New insights on Tournaisian–Visean (Carboniferous, Mississippian) athyridide, orthotetide, rhynchonellide, and strophomenide brachiopods from southern Belgium

Bernard Mottequin and Eric Simon

ABSTRACT

Twelve selected Carboniferous species belonging to seven genera of the orders Athyridida, Orthotetida, Rhynchonellida, and Strophomenida (Brachiopoda) from southern Belgium are revised and/or discussed, and sometimes photographed for the first time since their first description dating back to the 19th century. The investigated material originates from the historical type areas of the Tournaisian and Visean stages (Tournai and Visé, respectively) and from the Waulsortian carbonate buildups developed in the Namur–Dinant Basin. Two species are new (*Leptagonia franca* sp. nov., *Serratocrista scaldisensis* sp. nov.), and a new name is proposed (*Nucleospira hannoniae* nom. nov.) to solve the primary homonymy between *Athyris globulina* de Koninck and *A. globulina* Waagen. Taxonomic discussion involves selection of the holotype of *Retzia intermedia* de Koninck (definitely not an athyridide) and of lectotypes for several species of athyridides (*Athyris globulina* de Koninck, *A. vittata* de Koninck, and *Retzia davidsoni* de Koninck), and strophomenides (*Orthis cylindrica* M'Coy, *Schellwienella radialiformis* Demanet, and *S. ornata* Demanet). The palaeoecology of the investigated species and their biotic interactions with other organisms (e.g., drill holes, epizoans) are described. The analysis of the published data on the athyridides, orthotetides, and strophomenides occurring in southern Belgium during the Devonian–Mississippian reveals that our knowledge of these suspension-feeders in this part of the southern margin of Laurussia is currently insufficient to assess the aftermath of the different biological crises that took place during this time span, notably the Hangenberg Crisis at the end of the Famennian.

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INTRODUCTION

The Tournaisian–Visean brachiopod assemblages are generally characterized by the predominance of productides and spiriferides (e.g., Curry and Brunton, 2007) that proliferated in numerous shallow water environments. This is especially true in southern Belgium, which is the historical type area of the Tournaisian and Visean stages (Hance et al., 2006a, 2006b), where brachiopods commonly occur in the mixed carbonate-siliciclastic shelf–ramp environments that stretched from southern Belgium and northern France to southern Ireland across southern Wales and south-western England during the Tournaisian–Visean time span (Figure 1). Carboniferous brachiopods from Western Europe received attention very early in the history of palaeontology, notably in Ireland and in the UK (e.g., Martin, 1793, 1809; Phillips, 1836; M'Coy, 1844; Davidson, 1858–1863). In Belgium, a large part of the Mississippian brachiopods was described in the pioneering works of de Koninck (e.g., 1843, 1847, 1851, 1887), de Ryckholt (1851), and Demanet (e.g., 1923, 1934, 1938, 1941), but most of them remain unrevised.

Besides representatives of the orders Productida and Spiriferida, the Tournaisian–Visean brachiopod assemblages from southern Belgium (Namur–Dinant Basin (Figure 1); see below) frequently include athyridides, orthotetides, and strophomenides. The athyridides were the first brachiopods to be described in this area (Léveillé, 1835).

The purposes of this paper are (1) the taxonomic description and/or revision of some athyridides, orthotetides, rhynchonellides, and strophomenides from the Tournaisian–Visean succession of southern Belgium (Namur–Dinant Basin), (2) to discuss their palaeobiology, and (3) to provide information on their Devonian–Carboniferous representatives (apart from the rhynchonellides).

GEOLOGICAL SETTING

Lower Carboniferous rocks outcrop in southern Belgium on both sides of the major Midi-Eifel fault zone, notably in the Brabant Parautochton, the Haine-Sambre-Meuse Overturned Thrust Sheets, and the Dinant Synclinorium (Hance et al., 1999; Belanger et al., 2012) (Figure 2). These Variscan structural elements constituted the Namur–Dinant Basin that developed along the southeastern margin of Laurussia during Devonian and Mis-
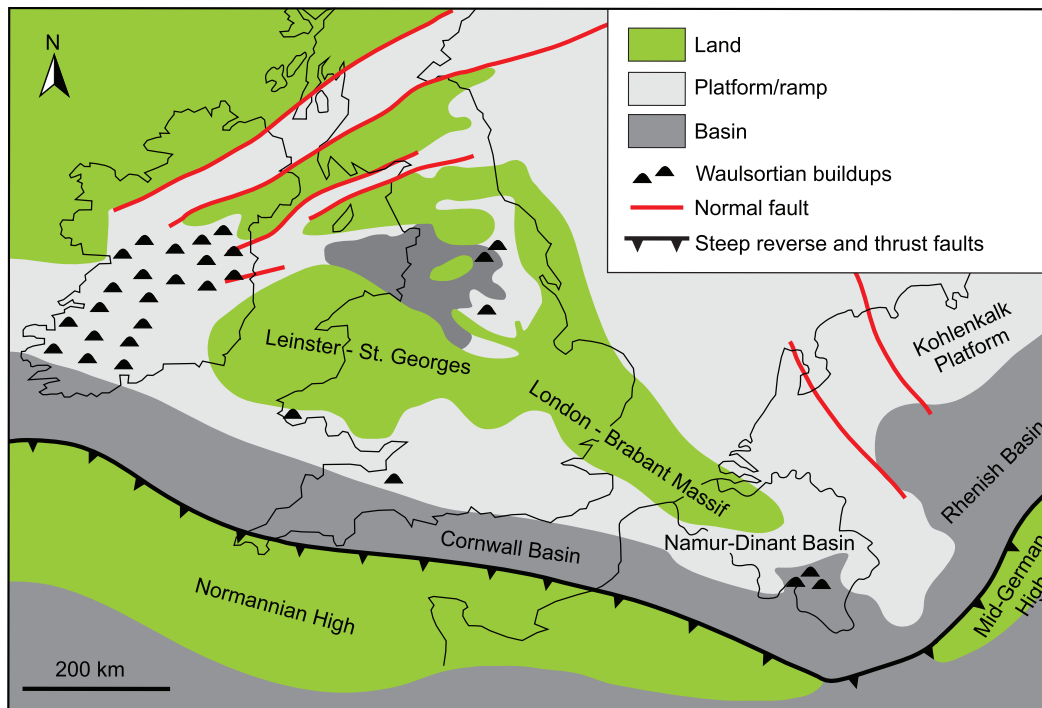
FIGURE 1. General context of Lower Carboniferous sedimentation in north-western Europe showing the distribution of emergent areas and Waulsortian buildups at the end of the Tournaisian (modified from Ziegler, 1990; Devuyst and Dehantschutter, 2007).
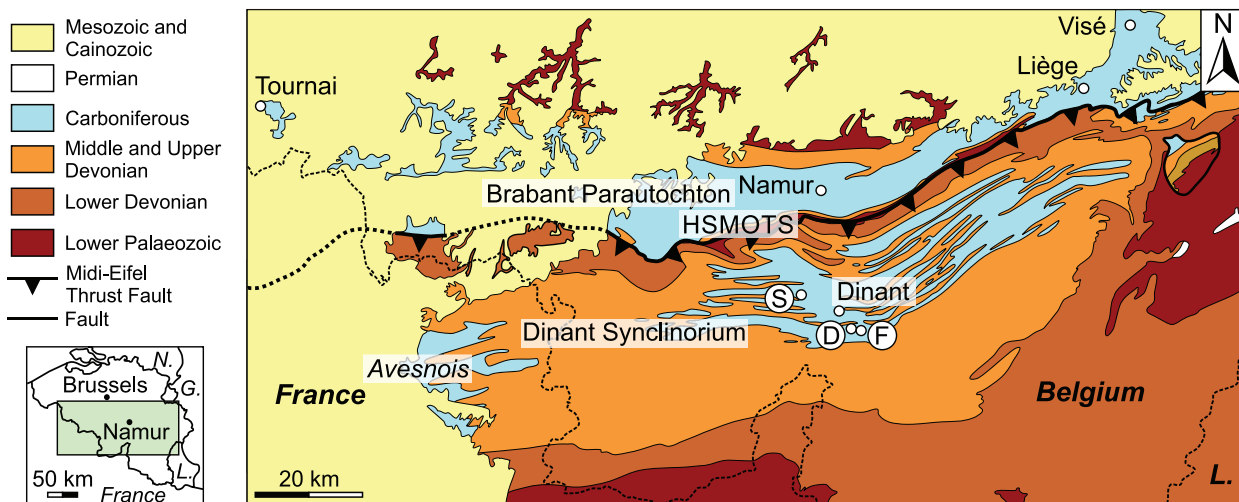
FIGURE 2. Schematic geological map of southern Belgium with location of the fossiliferous localities (modified from de Béthune, 1954). Abbreviations: D, Dréhance; F, Furfooz; G, Germany; HSMOTS, Haine-Sambre-Meuse Overturned Thrust Sheets; L, Grand Duchy of Luxemburg; N, The Netherlands; S, Sosoye.

