the peripheral band and with its lower edge running on the peripheral line. Labial slit short, extending about one eighth of the length of the last whorl. Base convex, with swollen surface and depressed axial region. Aperture sublanceolate, with prosocline, discontinuous peristome. Outer lip thin. Inner lip robust, covered by a callosity. The callus extends to the axial depression of the base where it forms a concave pad. Shell smooth. Selenizone delimited by very thin marginal spiral lines. Growth striae thin and scarcely visible, prosocline and prosocyrt on the spire, prosocyrt below the selenizone.

Remarks.—*Ptychomphalus rotellaeformis* (Dunker, 1847) is a species known from Upper Hettangian deposits of western Europe. It is characterised by a slightly angulated periphery and a smooth callus that completely fills and flattens the axial depression of the base.

The species was frequently quoted by previous authors. However, some of them refer to specimens likely belonging to other species. For example, the material illustrated by Gründel (2003: 3, pl. 1: 1–3) clearly differs from *P. rotellaeformis* in the presence of a prominent sutural band which forms a shallow spiral bulge. Moreover, the axial depression of the base bears a strong basal callus and is encircled by an outer spiral furrow. These characters are present also in the specimen ascribed by Dareste de la Chavanne (1912: 384, pl. 17: 2) to *Pleurotomaria* (*Cryptaenia*) *rotellaeformis*. They are reminiscent of *Pleurotomaria dewalquei* Terquem and Piette, 1865 (Terquem and Piette 1865: 59, pl. 4: 24, 25), although the presence of an outer furrow around the basal cavity is unclear in *P. dewalquei*.

The specimen ascribed by Sieberer (1907: 24, pl. 2: 4) to

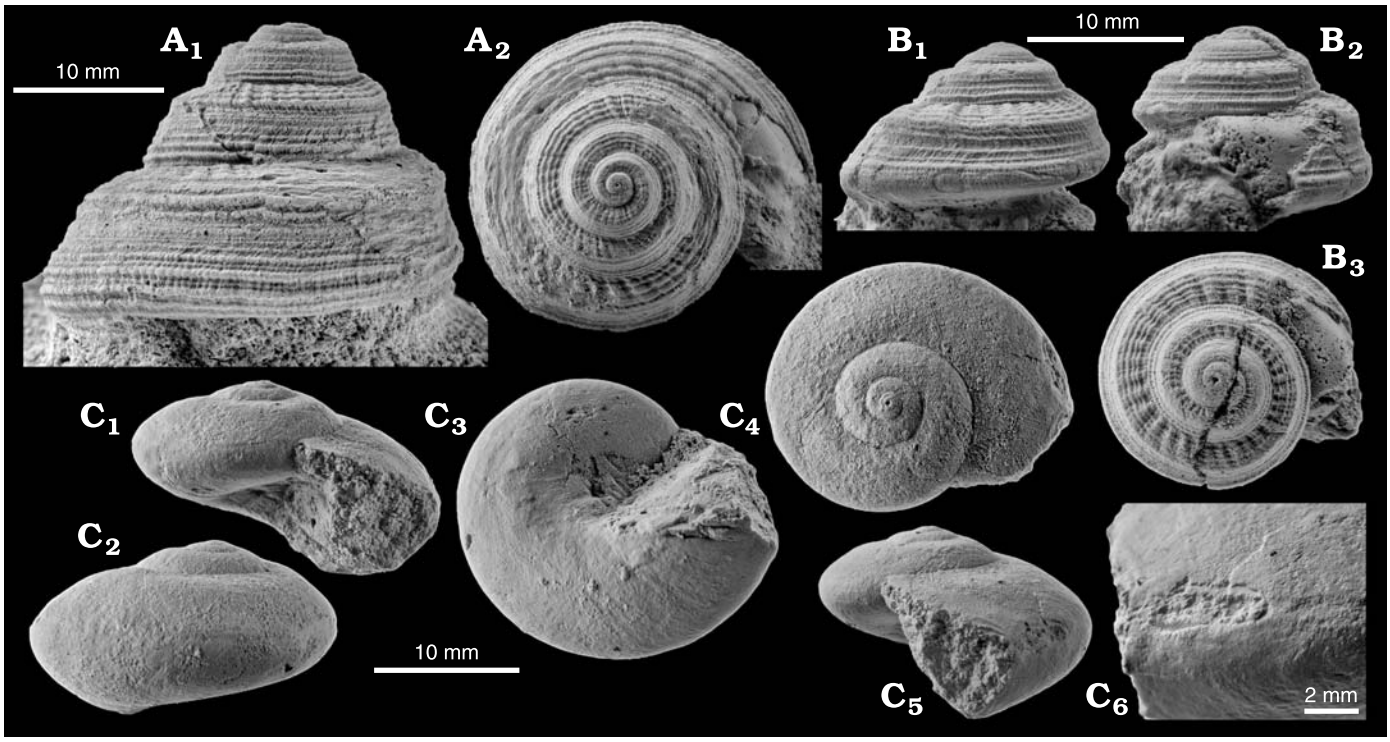

Fig. 12. Pleurotomariid and ptychomphalid gastropods from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**, **B**. *Anodomaria schroederi* sp.nov. A – Holotype, MNHNL BR342, dorsal (A_1) and apical (A_2) views. B – Paratype, MNHNL BR871, dorsal (B_1), lateral (B_2), and apical (B_3) views. **C**. *Ptychomphalus rotellaeformis* (Dunker, 1847), MNHNL BR364, apertural (C_1), dorsal (C_2), basal (C_3), apical (C_4), and lateral (C_5) views.

Cryptaenia rotellaeformis differs from the type material of Dunker's (1847) species in having a slightly more globose shape of the shell. This difference is here considered to represent species variability.

Other quotations of *P. rotellaeformis* (e.g., Quenstedt 1858; Dumortier 1864, 1867; Onetti 1915; Szente 1992) are not supported by sufficient data and/or concern poorly preserved specimens.

Ptychomphalus heliciformis (Eudes-Deslongchamps, 1849) is a Late Pliensbachian species very similar to *P. rotellaeformis*. Despite its rather different stratigraphical distribution, *P. heliciformis* was synonymised by Orbigny (1854) and Sieberer (1907) with Dunker's (1847) species. However, Fischer and Weber (1997: 155, pl. 25: 15, 16) considered it as a distinct species. These authors noted that the type material is lost and established a neotype and a paraneotype. These differ from *P. rotellaeformis* in a more rounded periphery and more convex whorl surface giving to the shell a slightly more turbiniform and less lenticular shape. Moreover, according to Fischer and Weber (1997), *P. heliciformis* has a more acute spire angle with respect to that of *P. rotellaeformis*. However, an extensive analysis of the known data concerning the two species seems to demonstrate a morphological continuity of these characters. Fischer and Weber (1997) mentioned also differences in the shape of the callus on the base, but they neither described them nor illustrated the basal view of the type material of *P. heliciformis*. According to the illustration made by Eudes-Deslongchamps (1949: 149, pl. 17: 2b) and Szabó (2009: 25, fig. 19B), in *P. heliciformis* the basal cavity is deeper and narrower than that of *P. rotellaeformis*. Moreover the callus on the axial depression of the base is thinner. It is not clear whether these differences are sufficient to keep the two species distinct. As underlined by Szabó (2009), only a full revision of all the material ascribed by previous authors to these species could give answers.

Stratigraphic and geographic range.—Early Hettangian (*Psiloceras planorbis* Zone), Halberstadt (Saxony-Anhalt, Germany); Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); Late Hettangian (*Schlotheimia angulata* Zone), Swabia (southern Germany).

Ptychomphalus caepa (Eudes-Deslongchamps, 1849)

Fig. 13.

1849 *Pleurotomaria coepa* [sic] sp. nov.; Eudes-Deslongchamps 1849: 150–151, pl. 17: 4a, b.
1854 *Pleurotomaria coepa* [sic] Eudes-Deslongchamps; Orbigny 1854: 399–400, pl. 348: 1, 2.
1855 *Pleurotomaria caepa* Eudes-Deslongchamps; Terquem 1855: 272, pl. 26: 2a–c.
1970 *Ptychomphalus rotellaeformis* (Dunker); Gaetani 1970: 389–390, pl. 31: 1–4.
1997 *Ptychomphalus caepa* (Eudes-Deslongchamps); Fischer and Weber 1997: 155, pl. 25: 13, 14.

Material.—Two specimens: MNHNL BR462, MNHNL BR682-1, Brouch, Upper Hettangian (*Schlotheimia angulata*