sissippian times. The Tournaisian–Visean lithostratigraphy of southern Belgium was summarized by Poty et al. (2002), and several sedimentation areas (see below) were recognized in the Namur–Dinant Basin by Poty (1997, 2016) and Hance et al. (2001) (Figure 3). During the upper Visean, the Visé–Maastricht sedimentation area was not connected to the Namur–Dinant Basin and

evolved to a graben that was open to the Campine Basin (Poty et al., 2002). The studied material comes from localities situated in the Hainaut (Tournai area), Dinant (Dréhance, Furfooz, Sosoye), and Visé–Maastricht (Visé) sedimentation areas.

Correlations of the Tournaisian (Hastarian, Ivorian) and Visean (Moliniacian, Livian, and Warnantian) Belgian substages, which are used here,
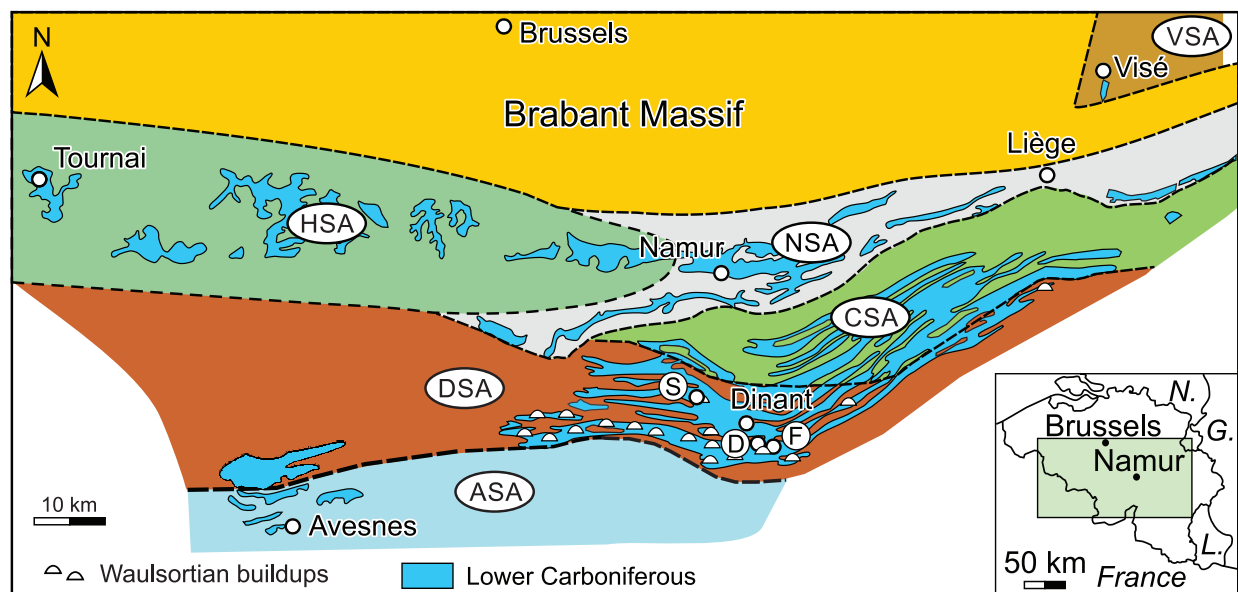
FIGURE 3. Late Tournaisian sedimentation areas in the Namur-Dinant Basin (not palinspastically restored; modified from Hance et al., 2001; Poty et al., 2006; Poty, 2016) with location of the fossiliferous localities. Abbreviations: ASA, Avesnois sedimentation area; CSA, Condroz sedimentation area; D, Dréhance; DSA, Dinant sedimentation area; F, Furfooz; G, Germany; HSA, Hainaut sedimentation area; L, Grand Duchy of Luxemburg; N, The Netherlands; NSA, Namur sedimentation area; S, Sosoye; VSA, Visé–Maastricht sedimentation area.
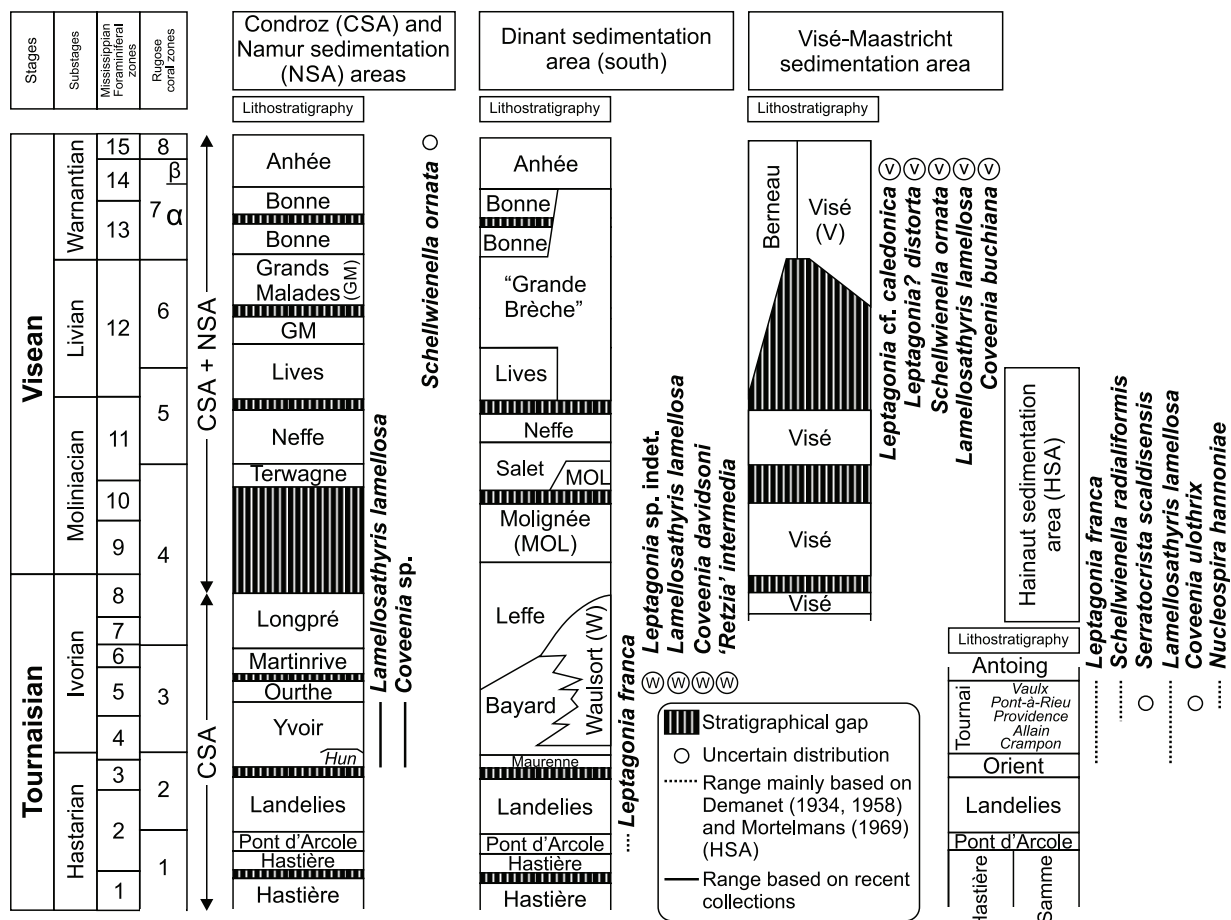
FIGURE 4. Distribution of the athyridides, orthotetides and strophomenides described and/or discussed herein within the essentially carbonate Tournaisian and Visean succession of southern Belgium (see text). Stratigraphy, lithostratigraphy (incompletely represented here for the Hainaut and Visé–Maastricht sedimentation areas; formations and members are in roman and italic letters, respectively), and biostratigraphy are adapted from Poty et al. (2002, 2006, 2014). The lenticular Vignobles Member is not represented here as it is rarely developed (it is comprised between the Vaulx Member of the Tournai Formation and the Antoing Formation). Note that the "Grande Brèche" is an informal stratigraphic unit resulting from the dissolution of evaporitic levels in the Grands Malades Formation; other brecciated horizons occur in the Lives Formation.