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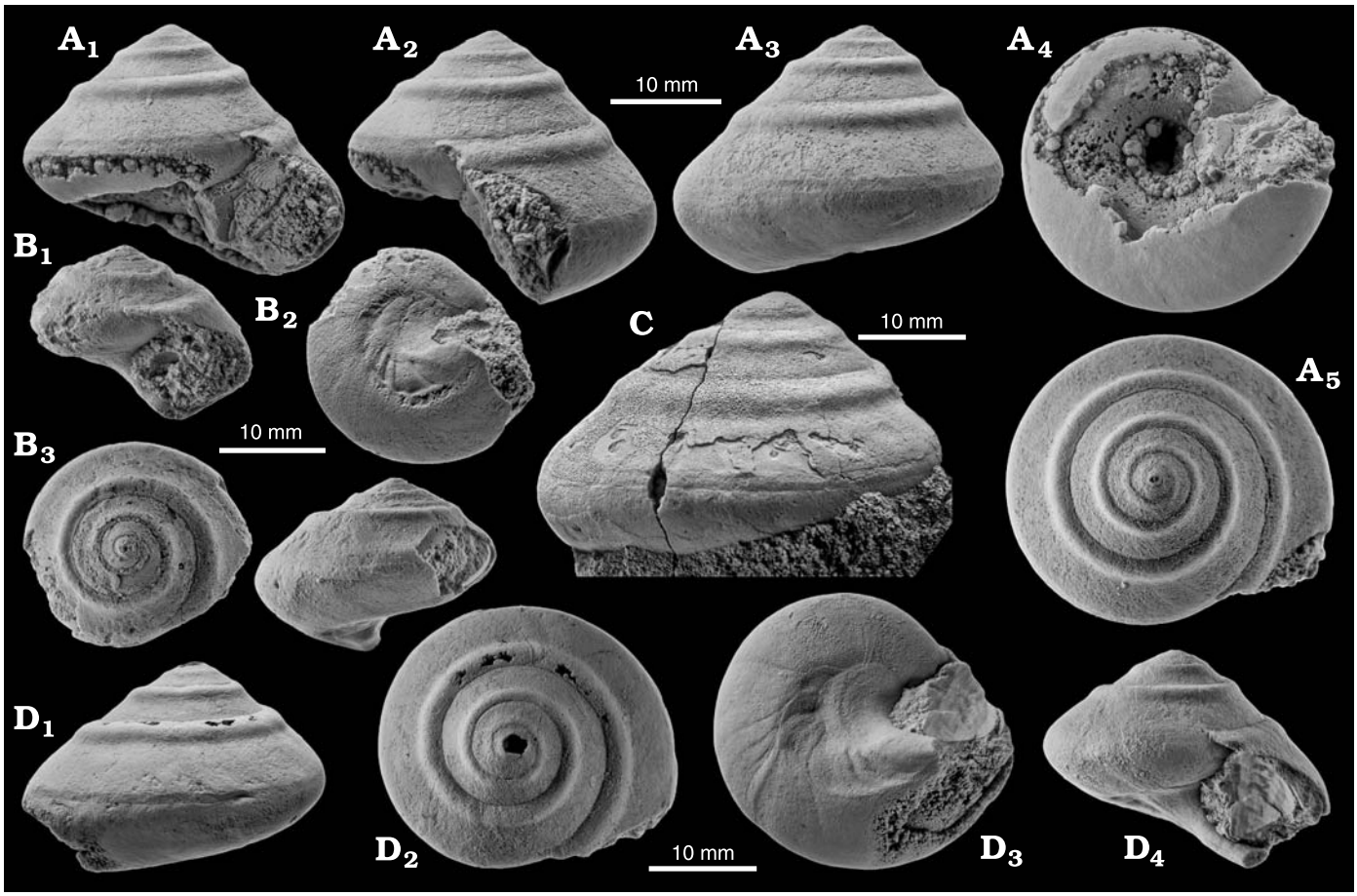

Fig. 13. Ptychomphalid gastropod *Ptychomphalus caepa* (Eudes-Deslongchamps, 1849) from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. MNHNL BR213-1, apertural (A_1), lateral (A_2), dorsal (A_3), basal (A_4), and apical (A_5) views. **B**. MNHNL BR810-1, apertural (B_1), basal (B_2), apical (B_3), and dorsal (B_4) views. **C**. MNHNL BR826-1, dorsal view. **D**. MNHNL BR213-2, dorsal (D_1), apical (D_2), basal (D_3), and apertural (D_4) views.

Zone, *Schlotheimia complanata* Subzone). Five specimens: MNHNL BR810 (two specimens), MNHNL BR826 (two specimens), MNHNL BR830, Brouch, Lower Hettangian (*Psiloceras planorbis* Zone, *Caloceras* beds). Fourteen specimens: MNHNL GL213 (eleven specimens), MNHNL GL426 (three specimens), Bridel quarry (Birgerkreiz), Luxembourg Sandstone Formation, exact stratigraphical level unknown. Five specimens: MNHNL GL271 (four specimens), MNHNL GL449, Steinfort, Luxembourg Sandstone Formation, exact stratigraphical level unknown. One specimen: MNHNL GL422, Kopstal (Biremdall), Luxembourg Sandstone Formation, Lower to Middle Hettangian. One specimen: MNHNL HE188, Mamer (Kaatzefiels), Strassen marl and limestone, lowermost Sinemurian (*Coroniceras* [*Arietites*] *bucklandi* Zone, *Belemnites brevis* beds).

Dimensions.—See Table 2.

Description.—Obtusely conical shell with cyrtoconical outline of the spire. Teleoconch composed of about six smooth whorls. Periphery smoothly angulated. Surface of whorls slightly concave, becoming slightly convex in the last growth stage. Suture not impressed. Peripheral angulation not exposed on spire. Selenizone scarcely visible, flush and moderately wide, running at the upper edge of periphery and not exposed on the spire. Slit short. Base convex and swollen, cryptomphalous. Aperture subcircular, with a marked sutural corner. Peristome discontinuous on the parietal lip. Inner lip arched, smoothly passing to the basal lip and provided with a strong callus. Callus extended greatly to the umbilical cavity and forming a large, circular, smooth pad which fills the wide umbilicus. Ornament made of a smooth, bulge-shaped subsutural carina appearing early during the growth. Whorl surface otherwise smooth. Base smooth. Selenizone bordered by thin marginal spiral threads. Growth lines faint, prosocline and prosocyrt on the spire, prosocyrt below the selenizone, opisthocyrt on the base, becoming prosocyrt on its axial region.

Remarks.—Eudes-Deslongchamps (1849: 150) erroneously established the name of the species as *Pleurotomaria coepa* Eudes-Deslongchamps, 1849, intending to refer to the Latin translation of the term "onion". Terquem (1855) corrected the name of the species, since its correct Latin spelling is *caepa*. This is also in accordance with Articles 32.5 and 33.2 (Comma 33.2.2) of the ICZN (1999). According to Fischer and Weber (1997), the holotype of *P. caepa* has been lost.

Thus, they designated a neotype and a paraneotype, based on the two specimens figured by Terquem (1855).

The analysis of the rich material from Luxembourg allows to recognise the ontogenetic characters and the variability of the species. The juvenile specimens have a relatively depressed spire and, consequently, the shell tends to have a lenticular shape. During the adult growth, the shell becomes obtusely conical, although the height of the spire is variable. The sutural bulge can be also variably prominent, but it is always distinct. In some specimens, it becomes feebly and irregularly undulated during the adult growth, without forming distinct nodes.

Ptychomphalus caepa differs from *Ptychomphalus rotellaeformis* (Dunker, 1847) in having a higher spire. Consequently, the shape of the shell is less lenticular. Moreover, the peripheral angulation is more distinct than in *P. rotellaeformis* and the suture is marked by a spiral bulge.

Ptychomphalus compressus (Sowerby, 1812) (Sowerby 1812: 33, pl. 10) differs from *P. caepa* in having more rounded whorls. The selenizone is elevated and forms a peripheral thread whereas in *P. caepa* the selenizone is flush.

Stratigraphic and geographic range.—Hettangian (*Alsatites liasicus* to *Schlotheimia angulata* Zones), Hettange-Grande (Lorraine, France); Hettangian, Dalheim (Luxembourg); Early Hettangian (*Psiloceras planorbis* Zone) and Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); Late Hettangian, Lombardy (Italy).

Ptychomphalus wehenkeli (Terquem and Piette, 1865)

Fig. 14.

1865 *Pleurotomaria wehenkeli* sp. nov.; Terquem and Piette 1865: 61, pl. 4: 29–31.

1988 *Ptychomphalus caepa* (Eudes-Deslongchamps); Meier and Meiers 1988: 31–32, pl. 7: 14a, b.

Material.—Forty-five specimens: MNHNL BR103, MNHNL BR116-1, MNHNL BR118-2, MNHNL BR123, MNHNL

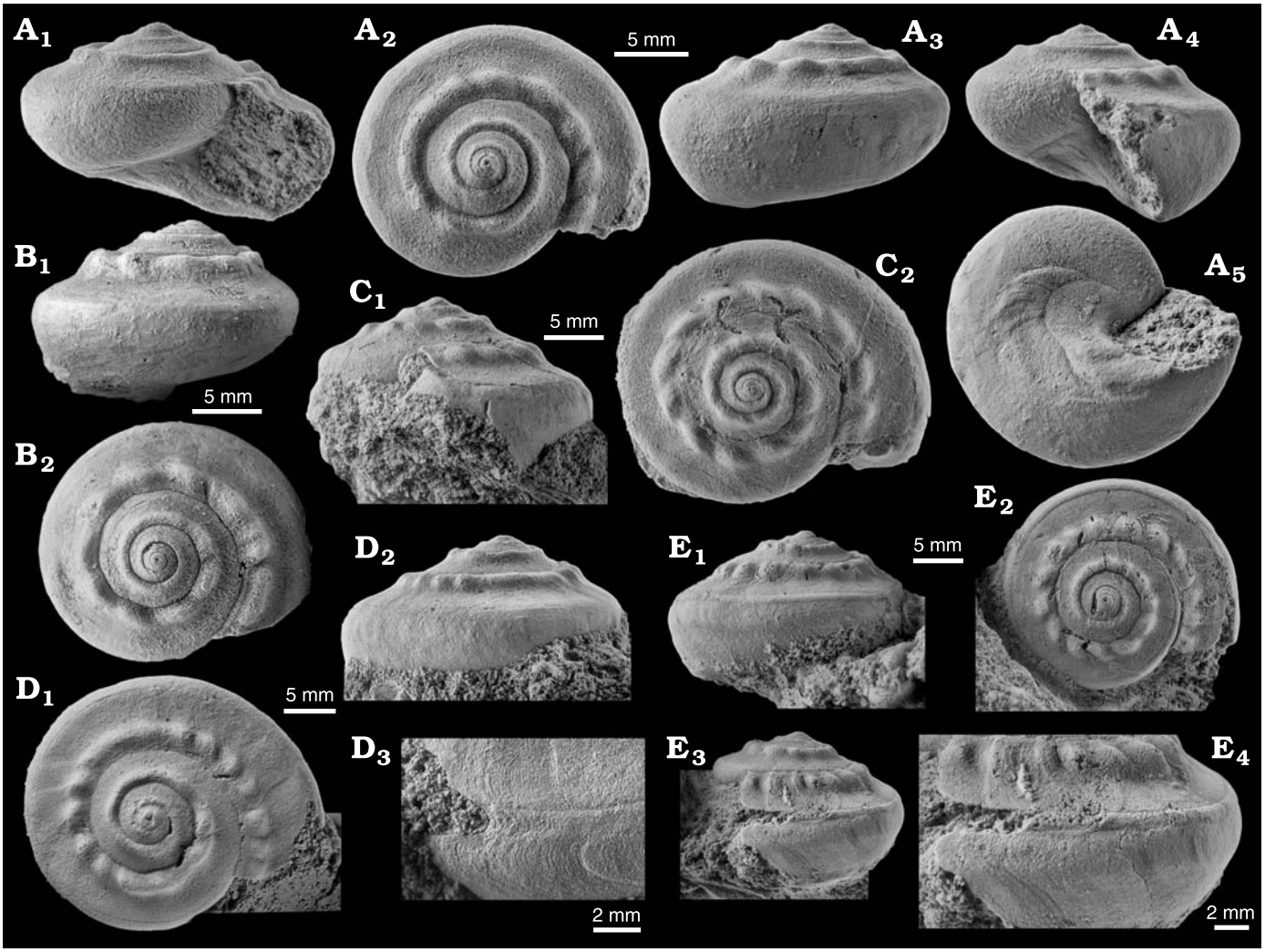

Fig. 14. Ptychomphalid gastropod *Ptychomphalus wehenkeli* (Terquem and Piette, 1865) from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. MNHNL BR368, apertural (A_1), apical (A_2), dorsal (A_3), lateral (A_4), and basal (A_5) views. **B**. MNHNL BR305-2, dorsal (B_1) and apical (B_2) views. **C**. MNHNL BR717, lateral (C_1) and apical (C_2) views. **D**. MNHNL BR545, apical (D_1) and dorsal (D_2) views, and detail of the selenizone area (D_3). **E**. MNHNL BR259, dorsal (E_1), apical (E_2), lateral (E_3) views, and detail of the slit and selenizone area (E_4).

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BR161, MNHNL BR176, MNHNL BR206, MNHNL BR221-1, MNHNL BR225, MNHNL BR233, MNHNL BR259, MNHNL BR270, MNHNL BR276, MNHNL BR279, MNHNL BR305-2, MNHNL BR306-1, MNHNL BR317, MNHNL BR341 (two specimens), MNHNL BR368, MNHNL BR455-1, MNHNL BR456, MNHNL BR467 (two specimens), MNHNL BR470, MNHNL BR472-2, MNHNL BR486, MNHNL BR499-1, MNHNL BR545, MNHNL BR562-2, MNHNL BR564, MNHNL BR656, MNHNL BR661, MNHNL BR694, MNHNL BR714, MNHNL BR717, MNHNL BR740 (two specimens), MNHNL HE101-1, MNHNL HE129, MNHNL HE144, MNHNL HE146, MNHNL HE147, MNHNL HE159, MNHNL HE178, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). One specimen: MNHNL GL379-2, Brouch, Luxembourg Sandstone Formation, exact stratigraphical level unknown.

Dimensions.—See Table 2.

Description.—Low-turbiniform, sublenticular-globose shell. Teleoconch composed of about five whorls. Surface of the whorls concave. Sutures slightly impressed. Periphery smoothly angulated, not exposed on the spire. Selenizone moderately wide, with its lower rim running along the line of the periphery. Surface of the selenizone flush on the juvenile and adult shell, becoming slightly convex to relatively prominent on the last whorl. Labial slit short, extending about one tenth of the length of the last whorl. Base convex, rather swollen. Aperture subcircular, with marked sutural corner. Peristome prosocline, discontinuous on the parietal lip. Inner lip arched, smoothly passing to the basal lip. Inner lip strengthened by a strong callus which extends to and covers the basal cavity. Early whorls sculptured with a smooth, bulge-shaped, subsutural spiral carina. On the post-juvenile shell, the carina bears strong, closely spaced, slightly prosocline nodes. Spire otherwise smooth. Selenizone smooth, delimited by very thin marginal spiral threads. Base smooth. Growth striae feeble, prosocline, evenly and markedly prosocyrt on the surface of the whorls, prosocyrt on the peripheral band below the selenizone, opisthocyrt on the base.

Remarks.—In *Ptychomphalus wehenkeli* (Terquem and Piette, 1865) the height to width ratio of the shell is moderately variable. Moreover, the nodes on the sutural bulge can be variably spaced and sized and they appear at different stages during the growth. The species differs from *Ptychomphalus caepa* (Eudes-Deslongchamps, 1849) in having a lower spire and the sutural spiral bulge ornamented with nodes. Moreover, the surface of the whorls is narrower and more concave.

Ptychomphalus wehenkeli represents the most abundant pleurotomarioidean species from Luxembourg. Joly (1907, 1908, 1936) reported it from several localities of Belgium and France. However, that author did not provide any illustration of his material.

Stratigraphic and geographic range.—Late Hettangian (*Schlotheimia angulata* Zone), Ardennes (France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg).

Family Trochotomidae Cox, 1960

Genus *Trochotoma* Eudes-Deslongchamps, 1843

Type species: *Trochotoma conuloides* Eudes-Deslongchamps, 1843. Calvados, Bathonian.

Trochotoma vetusta Terquem, 1855

Fig. 15.

1855 *Trochotoma vetusta* sp. nov.; Terquem 1855: 267–268, pl. 16: 10.
1867 *Trochotoma brocastellensis* sp. nov.; Moore 1867: 552, pl. 15: 29.
1934 *Ditremaria* (*Ditremaria*) *vetusta* (Terquem); Haber 1934: 366.
1966 *Trochotoma meneghinii* Gemmellaro; Bourrouilh 1966: 43–44, fig. 17.
1988 *Trochotoma vetusta* Terquem; Meier and Meiers 1988: 34, pl. 8: 17a–c.
2002 *Trochotoma* (*Trochotoma*) *vetusta* Terquem; Fischer et al. 2002: 444, fig. 3-1a, b.

Material.—Thirty-three specimens: MNHNL BR221-2, MNHNL BR320, MNHNL BR361, MNHNL BR375-2, MNHNL BR378, MNHNL BR418-2, MNHNL BR454, MNHNL BR455-2, MNHNL BR458, MNHNL BR460, MNHNL BR461, MNHNL BR465, MNHNL BR466, MNHNL BR469, MNHNL BR473-1, MNHNL BR533, MNHNL BR667, MNHNL BR678, MNHNL BR679, MNHNL BR680, MNHNL BR685, MNHNL BR698 (two specimens), MNHNL BR704, MNHNL BR705, MNHNL BR706, MNHNL BR708, MNHNL BR710, MNHNL BR713, MNHNL BR754, MNHNL HE123, MNHNL HE133 (two specimens), Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Trochiform, gradate shell composed of about six teleoconch whorls. Juvenile spire feebly cyrtoconical, adult spire coeloconical. Ramp narrow and convex, becomes increasingly pronuncied during growth. Outer whorl face flat to moderately convex, markedly wider than the ramp, oblique and forming an obtuse angulation with the ramp. Periphery marked by a spiral bulge on the juvenile and adult whorls. The peripheral bulge tends to vanish during growth of the last whorls where it becomes a rounded angulation. Suture moderately impressed, running in the middle of the peripheral carina and shifting slightly below it on the last whorl. Selenizone convex, placed on the angulation of the whorl surface. An exhalant hole (trema), seemingly elliptical and strongly elongate in spiral direction, forms before the last peristome. Selenizone reduced to a shell seam between the exhalant hole and the outer lip. Final part of the last whorl expanded. Base with well rounded surface and a broad, funnel-like umbilicus. Aperture elliptical, well-elongated in abaxial direction. Peristome strongly prosocline, discontinuous on the parietal lip. Inner lip strongly oblique, elongated within the umbilical cavity, almost straight and forming an obtuse, rounded angulation at the junction with the basal lip.