with other chronostratigraphic units, were discussed notably by Poty et al. (2006, 2014).

The material investigated herein mostly belongs to several very old collections (e.g., de Ryckholt, de Koninck, and Dewalque), of which the exact provenance is rarely known as is also the case for the stratigraphic level, although it is possible to constrain it with recent data (information are provided below). It is the reason for which we only indicate 'Tournai area' for the type locality of new species based on material from these old collections (see comment below).

The material from Tournai is from the Tournai Formation of Tournaisian age comprising dark, thin-bedded, siliceous, and argillaceous limestones with shaly and marly intercalations and with abundant chert nodules at some levels (Figure 4). Most

of the specimens from Tournai were collected in pocket solutions in which the specimens were silicified, but precise location and stratigraphic levels are generally lacking (see discussion in Demanet, 1958). Some of the specimens are from the former Dutoit quarry now flooded (see Demanet, 1958) and the active Lemay quarry at Vaulx, south-east of Tournai (see Hennebert, 1996). The Tournai Formation is comprised between the Orient and the Antoing formations. The Orient Formation (Tournaisian, latest Hastarian) includes dark grey calcareous shales, with crinoidal limestone beds (ca. 60 m thick) (e.g., Mortelmans, 1969; Poty, et al., 2002). The Antoing Formation (ca. 170 m thick; Tournaisian–Visean [mostly Ivorian to Moliniacian]) lithologically resembles the Tournai Formation, but the beds are

slightly thicker (e.g., Poty et al., 2002). Six members have been identified within the Tournai Formation, which is up to 145 m thick in its type area. They are from the base to the top: the Crampon, Allain, Providence, Pont-à-Rieu, Vaulx, and Vignobles members (see description in Poty et al., 2002) (Figure 4). Where the lenticular Vignobles Member is not developed as represented in Figure 4, the Vaulx Member, extends up to a thin clay marker probably of volcanic origin (Gaillard et al., 1999) known as the 'Gras Délit' (Poty et al., 2002), which marks the top of the formation. The limestones (mudstones, wackestones, and sometimes packstones [see Hennebert, 1996]) of the Tournai Formation are still intensively quarried for the production of cement, aggregate, and building stone and exposed in large and deep quarries. The Tournai Formation represents the nearly *in situ* accumulation of remains from a crinoid–brachiopod–bryozoan community with associated tabulate and solitary rugose corals, gastropods, bivalves, nautiloids, and trilobites; plurilocular foraminifers are very scarce and algae are almost absent (Hennebert, 1996 (see also for sedimentological and bathymetric interpretation); Gaillard et al., 1999). The biostratigraphical range of this formation, in terms of the Mississippian Foraminifer Zones (MFZ) of Devuyst and Hance (in Poty et al., 2006), spans the interval MFZ4 to MFZ5 (top of the Hastarian and lower part of the Ivorian) according to Hance et al. (2006a). For more details concerning the Tournai Formation, as well as the Lower Carboniferous succession in the Tournai area, see Hennebert and Doremus (1997a, 1997b) and Poty et al. (2002). Due to the scarcity of the microfossils (foraminifers, conodonts), correlations with the well-dated sections of the Namur–Dinant Basin are not possible (Mortelmans, 1973; Poty et al., 2002), but detailed studies on brachiopods may bring new elements for correlation in the future.

The material from Dréhance (de Koninck, 1887), Furfooz (de Koninck, 1887), and Sosoye (Demanet, 1923) (Figures 2–3) was recovered from Waulsortian carbonate buildups (Waulsort Formation; Figure 4) that developed in a ramp setting during the Tournaisian (Ivorian) and only occur within the Dinant sedimentation area (e.g., Lees, 1982, 1997, 2006; Hance et al., 2001) (Figures 3-4). The Waulsort Formation, of which the thickness varies between 0 and 300 m, includes a large range of massive limestones and diagenic dolostones (Poty et al., 2002). Its biostratigraphical range spans the interval MFZ4 (top of the Hastar-

ian) to MFZ8 (top of Ivorian) according to Hance et al. (2006a).

The Visé Formation (Ivorian–Warnantian, with stratigraphic gaps; MFZ8–MFZ14) crops out exclusively in a series of disused quarries south of Visé (Figures 2-4) (e.g., Pirlet, 1967; Hance et al., 2006b). Most of the fossils from Visé have been recovered from quarry F–G (e.g., Demanet, 1958; Pirlet, 1967; Poty, 1982; Hance et al., 2006b; Poty and Delculée, 2011), where exposures still exist although the rocks are unfortunately inaccessible. Its thickness is comprised between zero and several hundreds of meters due to major syn-sedimentary tectonics (e.g., Poty and Delculée, 2011). Four main facies composed of pale to grey limestones are distinguished among this lithostratigraphic unit (see Poty et al., 2002 for more details). Most of the macrofossils that contributed to the fame of the Visean fauna were collected within buildups composed of massive algal and bioclastic boundstones (Poty et al., 2002) belonging to the MFZ14. According to Aretz and Chevalier (2007), this particular lithofacies is close to the Cracoean facies of England (Mundy, 1994), which are also well-known for their rich brachiopod fauna (e.g., Brunton and Mundy, 1994).

MATERIAL AND METHODS

The bulk of the material investigated is curated at the Royal Belgian Institute of Natural Sciences (prefixed RBINS), Brussels, and complemented by specimens housed at the Department of Geology (palaeontological collections) of the University of Liège (prefixed ULg.PA). Additional material is housed at the Natural History Museum (prefixed BMNH), London, and at the National Museum of Ireland (Geological Collection, Natural History Division; prefixed NMING), Dublin.

SYSTEMATIC PALAEONTOLOGY

The supraspecific classification follows Cocks and Rong (2000) for Order Strophomenida, Williams and Brunton (2000) for Suborder Orthotetidina, and Alvarez and Rong (2002) and Alvarez (2007) for Order Athyridida. Only the illustrated material is registered.

Most of the synonymy lists refer only to the material from southern Belgium. The first monograph on Mississippian faunas from southern Belgium by de Koninck was published in several fascicules between 1842 and 1844, which are conventionally found in libraries as a bound volume cited with this combined date (Godefroid et al.,

2006). De Koninck (1847, 1851, 1887) invariably cited 1843 for his earlier work on brachiopods. As explained by Mottequin and Simon (2017), we have here opted for 1843 in conformity with de Koninck's works. It is useful to stress here on the fact that a large part of Demanet's (1934) monograph is based on an unpublished work of de Koninck, which would have been included in a monograph to be published in the Annales du Musée royal d'Histoire naturelle de Belgique, but the latter died in 1887 before completing his opus.