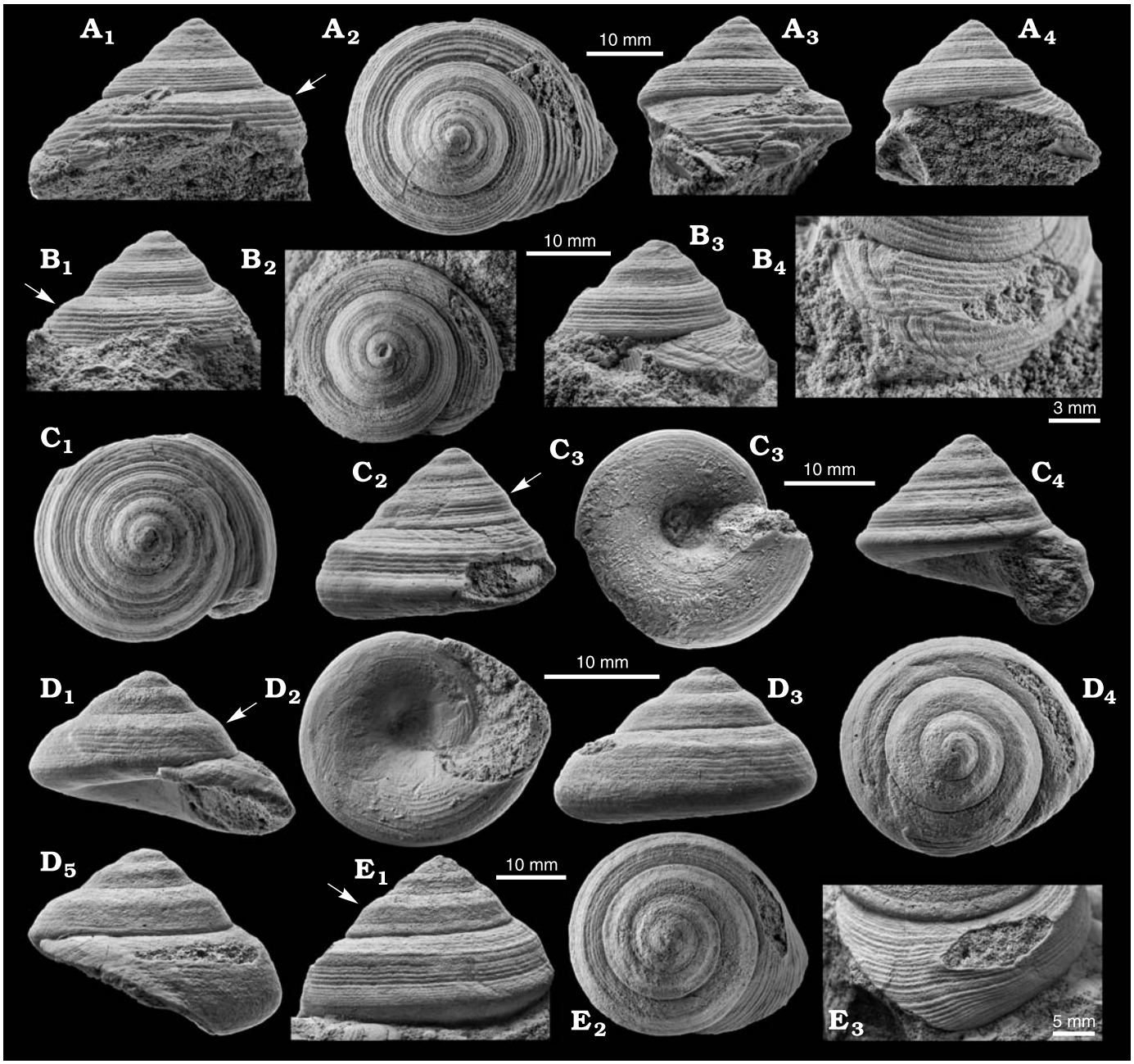

Fig. 15. Trochotomid gastropod *Trochotoma vetusta* Terquem, 1855 from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. MNHNL BR704, dorsal (A_1), apical (A_2), lateral (A_3), and apertural (A_4) views. **B**. MNHNL BR754, dorsal (B_1), apical (B_2), subapertural (B_3) views, and detail of the exhalant hole and of the shell seam (B_4). **C**. – MNHNL BR710, apical (C_1), dorsal (C_2), basal (C_3), and apertural (C_4) views. **D**. MNHNL BR361, apertural (D_1), basal (D_2), dorsal (D_3), apical (D_4), and lateral (D_5) views. **E**. MNHNL BR705, dorsal (E_1) and apical (E_2) views, and detail of the exhalant hole and of the shell seam (E_3). The arrow indicates the position of the selenizone.

Ornament consists of dense, distinct and unevenly sized spiral threads covering the whole surface of the whorls and are separated by narrower interspaces. The ramp can be crossed by feeble collabral striae. Base ornamented with spiral threads which are thinner and more widely spaced than those of the spire. Selenizone hidden by the spiral ornament, coinciding with a duplicated spiral thread which is wider than the others. Growth striae strongly prosocline and evenly prosocyrt on the spire, opisthocyrt on the base.

Remarks.—The species is rather variable in spire height, ramp, and outer whorl face inclinations, as well as in the prominence of the peripheral carina and of the ornament. Owing to that variability, and to the general shape of the shell, *Trochotoma brocastellensis* Moore, 1867 is here included in the synonymy of *Trochotoma vetusta* Terquem, 1855.

Trochotoma meneghinii Gemmellaro, 1879 (Gemmellaro 1879: 367, pl. 28: 11, 12) differs from *T. vetusta* in having a more acute spire and a conical shape of the shell owing to a

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narrower ramp. Moreover, in *T. meneghinii* the periphery is smoothly angulated whereas in *T. vetusta* it is marked by a slightly bulge-shaped carina. In agreement with Fischer et al. (2002: 444), the specimen described by Bourrouilh (1966) as *T. meneghinii* should be referred to *T. vetusta*.

Stratigraphic and geographic range.—Hettangian, Hettange-Grande (Lorraine, France); Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg); earliest Sinemurian (*Coroniceras* [*Arietites*] *bucklandi* Zone), Brocastle (South Wales, United Kingdom); Early Sinemurian, central Apennines (Italy); Late Sinemurian (*Echioceras raricostatum* Zone) to earliest Carixian, Eastern High Atlas (Morocco).

Trochotoma clypeus Terquem, 1855

Fig. 16A.

1855 *Trochotoma clypeus* sp. nov.; Terquem 1855: 268, pl. 16: 9.
1934 *Ditremaria* (*Ditremaria*) *clypeus* (Terquem); Haber 1934: 332–333.

Material.—Two specimens: MNHNL BR124, MNHNL BR305-1, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Trochiform, low conical-gradate shell consisting of about five whorls. Early whorls strongly convex. Adult whorls bearing a rounded angulation delimiting a flat to slightly convex, relatively broad and feebly oblique ramp. Outer whorl face flat to slightly concave. Periphery exposed on spire and marked by a strong spiral bulge. Sutures impressed, running along the mid-line of the peripheral bulge. Selenizone slightly elevated, placed at the angulation of the whorls. Ornament made of dense, somewhat strong and subregularly sized spiral threads separated by thin interspaces. Three to four threads run on the ramp and four to five on the outer whorl face. Selenizone corresponding to a duplicated spiral thread which is slightly wider than the spiral threads of the ornament. Peripheral bulge bearing thin spiral threads. Ramp ornamented also by fairly prosocline, unevenly sized and spaced collabral riblets. Growth striae strongly prosocline and widely prosocyrt on the spire.

Remarks.—Although the specimens have the base embedded into the sediment, they correspond well to the description and illustration of *Trochotoma clypeus* Terquem, 1855. The only difference concerns the size which is smaller in Terquem's (1855) type specimen which, therefore, most probably represents a juvenile shell. According to Terquem (1855), *T. clypeus* shows a slightly concave base with funnel-like umbilicus. This is a typical feature of the species belonging to the genus *Trochotoma* Eudes-Deslongchamps, 1843.

Trochotoma clypeus differs from *Trochotoma vetusta* Terquem, 1855 in having a smaller size, a more obtuse apical angle, and more rounded juvenile whorls. Moreover, in *T. clypeus* the ramp is sculptured with a stronger collabral ornament.

Stratigraphic and geographic range.—Late Hettangian (*Schlotheimia angulata* Zone), Hettange-Grande (*Lorraine, France);* Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg).

Suborder Trochina Cox and Knight, 1960
Superfamily Turbinoidea Rafinesque, 1815
Family Turbinidae Rafinesque, 1815
Subfamily Angariinae Gray, 1857
Genus *Meiersia* nov.

Type species: *Meiersia disarmata* sp. nov. (see below). Late Hettangian, Luxembourg; see below.

Etymology: The genus is dedicated to Kurt Meiers, passionate collector of fossils cooperating with the National Museum of Natural History of Luxembourg.

Diagnosis.—Adult shell sinistral, discoidal-lenticular and with almost flat spire. Base swollen and widely umbilicated. Aperture subcircular to subtrapezoidal, weakly angulated at the periphery. Peristome with upper part of outer lip slightly convex to almost straight. Periphery corresponding to a sharp flange bearing dense crenulations or distinct and widely spaced spines. Base smooth, evenly convex to subangulated in its median part. Growth lines strong.

Remarks.—We identified two species belonging to *Meiersia* gen. nov., namely the type species *Meiersia disarmata* sp. nov. and *Meiersia calcar* (Orbigny, 1853) (Orbigny 1853: 378, pl. 340: 5–7; Fischer and Weber 1997: 150, pl. 21: 3) a species known from the Pliensbachian sediments of Calvados (France). Koken (1896, 1897) ascribed the latter species to the genus *Asperilla* Koken, 1896. However, the type species of *Asperilla*, *Asperilla coronoserra* (Quenstedt, 1884) (= *Delphinula longispina* Rolle, 1860) from the Kimmeridgian of Swabia (southern Germany) is characterised by a dextral shell provided with a strong spiral cord on the central part of the base (Quenstedt 1884: 413, pl. 201: 45, 46; Brösamlen 1909: 237, pl. 19: 15). These aspects clearly differentiate *Asperilla* from *Meiersia*. Moreover, *A. coronoserra* is provided with a further, narrower spiral cord at the periumbilical edge.

Cossmann (1916) and Fischer and Weber (1997) treated *Asperilla* as subgenus of *Platyacra* Ammon in Zittel, 1882. *Platyacra* differs from *Meiersia* in having a characteristic dimorphic shell. In the former genus the early spire is planispiral with a concave apical side, and the adult shell is pagodiform due to the peripheral carina placed much above the suture. On the contrary, in *Meiersia* the early spire, though strongly depressed, shows the first observable whorls convex. Moreover, the adult shell is lenticular and with the peripheral carina in contact to the suture.