Phylum BRACHIOPODA Duméril, 1805
Subphylum RHYNCHONELLIFORMEA Williams et al., 1996
Class STROPHOMENATA Williams et al., 1996
Order STROPHOMENIDA Öpik, 1934
Superfamily STROPHOMENOIDEA King, 1846
Family RAFINESQUINIDAE Schuchert, 1893
Subfamily LEPTAENINAE Hall and Clarke, 1894
Genus LEPTAGONIA M'Coy, 1844

Type species. *Producta analoga* Phillips, 1836, from the Visean Pendleside Limestone Group of Bowland, Yorkshire, England.

Leptagonia franca sp. nov.
Figures 4-8, Table 1

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p	1843	*Leptaena depressa;* de Koninck, p. 215, pl. 13, fig. 6a-c (labelled *Leptaena depressa* var. *analoga* Sowerby in the plate legend).
p	1851	*Leptaena analoga*; de Koninck, p. 653.
p	1868	*Strophomena (Producta) analoga;* Dewalque, p. 333.
p	1881	*Strophomenes (Producta) analoga;* Mourlon, p. 47.
v	1933	*Leptaena analoga*; Maillieux, p. 92.
v	1934	*Leptaena analoga* (Phillips); Demanet, p. 61, text-figs. 11-14, pl. 5, figs. 1-14.
	1950	*Leptaena analoga* Wilckens (*sic*); Termier and Termier, pl. 82, figs. 19-20.
p	1958	*Leptaena analoga* (Phillips); Demanet, p. 123, 126, 130.
p	1969	*Leptaena analoga* (Phill.); Mortelmans, p. 31 (only those from the Tournai Formation).
v	2017	*Leptagonia* sp. indet.; Mottequin and Simon, fig. 12d.

Etymology. From *francus, a, um* (Latin: of or belonging to the Franks, Frank), in reference to the rich Frank history of the town of Tournai.

Holotype. RBINS a5891 (Demanet, 1934, pl. 5, fig. 1) from Tournai (Tournai Formation) (Figure 5.1-6).

Paratypes. RBINS specimens from Tournai (Tournai Formation) illustrated by Demanet (1934) a5829 (pl. 1, fig. 30) (Figure 6.1-6), a5892 (pl. 5, fig. 2) (Figure 5.7-12), a5893 (pl. 5, fig. 3), a5894 (pl. 5, fig. 4), a5895 (pl. 5, fig. 5) (Figure. 6.7-12), a5896 (pl. 5, fig. 6) (Figure 7.1), a5897 (pl. 5, fig. 7) (Figure 7.10-13), a5898 (pl. 5, fig. 8), a5899 (pl. 5, fig. 9) (Figure 7.9), a5902 (pl. 5, fig. 12) (Figure 7.4-5), a5903 (pl. 5, fig. 13) (Figure 7.8), a5904 (pl. 5, fig. 14), a5905 (text-fig. 11), a5906 (text-fig. 13), a5907 (text-fig. 14) and herein a13099 (Figure 5.13-18), a13100 (Figure 6.13-17), 13101 (Figure 6.18-22), a13102 (Figure 6.23-27), a13103 (Figure 7.2), a13104 (Figure 7.6-7).

Additional material. RBINS: two ventral valves and 27 articulated specimens.

**Type locality.** Tournai area (Figures 2-3), southern Belgium.

Type stratum. Tournai Formation, Tournaisian (Figure 4).

Diagnosis. Shell large (up to 70 mm in width), with a subtrapezoidal to subrectangular outline in juveniles, but transversally subrectangular in mature specimens; cardinal extremities slightly mucronate in juveniles, but becoming acute to subrounded (due to development of lamellose shelly expansions) in mature specimens. Shell parvicostellate and rugate, with 11–15 costae in 5 mm at 10 mm from the dorsal umbo; 15–22 rugae on ventral disc. Ventral muscle field subdiamond-shaped, raised anterolaterally, and anteriorly on a low pseudo-spondylium. Dorsal muscle platform raised above valve floor extending to about half length of the disc; dental sockets deep, well-defined; socket plates strongly divergent; dorsal marginal ridge well developed, with numerous mantle canals developed anteriorly and antero-laterally to it.

Description. Shell large (up to 70 mm in width), markedly wider than long, widest at hinge line in juveniles or posteriorly to hinge line in mature specimens, concavoconvex in lateral profile with sharp, dorsally directed geniculation, with a subtrapezoidal to subrectangular outline in juveniles, but transversally subrectangular in mature specimens; anterior commissure rectimarginate; anterior margin slightly rounded or emarginate; cardinal extremities slightly mucronate in juveniles, but becoming acute to subrounded (due to development of lamellose shelly expansions) in mature specimens.
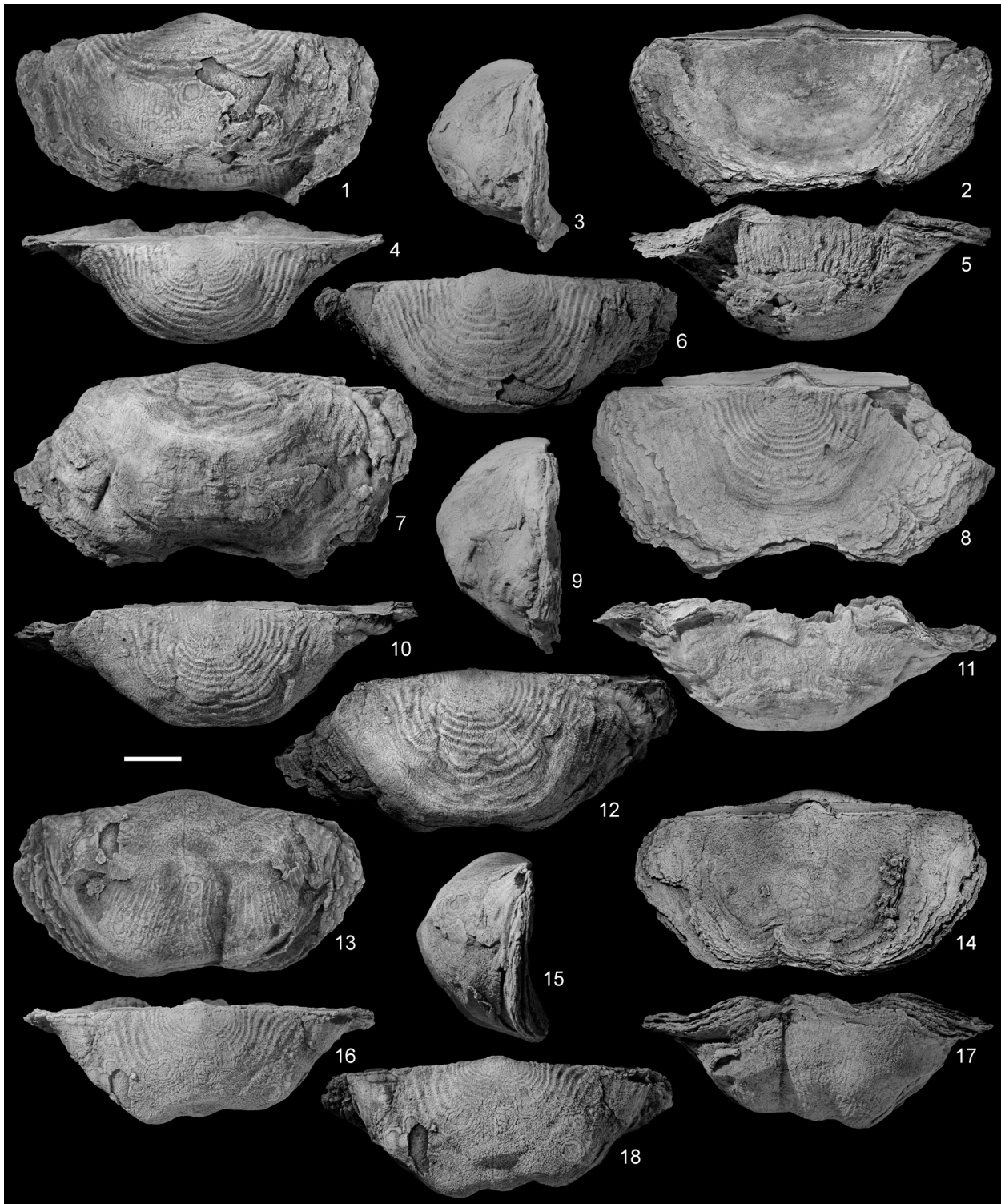
FIGURE 5. *Leptagonia franca* sp. nov. from the Tournai area, Tournai Formation (Tournaisian). **1-6,** RBINS a5891 (holotype), articulated specimen, almost complete, in ventral (perpendicular to the surface of the alae), dorsal, lateral, posterior, anterior, and ventral (perpendicular to the disc) views. **7-12,** RBINS a5892, articulated specimen, almost complete, in ventral (perpendicular to the surface of the alae), dorsal, lateral, posterior, anterior, and ventral (perpendicular to the disc) views. **13-18,** RBINS a13099, articulated specimen (with an auloporid tabulate fixed to its right ventral flank), almost complete, in ventral (perpendicular to the surface of the alae), dorsal, lateral, posterior, anterior, and ventral (perpendicular to the disc) views. Scale bar equals 10 mm.
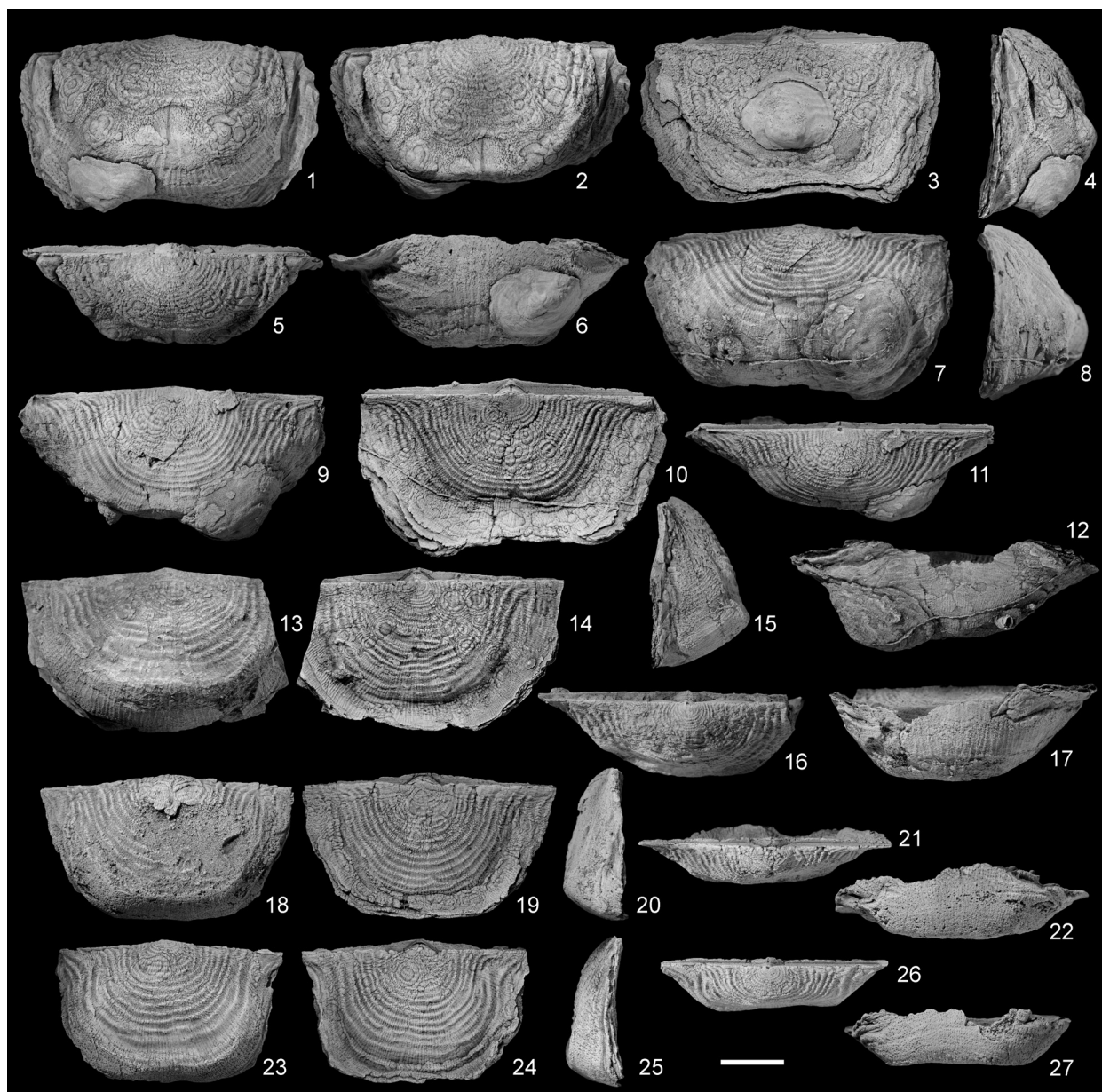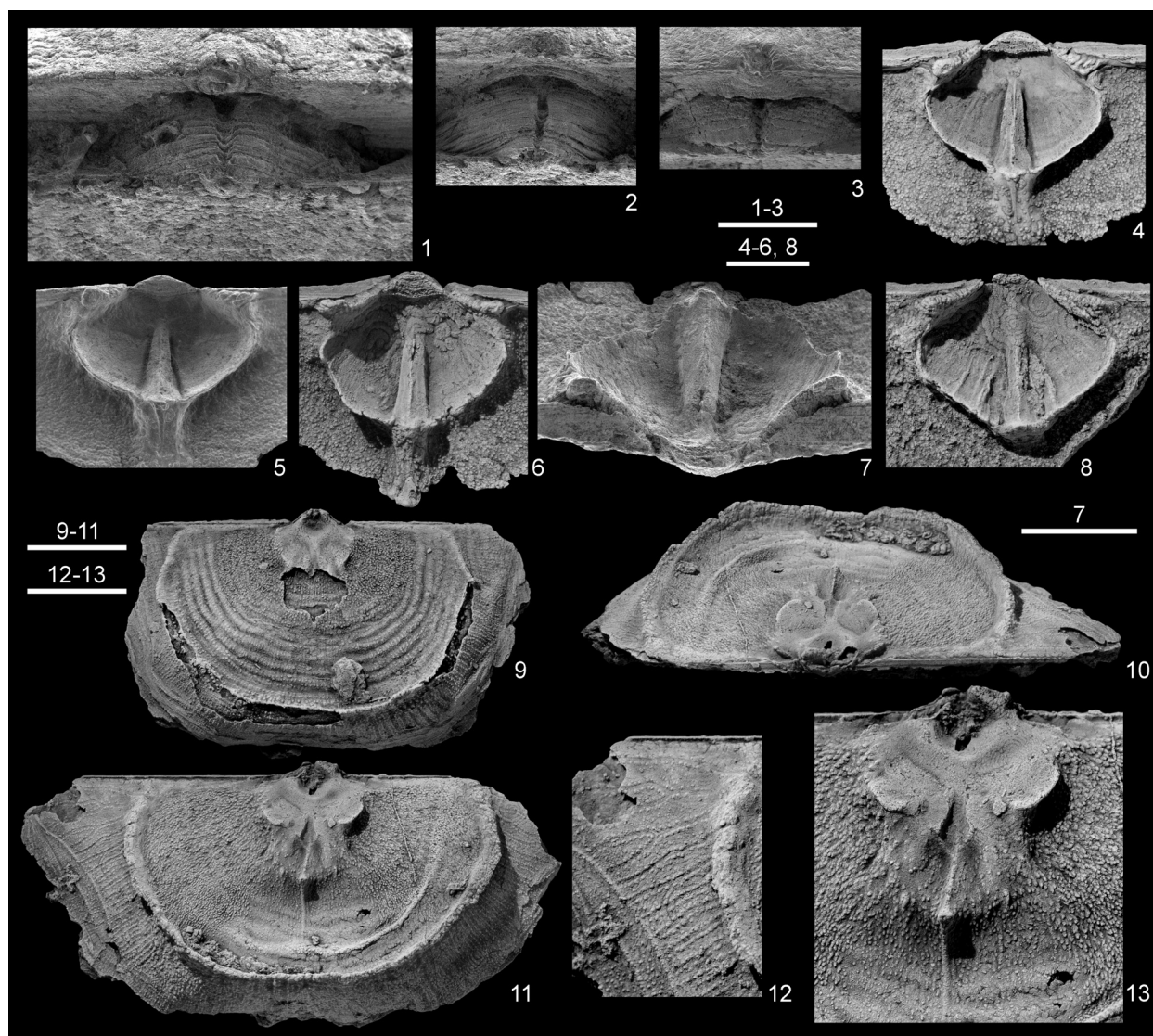
FIGURE 6. *Leptagonia franca* sp. nov. from the Tournai area, Tournai Formation (Tournaisian). **1-6,** RBINS a5829, complete articulated specimen (with *Petrocrania*? *ryckholtiana* (de Koninck, 1843) attached to ventral and dorsal valves) in ventral (orientation as in Figure 5.1), ventral (perpendicular to the visceral disc), dorsal, lateral, posterior, and anterior views. **7-12,** RBINS a5895, complete articulated specimen (with *Petrocrania*? *ryckholtiana* and microconchid attached to ventral valve), in ventral (orientation as in Figure 5.1), lateral, ventral (perpendicular to the visceral disc), dorsal, posterior and anterior views. **13-17,** RBINS a13100, articulated specimen, almost complete, in ventral (orientation as in Figure 5.1), dorsal, lateral, posterior, and anterior views. **18-22,** RBINS a13101, articulated specimen, almost complete, in ventral (orientation as in Figure 5.1), dorsal, lateral, posterior and anterior views. **23-27,** RBINS a13102, articulated specimen, almost complete, in ventral (orientation as in Figure 5.1), dorsal, lateral, posterior, and anterior views. Scale bar equals 10 mm.