The specimen from the Pliensbachian of Calvados (France) ascribed by Cossmann (1916: 208, pl. 9: 10–12) to *Platyacra* (*Asperilla*) *calcar* (Orbigny, 1853) is a sinistral shell which is distinguished from the holotype of Orbigny's (1853) species by a more marked periumbilical angulation bearing small nodes, and in the presence of some spiral threads on the surface of the base, between the peripheral

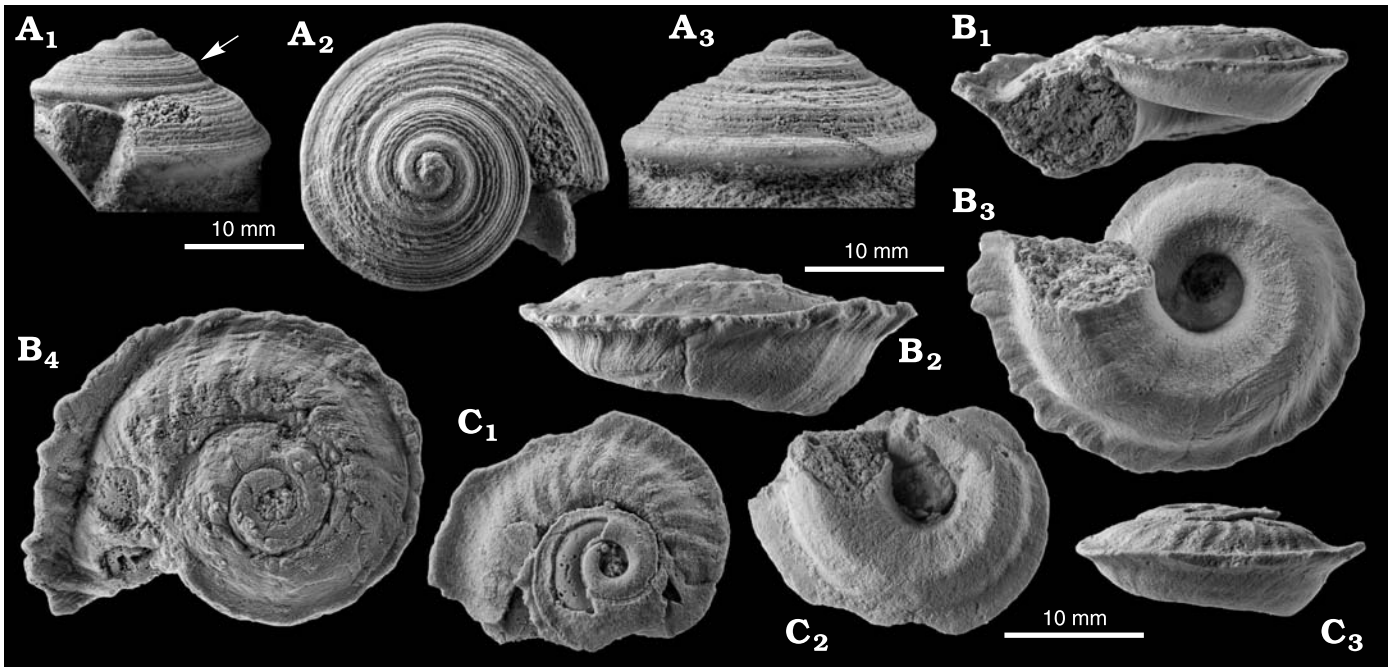

Fig. 16. Trochotomid and turbinid gastropods from Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Early Jurassic. **A**. *Trochotoma clypeus* Terquem, 1855, MNHNL BR305-1, lateral (A_1), apical (A_2), and dorsal (A_3) views. The arrow indicates the position of the selenizone. **B**, **C**. *Meiersia disarmata* sp. nov. **B**. Holotype, MNHNL BR358, apertural (B_1), dorsal (B_2), basal (B_3), and apical views. **C**. Paratype, MNHNL BR873, apical (C_1), basal (C_2), and dorsal (C_3) views.

flange and the basal angulation. Moreover, the spines on the peripheral flange are more numerous and denser. That specimen could belong to a distinct species of *Meiersia*. In this case, the interspecific variation of the genus would be wider than here described.

The material described by Haas (1953: 35, pl. 2: 27, 28, 33, 34) as ?*Platyacra* (*Asperilla*) sp., from the Late Triassic of Peru exhibits general characters reminiscent of *Meiersia*. This would demonstrate a Triassic origin of the genus. However, its poor preservation prevents a safe supraspecific attribution.

Stratigraphic and geographic range.—?Late Triassic, Peru; Late Hettangian, Luxembourg; Late Pliensbachian, Calvados (France).

Meiersia disarmata sp. nov.

Fig. 16B, C.

1988 *Asperilla calcar* (Orbigny); Meier and Meiers 1988: 35, pl. 8: 18a–c.

Etymology: From Latin *disarmata*, without arms; referred to the absence of spines on the peripheral flange.

Type material: Holotype: specimen MNHNL BR358 (Fig. 16B). Paratypes: six specimens: MNHNL BR758, MNHNL BR869, MNHNL BR870, MNHNL BR872, MNHNL BR873, MNHNL BR874.

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

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

Dimensions.—See Table 2.

Diagnosis.—Base provided with a smooth median spiral angulation which almost disappears during the last growth stages. Peripheral flange densely crenulated, without spines.

Description.—Sinistral shell with flat spire, consisting of about five whorls. Exposed surface of whorls feebly and evenly convex, delimited by slightly incised sutures. Last whorls slightly bending downward during the final growth. Periphery marked by a sharp, prominent, slightly upward curved flange which is covered by the previous whorls on the spire and becomes slightly exposed on the last whorl. Base strongly convex, widely phaneromphalous. Median band of the surface of the base marked by a spiral angulation which tends to disappear on the last whorl. Umbilical edge bearing a smooth, rounded angulation. Basal angulation running nearly at the mid-distance between the periumbilical angulation and the peripheral flange. Aperture rounded-trapezoidal. Peristome angulated at the peripheral flange. Basal angulation ending on the peristome at the junction of the outer lip with the basal lip. Peristome feebly angulated by the periumbilical angulation at the junction of the inner lip with the basal lip. Apart from the peripheral flange the shell is essentially smooth. Outer rim of peripheral flange densely crenulated and lacking spines. Very shallow, wrinkle-shaped collabral ribs can originate from the crenulations of the peripheral flange. They tend to fade out towards the suture, and on the peripheral band of the base. Growth lines very strong, prosocline and distinctly prosocyrt on the whorl surface, opisthocyrt on the base, acutely backward angular on the peripheral flange.

Remarks.—The variability of this species concerns the angulations of the base and the elements of the ornament. Both the basal and periumbilical angulations vary in strength. The collabral ribs are of variable strength and distribution.

Meiersia disarmata sp. nov. is very close to *Meiersia*

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calcar (Orbigny, 1853), from the Upper Pliensbachian deposits of Calvados (France). However, Orbigny's (1853) species differs from *M. disarmata* in the peripheral flange, which has long, widely and evenly spaced spines (seven to eight on the last whorl). Moreover, in the holotype of *M. calcar*, the basal angulation is absent or obscure.

Stratigraphic and geographic range.—Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg).

Superfamily Eucycloidea Koken, 1897

Remarks.—Here the Eucycloidea Koken, 1897 are interpreted in agreement with Szabó (1995) and Conti and Monari (2001). Recently Kano (2008), based on a phylogenetic analysis of molecular data, assigned the family Eucyclidae Koken, 1897 to the superfamily Seguenzioidea Verrill, 1884, although admitting that the eucyclids and seguenziids show strong differences in the shell morphology and anatomy.

On the contrary, Bandel (2010) reaffirmed the distinction between the Seguenzioidea and the Eucycloidea, mainly based on the study of Triassic taxa. Considering that the eucycloideans are essentially represented by Mesozoic taxa, this approach seems to be more convincing. However, in contrast to Conti and Monari (2001), Bandel (2010) excluded from the Eucycloidea the family Cirridae Cossmann, 1916, which he previously ascribed to a distinct superfamily (Bandel 1993; Frýda et al. 2008 and references therein).

Family Eucyclidae Koken, 1897

Genus *Eucyclus* Eudes-Deslongchamps, 1860

Type species: *Eucyclus obeliscus* Eudes-Deslongchamps, 1860. Pliensbachian, Calvados (France).

Eucyclus sp.

Fig. 17A.

Material.—One specimen: MNHNL GL205, Luxembourg Sandstone Formation, Hettangian–Lower Sinemurian, exact locality and stratigraphical level unknown.

Dimensions.—See Table 2.

Description.—Shell large, turbiniform with strongly impressed suture. Whorls strongly convex, angulated at the periphery. Angulation at about middle of the whorl. Base distinctly convex, anomphalous. Aperture semicircular, angular at the termination of the periphery on the outer lip and slightly elongated at the base of the columella. Peristome seemingly discontinuous at the parietal lip. Columellar lip straight and subvertical. Ornament mainly consisting of strong spiral cords. Periphery marked by a spiral keel bearing widely spaced and robust nodes, about twelve on the last whorls. Base ornamented with six strong spiral cords. The spiral cord below the peripheral keel bears low nodes. The other spiral cords of the base are slightly nodose or wavy. The nodes on the peripheral angulation and on the spiral cords of the base are roughly aligned to each other in axial direction, seemingly formed by intersection of the spiral ornament with low and feeble collabral wrinkles. Weak traces on the inner mould of two spiral cords on the ramp. Growth lines strong, forming a pattern of dense threads which make strongly rough the interspaces between the spiral cords.

Remarks.—The shell is only preserved on the last whorl of the present specimen. Another whorl is preserved on the internal mould and the apex is missing. Shape and ornament are typical for the genus *Eucyclus* Eudes-Deslongchamps, 1860. Moreover, the external ornament is partly reflected on the inner mould surface which is a characteristic feature of the members of the family Eucyclidae Koken, 1897 (e.g., Conti and Monari 1991: pl. 8: 10–18; 1995: pl. 2: 12–14; 2001: fig. 8, 15; Szabó 1995: pl. 7: 13). The general habitus and especially the large size of the shell distinguish the specimen from other coeval *Eucyclus* species. However, its very poor preservation prevents more detailed comparisons.

Family Cirridae Cossmann, 1916

Genus *Spirocirrus* Cossmann, 1916

Type species: *Turbo calisto* Orbigny, 1853. Late Bathonian, Calvados (France).

Remarks.—According to Bandel (1993), *Spirocirrus* Cossmann, 1916 is a synonym of *Scaevola* Gemmellaro, 1879, and the type species of *Scaevola*, namely *Scaevola intermedia* Gemmellaro, 1879 (Gemmellaro 1879: 342, pl. 27: 7–9), differs from type species of Cossmann's (1916) genus, *Spirocirrus calisto* (d'Orbigny, 1853) (Orbigny 1853: 345, pl. 332: 9, 10; Fischer and Weber 1997: 140, pl. 21: 6), only in having a lower spire. However, other characters also differentiate *S. intermedia* from *S. calisto*. For example, *S. intermedia* has rounded whorls and is ornamented with collabral ribs which smoothly pass onto the base, whereas in *S. calisto* the juvenile whorls are roughly biangulated and become rounded only during the last growth stage, and the collabral ribs end or become much less prominent along the lower angulation.

Spirocirrus weisi sp. nov.

Fig. 17B, C.

1907 *Trochus* sp.; Joly 1907: 53, pl. 1: 1a–d.

1988 *Spirocirrus calisto* (Orbigny); Meier and Meiers 1988: 28, pl. 4: 9a, b.

Etymology: The species is dedicated to Robert Weis (National Museum of Natural History of Luxembourg).

Type material: Holotype: specimens MNHNL BR299 (Fig. 17B). Paratypes: one specimen: MNHNL BR374.

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

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

Dimensions.—See Table 2.

Diagnosis.—Sinistral, high turbiniform shell. Umbilicus very narrow. Aperture rounded with continuous peristome on the parietal lip. Outer face of whorls delimited by two weak angulations of which the lower one is more pronounced. Angulations fading on the last whorl. Collabral ornament made of varicose, swollen and widely spaced ribs

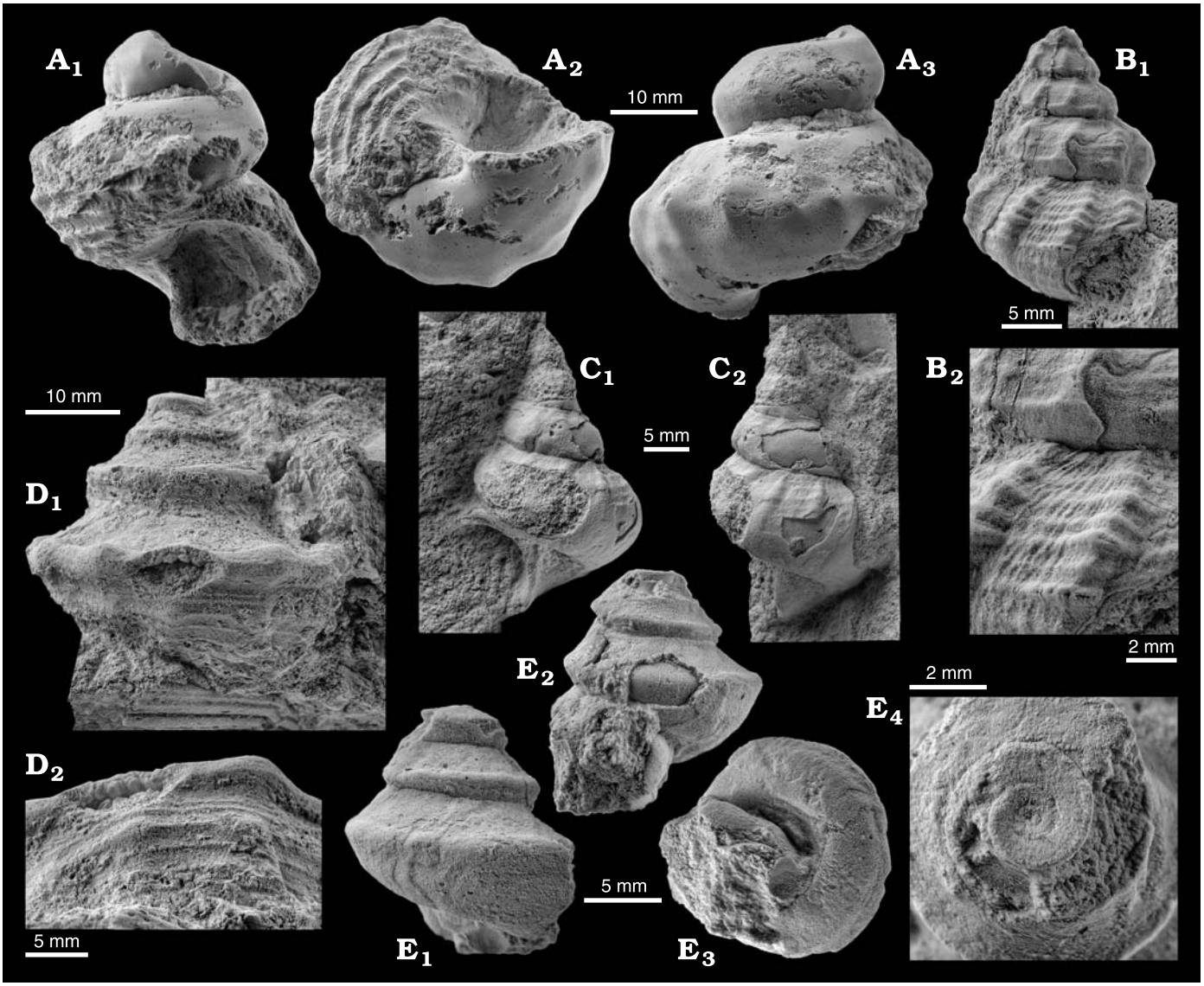

Fig. 17. Eucycloidean gastropos from Luxembourg Sandstone Formation, Early Jurassic. **A**. *Eucyclus* sp., MNHNL GL205, apertural (A_1), basal (A_2) and dorsal (A3) views, Hettangian–Early Sinemurian, exact locality and stratigraphical level uncertain. **B**–**E**. Brouch (Mersch, Grand-Duchy of Luxembourg), Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone). **B**, **C**. *Spirocirrus weisi* sp. nov., **B**. Holotype, MNHNL BR299, lateral view (B_1) and detail of the ornament (B_2). **C**. Paratype, MNHNL BR374, apertural (C_1) and subdorsal (C_2) views. **D**, **E**. *Platyacra* aff. *sinistrorsa* (Terquem, 1855). **D**. MNHNL BR373, dorsal view (D_1) and detail of the ornament of the base (D_2). **E**. MNHNL BR876, dorsal (E_1), subapertural (E_2), and basal (E_3) views, and detail of the apical spire (E_4).

which become much less prominent on the lower angulation of the outer whorl face. Spiral ornament composed of three primary spiral cords which alternate with secondary spiral cords on the juvenile shell and form elongated nodes on the collabral ribs. Secondary spiral cords becoming as thick as the primary ones on the last whorl. Base ornamented with few and well spaced spiral cords.

Description.—Sinistral, high turbiniform shell. Whorls strongly convex separated by strongly impressed and oblique sutures running well below the periphery. Periphery of the juvenile whorls delimited by two weak and rounded angulations, of which the lower one is slightly more pronounced. The periphery becomes rounded on the last whorl. Last whorl relatively swollen. Base evenly convex, narrowly umbilicated. Aperture circular. Peristome slightly prosocline, continuous along the parietal lip. Inner lip weakly reflected outwards. Outer lip not observable. Ornament composed of collabral ribs and spiral cords. About ten, regularly spaced prosocline collabral ribs on the adult shell, which are varicose, swollen and rounded. Three primary spiral cords ornament the juvenile shell and form spirally elongated nodes overlapping the collabral ribs. The uppermost cord runs on the ramp, whereas the other two ones delimit the outer face of the whorl. Thinner spiral cords appear during growth which rapidly become almost as thick as the primary cords. Last whorl ornamented with six strong spiral cords. The collabral ribs become less prominent in correspondence to the spiral cord marking the lower angulation. Base ornamented with spiral cords separated by inter-

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vals which are much wider than those on the whorls. Growth lines prosocline and slightly prosocyrt on the whorls, feebly opisthocyrt on the base. They form dense and thin growth threads.

Remarks.—*Spirocirrus weisi* sp. nov. represents the oldest member of the genus *Spirocirrus*, a genus previously known from Late Toarcian to Bathonian of the northern Paris Basin and England (Orbigny 1853; Hudleston 1892; Cossmann 1900, 1916; Fischer and Weber 1997). The species has strong similarities with *Spirocirrus calisto* (Orbigny, 1853), from the Late Bathonian of the Paris Basin (Orbigny 1853; Cossmann 1885, 1900, 1916; Fischer and Weber 1997). On the basis of that similarity, Meier and Meiers (1988) assigned the specimens from Luxembourg to *S. calisto*. However, *S. calisto* differs from *S. weisi* in having more thinner and denser spiral threads on the spire and on the base. Moreover, in *S. calisto* the lower spiral thread of the peripheral band is thicker and the associated angulation is more pronounced. The peripheral angulations are more persistent on the last whorl in *S. calisto*, whereas in *S. weisi* they fade out so that the last whorl is almost rounded.

The specimen described by Joly (1907) as *Trochus* sp. differs from the holotype of *S. weisi* only in being smaller. It is interpreted here as a juvenile specimen of that species.

Scaevola busambrensis Gemmellaro, 1879 (Gemmellaro 1879: 341, pl. 27: 1, 2), from the Sinemurian carbonate platform sediments of north-western Sicily (Italy) probably belongs to the genus *Spirocirrus* Cossmann, 1916. It differs from *S. weisi* in having three strong spiral carinae on the adult shell and in having thin and dense spiral threads on the base.

Stratigraphic and geographic range.—Late Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone), Brouch (Luxembourg). Late Hettangian (*Schlotheimia angulata* Zone), Metzert (Belgium).

Genus *Platyacra* Ammon in Zittel, 1882

Type species: *Trochus impressus* Schafhäutl, 1863. ?Hettangian–Sinemurian, Bavaria (southern Germany), see Suess et al. (2005).

Platyacra aff. *sinistrorsa* (Terquem, 1855)

Fig. 17D, E.

1988 *Platyacra sinistrorsus* [sic] (Deshayes); Meier and Meiers 1988: 29, pl. 4: 10a, b.