Ventral visceral disc shorter than trail in mature specimens, moderately convex longitudinally and transversally, subtrapezoidal in outline; umbo small; beak short; interarea low, striated parallel to hinge, apsacline to almost orthocline, weakly concave; apical foramen small (Figure 7.1-3); delthyrium broad, triangular, closed apically by a convex, striated pseudodeltidium; median depression developed anteriorly to geniculation in mature specimens.

FIGURE 7. *Leptagonia franca* sp. nov. from the Tournai area, Tournai Formation (Tournaisian). **1-3,** Detail of the small pseudodeltidium and apical foramen of three articulated specimens with the ventral valve on top: RBINS a5896 (**1**), RBINS a13103 (**2**), and RBINS a5895 (**3**). **4-5,** RBINS a5902, incomplete ventral valve showing the posterior morphology. **6-7,** RBINS a a13104 , incomplete ventral valve interior showing the posterior morphology and posterior view notably displaying the prominent teeth. **8,** RBINS a5903, incomplete ventral valve interior showing the posterior morphology. **9,** RBINS a5899, almost complete dorsal valve interior in ventral view. **10-13,** RBINS a5897, almost complete dorsal valve interior in posterior and ventral views, detail of the lateral vascular canals, and close-up of the cardinal process and the muscular field. Scale bars equal 2.5 mm (1-3), 5 mm (4-8, 12-13), 10 mm (9-11).

Dorsal visceral disc flat longitudinally and transversally; trail shorter than disc; interarea clearly less developed than the ventral one, flat, apsacline, divided by convex, striated, medially grooved chilidium (Figure 7.1-3).

Shell parvicostellate and rugate, with 11–15 costae (n=8) in 5 mm at 10 mm from the dorsal umbo. Between 15 and 22 rugae on ventral disc; prominent on both discs and absent on trails.

Ventral interior (Figure 7.4-8) with small teeth, supported by short dental plates; muscle field sub-diamond-shaped, raised anterolaterally and anteriorly on a low pseudospondylium; diductor scars large, fan-shaped, radially striated; adductor scars separating the diductors, raised on a prominent median ridge widening anteriorly and divided by a thin myophragm; base of the adductor ridge extends slightly anterior to the pseudospondylium
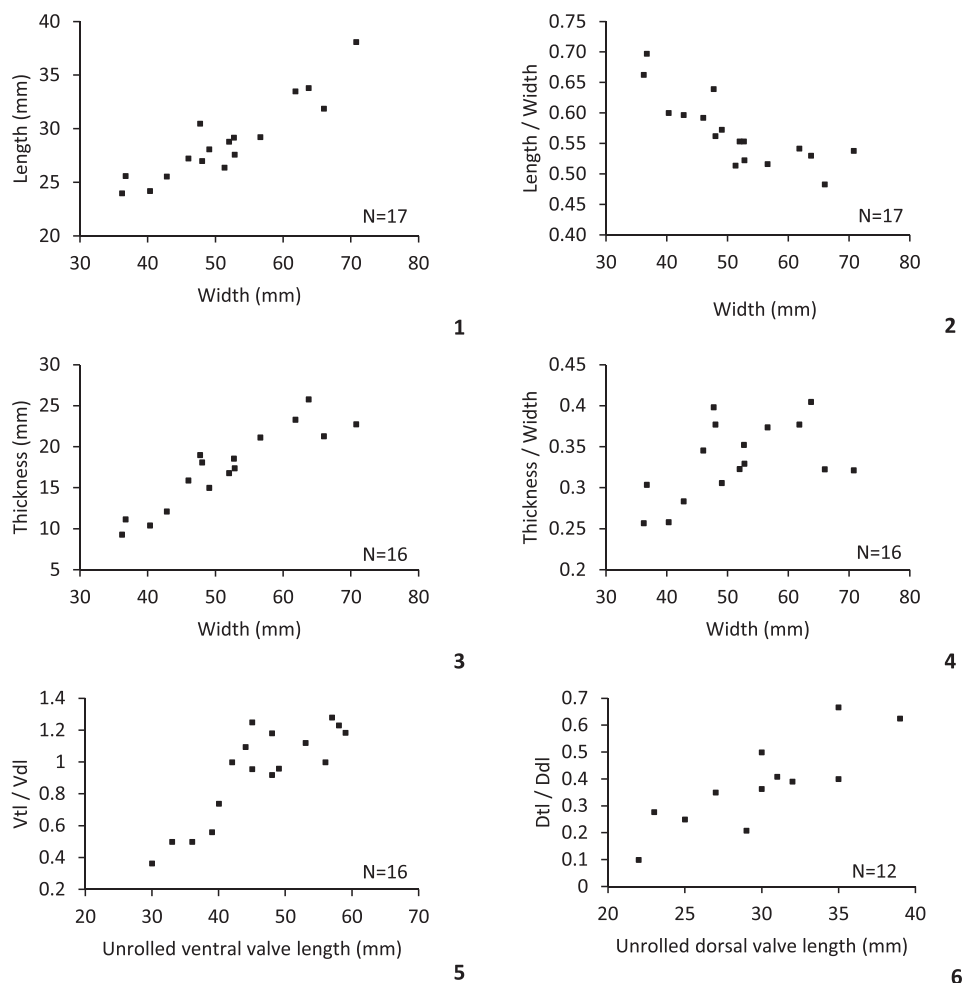
FIGURE 8. Scatter diagrams of *Leptagonia franca* sp. nov. N: number of specimens measured. **1,** Relation between shell width and length. **2,** Relation between shell width and shell length/shell width ratio. **3,** Relation beween shell width and thickness. **4,** Relation between shell width and shell thickness/shell witdth ratio. **5,** Relation between unrolled ventral valve length and ratio between unrolled ventral trail length (Vtl) and unrolled ventral disc length (Vdl). **6,** Relation between unrolled dorsal valve length and ratio between unrolled dorsal trail length (Dtl) and unrolled dorsal disc length (Ddl).

as a rounded buttress onto valve floor; mantle canals not observed.