Material.—Two specimens: MNHNL BR373, MNHNL BR876, Brouch, Upper Hettangian (*Schlotheimia angulata* Zone, *Schlotheimia complanata* Subzone).

Dimensions.—See Table 2.

Description.—Sinistral, dimorphic shell. Early shell planispiral anisostrophic composed of about four whorls. Its apical side is concave and consists of flat whorls which are delimited by a sharp peripheral angulation which is not prominent on the spire surface. Suture running near the peripheral angulation. Adult spire pagodiform, consisting of about three whorls. The peripheral angulation becomes well-exposed on the spire. It delimits a wide and steep ramp, and a relatively narrow outer whorl face which is inclined opposite to the ramp. Last whorl with peripheral angulation slightly below mid-whorl. Suture oblique and impressed, running at or near to an obtuse angulation of the base. Base distinctly convex, with a wide umbilicus encircled by a periumbilical angulation. Apertural region not preserved. Main spiral ornament made of a strong peripheral keel and of a spiral cord marking the angulation of the base. Outer whorl face and base of the adult spire ornamented with subequally sized and widely spaced spiral threads. There are two spiral threads on the outer whorl face and four on the base below the spiral cord marking the angulation of the base. Peripheral keel crenulated by shallow, widely spaced, spirally elongated nodes. About twelve nodes on the last whorl forming shallow undulations on the ramp and on the base. The basal cord bears also shallow nodes axially aligned with those of the peripheral keel. Growth striae prosocline and prosocyrt on the ramp, seemingly opisthocyrt on the base.

Remarks.—The material is poorly preserved. The largest specimen (MNHNL BR373) is partly embedded in the sediment. The other specimen (MNHNL BR876) is an incomplete adult shell seemingly preserving obscure traces of a fine spiral ornament on the ramp. The specimens are closely reminiscent of the material on which Terquem (1855: 264, pl. 15: 14) erected *Trochus sinistrorsus* Terquem, 1855. However, Terquem's (1855) species, which was refigured by Cossmann (1916: 207, pl. 9: 8, 9) and assigned by him to the genus *Platyacra* Ammon in Zittel, 1882, exhibits some differences with respect to the material described here. In particular, the type material of *P. sinistrorsa* is smaller in size and lacks spiral cords on the outer whorl face and base. Moreover, it has less pronounced nodes undulating the peripheral keel. The ramp is ornamented with distinct collabral ribs which form nodes at the upper suture.

Platyacra impressa (Schafhäutl, 1863) (Zittel 1882: 190, fig. 237; Ammon 1893: 169, fig. 7), type species of the genus *Platyacra*, is also smaller in size and with a slightly narrower adult spiral angle. Moreover, the base lacks a spiral cord and the ramp is crossed only by growth striae.

The specimens described here most likely belong to a species different from both *P. sinistrorsa* (Terquem, 1855) and *P. impressa*. However, both present specimens are so poorly preserved that species identification is not recommended.

Evolutionary and palaeobiogeographical considerations

The systematic analysis of the Early Jurassic fauna of the Luxembourg Sandstone Formation resulted in the identification of twenty-two species belonging to Patellogastropoda, Neritimorpha, and Vetigastropoda. Eleven genera, nine families and six superfamilies were identified (Table 3). From a prelimi-

Table 3. List and taxonomic repartition of the species described here. Abbreviation: n, number of specimens.

Taxa	n	Figs.
Subclass Eogastropoda Ponder and Lindberg, 1996		
?Superfamily Lottioidea Gray, 1840		
?Family Acmaeidae Forbes, 1850		
Scurriopsis (*Scurriopsis*) *schmidti* (Dunker, 1844)	16	5A–C
Scurriopsis (*Hennocquia*) *hettangiensis* (Terquem, 1855)	44	5D–I
Subclass Neritimorpha Koken, 1896		
Superfamily Neritoidea Rafinesque, 1815		
Family Neridomidae Bandel, 2008		
Neridomus liasina (Dunker, 1844)	10	6A–F
Neridomus cannabis (Terquem, 1855)	5	7A–D
Superfamily Neritopsoidea Gray, 1847		
Family uncertain		
Bandelopsis? cf. *exigua* (Terquem, 1855)	4	8A, B
Bandelopsis? sp.	1	8C
Subclass Archaeogastropoda Thiele, 1925		
Superfamily Pleurotomarioidea Swainson, 1840		
Family Pleurotomariidae Swainson, 1840		
Pleurotomaria wanderbachi Terquem, 1855	7	9A–D
Pleurotomaria hettangiensis Terquem, 1855	6	10A–D
Pleurotomaria cf. *hettangiensis* Terquem, 1855	1	10E
Pleurotomaria hennocquii Terquem, 1855	1	11A
Pleurotomaria cognata Chapuis and Dewalque, 1853	3	11B, C
Pleurotomaria sp.	1	11D
Anodomaria schroederi sp. nov.	2	12A, B
Family Ptychomphalidae Wenz, 1938		
Ptychomphalus rotellaeformis (Dunker, 1847)	2	12C
Ptychomphalus caepa (Eudes–Deslongchamps, 1849)	28	13A–D
Ptychomphalus wehenkeli (Terquem and Piette, 1865)	45	14A–E
Family Trochotomidae Cox, 1960		
Trochotoma vetusta Terquem, 1855	33	15A–E
Trochotoma clypeus Terquem, 1855	2	16A
Superfamily Turbinoidea Rafinesque, 1815		
Family Turbinidae Rafinesque, 1815		
Meiersia disarmata sp. nov.	7	16B, C
Superfamily Eucycloidea Koken, 1897		
Family Eucyclidae Koken, 1897		
Eucyclus sp.	1	17A
Family Cirridae Cossmann, 1916		
Spirocirrus weisi sp. nov.	2	17B, C
Platyacra aff. *sinistrorsa* (Terquem, 1855)	2	17D, E

nary account, other twenty-six species, currently under study, belong to higher Prosobranchia (Pseudomelanoidea, Zygopleurodea, Stromboidea, and Purpurinidae), Heterobranchia (Mathildidae) and Opistobranchia. This implies a high suprasspecific diversity.

The fauna is dominated by pleurotomarioideans representing the genera *Ptychomphalus*, *Pleurotomaria*, and *Trochotoma*, and by the patellogastropod genus *Scurriopsis* both in number of species and specimens. The neritimorph genus *Neridomus* is also well represented.

Ptychomphalus first occurred in the late Middle to Late Triassic of the southern Alps (Bandel 2009). Several species are known from the Early Jurassic of the western Europe and of the central region of western Tethys which clearly reflects a major radiation of this genus, although a detailed systematic revision may reveal synonymies, which will decrease the number of species involved (Gründel and Nützel 1998). The species radiation was seemingly fast and took place in Hettangian times in the eastern and western Paris Basin. In fact, apart from the species described here, six other species described by Terquem (1855), Terquem and Piette (1865), Joly (1907), and Dareste de la Chavanne (1912) probably belong to the genus *Ptychomphalus*, namely *Pleurotomaria lens* Terquem, 1855; *Pleurotomaria nucleus* Terquem, 1855; *Pleurotomaria dewalquei* Terquem and Piette, 1865; *Pleurotomaria jamoigniaca* Terquem and Piette, 1865; *Pleurotomaria nicklesi* Joly, 1907; and *Pleurotomaria* (*Cryptaenia*) *planispira* Dareste de la Chavanne, 1912. A peak of species radiation occurred in the Sinemurian to Pliensbachian time and *Ptychomphalus* expanded over a wide area of European epicontinental shelf (Sowerby 1812, 1818; Eudes-Deslongchamps 1849; Schrüfer 1861; Sieberer 1907; Gründel and Nützel 1998; Gründel 1999, 2007; Gründel and Koppka 2007; Schubert et al. 2008), the central region of the western Tethys (Gemmellaro 1874, 1911; Szabó 1980, 2009; Conti and Monari 1991; Conti et al. 2007; Monari et al. 2008) and North Africa (Bourrouilh 1966). *Ptychomphalus* is unknown from sediments younger than the Pliensbachian.

Pleurotomaria presumably originated in the Triassic of the western Pacific region (Begg and Grant-Mackie 2003), but the major radiation occurred in the early Middle Jurassic of the western European epicontinental seas (e.g., Orbigny 1856; Eudes-Deslongchamps 1849; Hudleston 1895; Sieberer 1907; Fischer and Weber 1997). The presence of at least five species in the Hettangian to earliest Sinemurian sediments of Luxembourg suggests an early radiation slightly after the end-Triassic crisis.

The evolutionary history of *Trochotoma* is characterised by a major Sinemurian adaptive radiation involving the European epicontinental shelf (Rollier 1918; Haber 1934), and the marginal and intratethyan carbonate platforms, such as the Northern Calcareous Alps (Austria) (Ammon 1893; Haber 1934), the Apennines Platform (central Italy) (Fischer et al. 2002), the Trapanese Platform (western Sicily, Italy) (Gemmellaro 1879; Haber 1934) and the High Atlas (Bourrouilh 1966). As mentioned above for the other pleurotomarioidean taxa, the occurrence of a number of species in the Hettangian sediments (Terquem 1855; Henry 1876; Rollier 1918, and herein) demonstrates that the diversification started very early in the Jurassic.

Several Jurassic species of *Scurriopsis* were listed by Haber (1932). However, most of them lack information on the shape of the muscle scar, the protoconch and the structure of the shell wall. Recent systematic analyses (e.g., Hedegaard et al. 1997; Fuchigami and Sasaki 2005) demonstrate that these characters are of high importance for the identification and taxonomic placement of the limpet-shaped gastropods. This makes the reconstruction of the evolutionary history of these limpets difficult and their significance in Hettangian faunas remains debatable. Neverthless, the definitive presence of two subgenera, namely *Scurriopsis* s.s. and *Scurriopsis* (*Hennocquia*), in the faunas from Luxembourg and their wide distribution indicate an adaptive radiation of the genus during the Hettangian.

Neridomus is merely accessory in the Hettangian faunas of northern Germany, Paris Basin, Lusitatian Basin (Portu-

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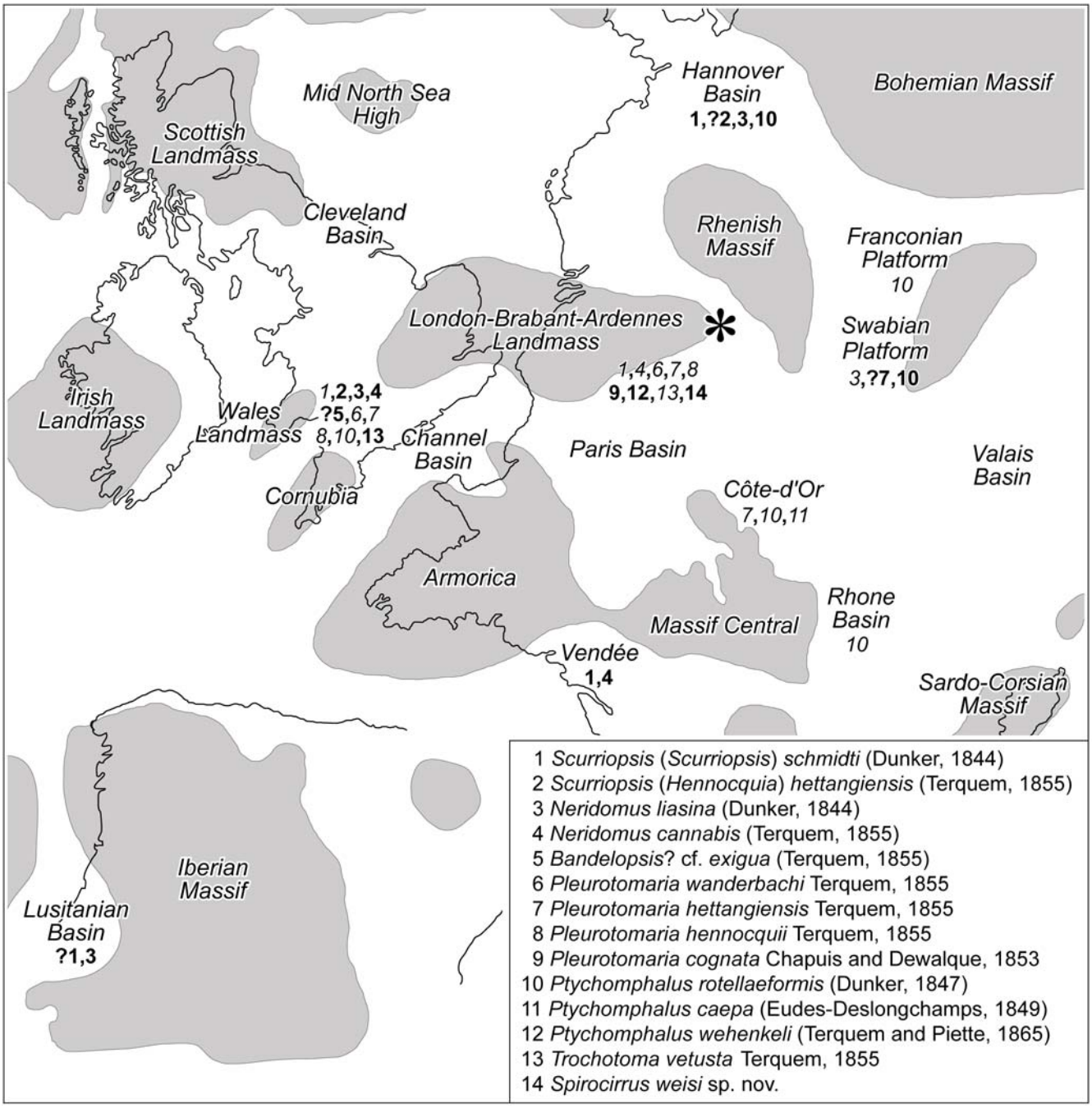

Fig. 18. Hettangian to earliest Sinemurian palaeogeographical distribution of the species described here in the western European epicontinental seas. Occurrences corresponding to the synonymies listed in the systematic part are in bold. Occurrences from sources lacking an illustration of the species concerned are in italics.

gal) and southern Hungary (e.g., Dunker 1847; Böhm 1901; Chartron and Cossmann 1902; Cossmann 1925; Szente 1992), being represented by single species. On the contrary, it seems to be a characteristic faunal element of the Upper Hettangian sediments of Luxembourg where it is present with at least two species and a large number of specimens (Terquem 1855; Terquem and Piette 1865; Joly 1907, and herein). The genus is highly diversified in the Early Sinemurian carbonate platform faunas from the north-western Sicily (Italy) (Gemmellaro 1879; Cossmann 1925).

Among the accessory genera, i.e., genera occurring in the fauna from Luxembourg with a single species and few specimens (Table 3), the first occurrence of *Anodomaria* and *Spirocirrus* is remarkable. During the Late Sinemurian to Pliensbachian, *Anodomaria* spread in those western Tethyan areas where a pelagic sedimentation took place as a result of the drowning of the carbonate platforms, i.e., the Bakony Mountains (Hungary), the Northern Calcareous Alps (Austria) and the Sicani Mountains (western Sicily, Italy) (Gemmellaro 1874; Szabó 1980, 2008, 2009; Conti et al. 2007). In

contrast, *Spirocirrus* speciated rapidly during the Late Toarcian to Early Bajocian mainly in a restricted area including the northern Paris Basin and England (Hudleston 1892; Cossmann 1916). *Spirocirrus* occurs also in the Aalenian (Sturani 1964) coral-bearing facies of the Trento Platform (Dal Piaz 1912; Cossmann 1916). *Spirocirrus calisto* (d'Orbigny, 1853), from the Bathonian deposits of northern France (Cossmann 1885, 1900, 1916; Fischer and Weber 1997) represents the last occurrence of the genus.

The knowledges about *Platyacra* are rather poor as the genus is represented by few species. The type species, *Platyacra impressa* (Schafhäutl, 1863) comes from the supposed Hettangian–Sinemurian sediments of Bavaria (southern Germany) (Schafhäutl 1863; Ammon 1893; Seuss et al. 2005). Two species, namely *Platyacra sinistrorsa* (Terquem, 1855) and *Platyacra* aff. *sinistrorsa* occur in the Luxembourg Sandstone Formation (Terquem 1855, and herein). *Cirrus normanianus* Orbigny, 1853, a Late Pliensbachian species from Calvados (northern France) which was assigned to *Platyacra* by Cossmann (1916) and Fischer and Weber (1997) would represent the youngest species known for the genus. However, some differences from the type species, such as a lower spire and more rounded whorls, could indicate its membership of another genus.

The palaeobiogeographical data highlight a very wide distribution of the gastropod species here described, including the whole western European epicontinental shelf, from the Hannover Basin (northern Germany) to the Lusitanian Basin (Portugal) (Fig. 18). The fauna from Luxembourg shows the closest similarities with those from the northern Germany described by Dunker (1844, 1847) and from the South Wales (United Kingdom) quoted by Tawney (1866) and Moore (1867).

The similarities between the Luxembourg fauna and those from the northern Germany could reflect an open communication of that area with the Luxembourg region. Indeed, during the Early Jurassic times the latter region acted as a seaway between the London-Brabant-Ardennes Landmass and the Rhenish Massif connecting the Paris Basin with the northern Germany epicontinental seas (De Graciansky et al. 1998). The sediments of northern Germany are older (Early Hettangian, *Psiloceras planorbis* Zone) than those of Luxembourg (Late Hettangian, *Schlotheimia angulata* Zone). This is in agreement with De Graciansky et al. (1998) who suggested that during the Hettangian to earliest Sinemurian time span the western Europe was a subject of a wide east to west marine transgression, from the basins of the northern Germany to the Paris Basin through the Luxembourg seaway.

The similarities between the Luxembourg fauna and those from the South Wales are likely even more marked than resulting from this analysis and shown in Fig. 18. In fact, Moore (1867) listed about fifty other species from South Wales which were also quoted by Terquem (1855) for the Luxembourg Sandstone Formation. This information seems to be significant, although historical data mentioned above should be verified by a detailed systematic revision. Such correspondence most likely reflects both a time correspondence and some palaeonvironmental similarities between the two regions. In fact, according to Bradshaw et al. (1992) and Simms et al. (2002) the lowermost Jurassic deposits of South Wales consist mainly of bioclastic calcarenites and gravel-grade conglomerates deposited on shores related to the presence of small islands or shoals between the London-Brabant-Ardennes and the Wales Landmasses. Thus, they formed in a coastal, high-energy environment which is partly comparable to that of the Luxembourg Sandstone Formation.The age of these sediments in South Wales changes geographically from the Early Hettangian to the Early Sinemurian (Hodges 1986, Simms et al. 2002), as is the case in the Luxembourg Sandstone Formation (Colbach 2005; Van de Bril et al. 2007; Van de Bril and Swennen 2008), although Bradshaw et al. (1992) maintained that in South Wales the effect of the presence of exposed lands on the sedimentation probably ended before the beginning of the Sinemurian.

A comprehensive interpretation of the evolutionary and palaeobiogeographical data presented above should take into consideration that only a part of the gastropod collections of MNHNL is analysed here. Moreover, it should also consider the fact that most of the available information on the Early Jurassic gastropods concerns the western Europe. Nonetheless, this study highlights that during the Early Jurassic, most of the characterising genera showed a strong species radiation and a wide geographical distribution, trends probably favoured by a marine transgression over wide areas of the western European epicontinental shelf during the Hettangian to earliest Sinemurian time span. This radiation, including the first appearance of some accessory taxa, was already considerably advanced in the Late Hettangian. This suggests that the recovery of the gastropod diversity after the end-Triassic crisis was relatively fast in western Europe.

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