Dorsal interior (Figure 7.9-13) with stout, ventrolaterally oriented cardinal process lobes; muscle platform raised above the valve floor; cardinal process pit developed between the cardinal process lobes and the posterior margin of the muscle platform; posterior adductor scars more or less circular and separated by a median ridge terminating close to their anterior end, but variably developed among the examined material; anterior adductor scars markedly smaller and separated by a slender septum continuing anteriorly for a variable distance in front of the muscle platform and reaching its maximum height at the junction of the lateral ridges bounding the former, then decreasing rapidly

towards the anterior margin; dental sockets deep, well-defined; socket plates diverging at an angle of 142–159 degrees (n=2); outer surface of the marginal ridge including numerous traces of mantle canals; tubercles abundant, but variably developed following the specimens (compare Figure 7.9 and 7.11).

Dimensions (Figure 8, Table 1). The number of specimens measured is rather low due to lack of well-preserved material. For this reason, the mean value is given without standard error. Nonetheless, the unrolled ventral trail length/unrolled ventral disc length and unrolled dorsal trail length/unrolled dorsal disc length ratios analysed here show that an interrelation is probable.

TABLE 1. Measurements in mm of *Leptagonia franca* sp. nov. Abbreviations for tables 1–4: Ddl, unrolled length of dorsal disc; Dtl, unrolled length of dorsal trail; Hi, height of the ventral interarea; L, length of the shell; T, thickness of the shell; Vdl, unrolled length of ventral disc; Vtl, unrolled length of ventral trail; W, width of the shell; Wi, width of the ventral interarea.

|	W	L	Vdl	Vtl	Ddl	Dtl	T	L/W	T/W	Vtl/Vdl	Dtl/Ddl
N	17	17	17	17	13	13	16	17	16	17	12
Mean	51.4	28.9	23.8	22.2	21.6	8.1	17.4	0.57	0.33	0.93	0.38
MIN	36.2	24	20	8	18	2	9.3	0.48	0.26	0.36	0.10
MAX	70.8	38.1	28	32	25	15	25.8	0.70	0.40	1.28	0.67

Remarks. Until recently, Tournaisian leptaenines from Western Europe, but not only (see Bahram-manesh et al. (2011) for a non-exhaustive list of references), were identified as *Leptagonia analoga* (Phillips, 1836), whose lectotype was selected and illustrated by Brunton (1968) as subsequently did Brand (1972) and Cocks and Rong (2000). Phillips' species was described with great detail by Brunton (1968), Brand (1972), and Harper and Jeffrey (1996). As rightly proposed by Bassett and Bryant (2006), several features such as the outline of the muscular field could be used to discriminate all the forms identified as *L. analoga*, an opinion subsequently followed by Mottequin (2010) and Bahram-manesh et al. (2011). In order to concretise this point of view, a new large-sized species is here erected on the basis of the well-preserved material from the Tournai area, formerly illustrated by Demanet (1934). *Leptagonia franca* sp. nov. differs from *L. analoga* by its less elongate ventral disc, its more developed ventral trail, and its more inflated shell. Furthermore, its ornamentation is slightly coarser than in the latter and its ventral muscle field is subdiamond-shaped. Except the radial ornamentation, which is similar in both species, the same features plus a markedly distinct dorsal internal morphology are used to discriminate *L. franca* and *L. caledonica* Brand, 1972. Due to its distinctive external and internal features, *L. franca* cannot be confused with *L. simorini* (Sokolskaya in Sarytcheva et al., 1963) and *L. smithi* Brand, 1972. The new species differs from *L. convexa* (Weller, 1914) notably in its less elongate ventral disc and its more developed ventral trails. *Leptagonia franca* is clearly larger and has a coarser radial ornamentation than *L. missouriensis* Carter, 1968. Sanders (in Easton et al., 1958) erected *Leptaena cooperi* from the Represso Limestone of Sonora (Mexico), on the basis of a few incomplete specimens (see Carter, 1987), that he compared with the Belgian material illustrated by Demanet (1934). Indubitably, the internal morphology of both species is identical except some differences noted by Sanders (in Easton et al., 1958), such as the outline of the visceral disc (slightly more than semi-elliptical in *L. franca* vs. nearly completely elliptical in *L. cooperi*). Further material is however required to better describe the poorly known Mexican species.

Occurrence. Until now, *Leptagonia franca* is mainly known from the Tournai Formation in the eponymous area but also occurs in the Tournaisian succession of the Dinant Synclinorium, as evidenced by the specimens illustrated by Demanet (1934, pl. 5, figs. 10, 11) from the Hastarian Pont d'Arcole Formation. Its precise distribution in the Tournaisian succession would require a detailed survey of the complete Tournaisian succession, which is well beyond the scope of this paper. However, Demanet (1923, pl. 5, fig. 8) illustrated a ventral valve identified as *Strophomena analoga* from the Waulsort Formation at Sosoye in the Dinant sedimentation area (Figures 2-4). This specimen (RBINS a11747) characterized by its flat visceral disc and thin radial ornamentation (17 ribs per 5 mm at 10 mm from the umbo; 22 rugae) is re-illustrated herein (Figure 9.1-4) and left provisionally in open nomenclature due to the absence of additional material, and is thus identified as *Leptagonia* sp. indet.

Leptagonia cf. *caledonica* Brand, 1972
Figures 4, 9.5-26, 10-11

p	1843	*Leptaena depressa* Sowerby; de Koninck, p. 215, pl. 12, figs. 3, 5 (?), 6.
p	1851	*Leptaena analoga*; de Koninck, p. 653.
p	1868	*Strophomena (Producta) analoga;* Dewalque, p. 333.
p	1881	*Strophomenes (Producta) analoga;* Mourlon, p. 47.
v	1934	*Leptaena sinuata* de Koninck; Demanet, p. 74, pl. 6, figs. 6-7.
cf.*	1972	*Leptagonia caledonica* sp. nov. Brand, p. 61, text-figs. 1d, 2-3, pl. 9, figs. 1-7.
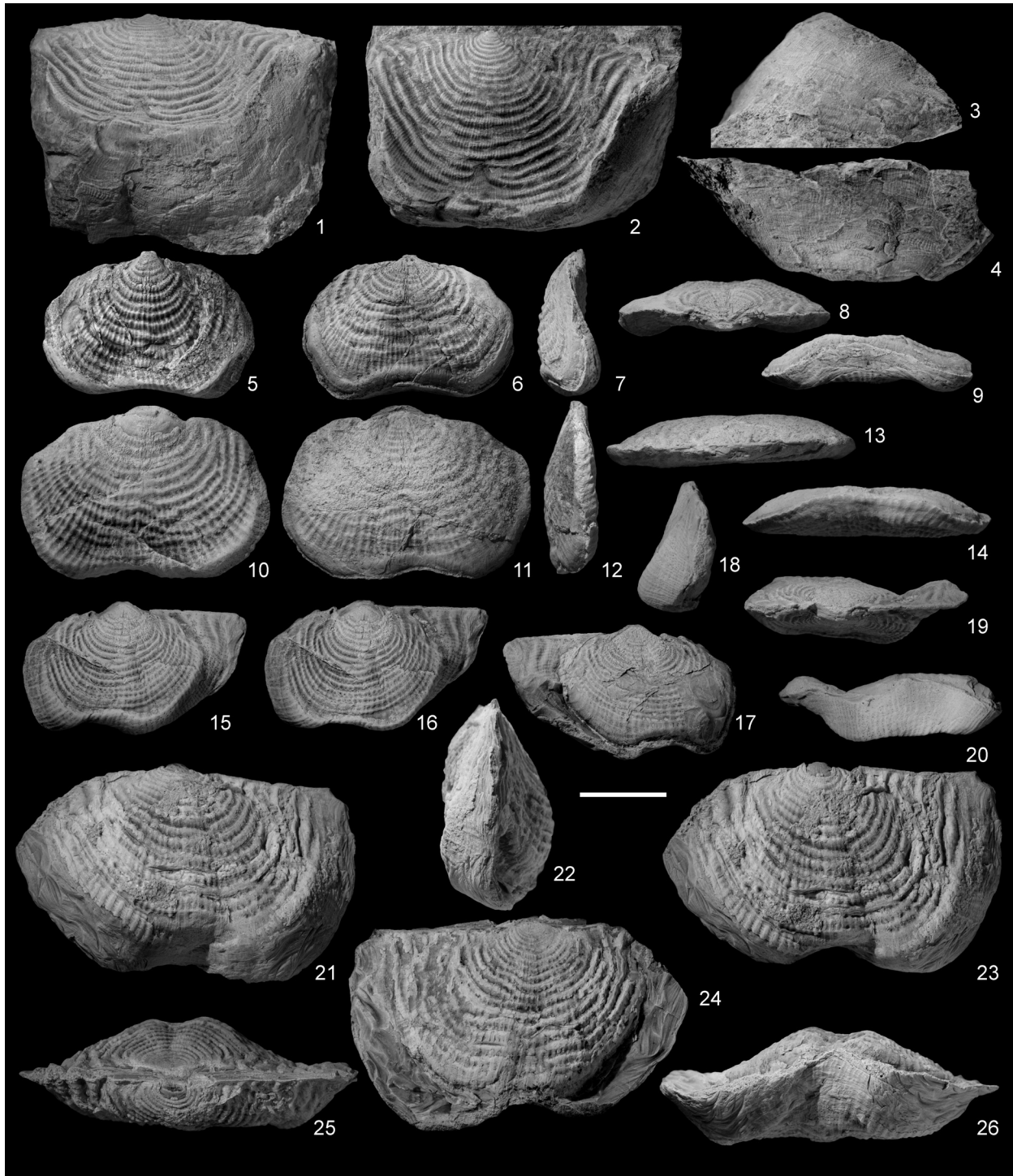
FIGURE 9. 1-4, *Leptagonia* sp. indet. from Sosoye, Waulsort Formation (Tournaisian, Ivorian), RBINS a11747, almost complete ventral valve in ventral, ventral (perpendicular to the disc), lateral and anterior views. **5-26,** *Leptagonia* cf. *caledonica* Brand, 1972 from Visé, Visé Formation (Visean, Warnantian). **5-9,** RBINS a5915, incomplete articulated specimen in ventral (perpendicular to the disc), dorsal, lateral, posterior, and anterior views. **10-14,** RBINS a5914, incomplete articulated specimen in ventral (perpendicular to the disc), dorsal, lateral, posterior, and anterior views. **15-20,** ULg.PA. 2016.12.25/1, articulated specimen, almost complete, in ventral, ventral (perpendicular to the disc), dorsal, lateral, posterior and anterior views. **21-26,** ULg.PA.2016.12.25/2, articulated specimen, almost complete, in ventral, lateral, ventral (perpendicular to the disc), dorsal, posterior, and anterior views. Scale bar equals 10 mm.
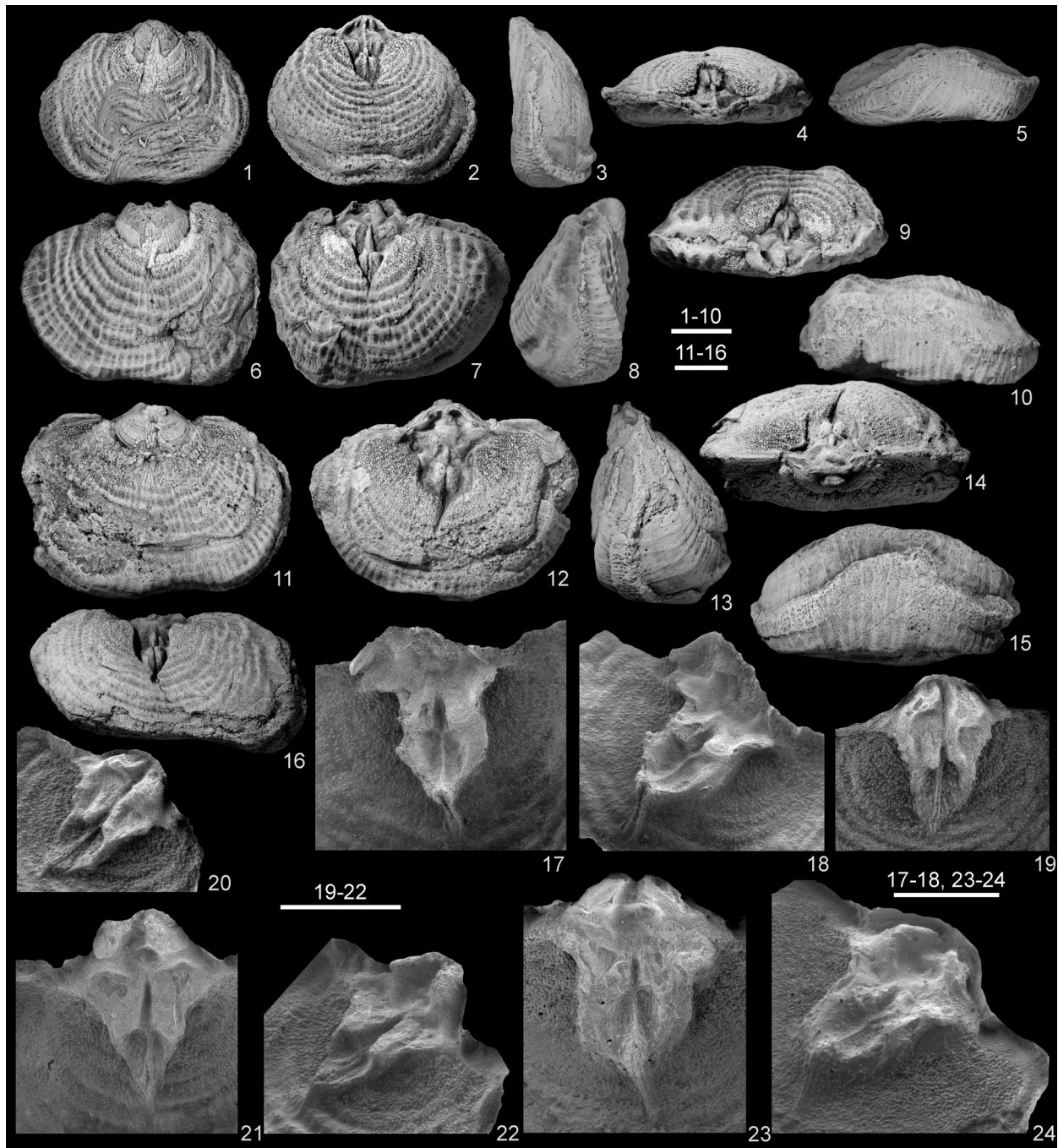
FIGURE 10. *Leptagonia* cf. *caledonica* Brand, 1972 from Visé, Visé Formation (Visean, Warnantian). **1-5, 19-20**, ULg.PA.2016.12.25/3, internal mould in ventral, dorsal, lateral, posterior and anterior views, and detail (SEM) of the muscular platform (latex cast). **6-10, 21-22,** ULg.PA.2016.12.25/4, internal mould in ventral, dorsal, lateral, posterior, and anterior views, and detail (SEM) of the muscular platform (latex cast). **11-15, 23-24,** ULg.PA.2016.12.25/5, internal mould in ventral, dorsal, lateral, posterior, and anterior views, and detail (SEM) of the muscular platform (latex cast). **16-18,** ULg.PA.2016.12.25/6, distorted internal mould in dorsal view and close-up (SEM) of the muscular platform (latex cast). Scale bars equal 5 mm.
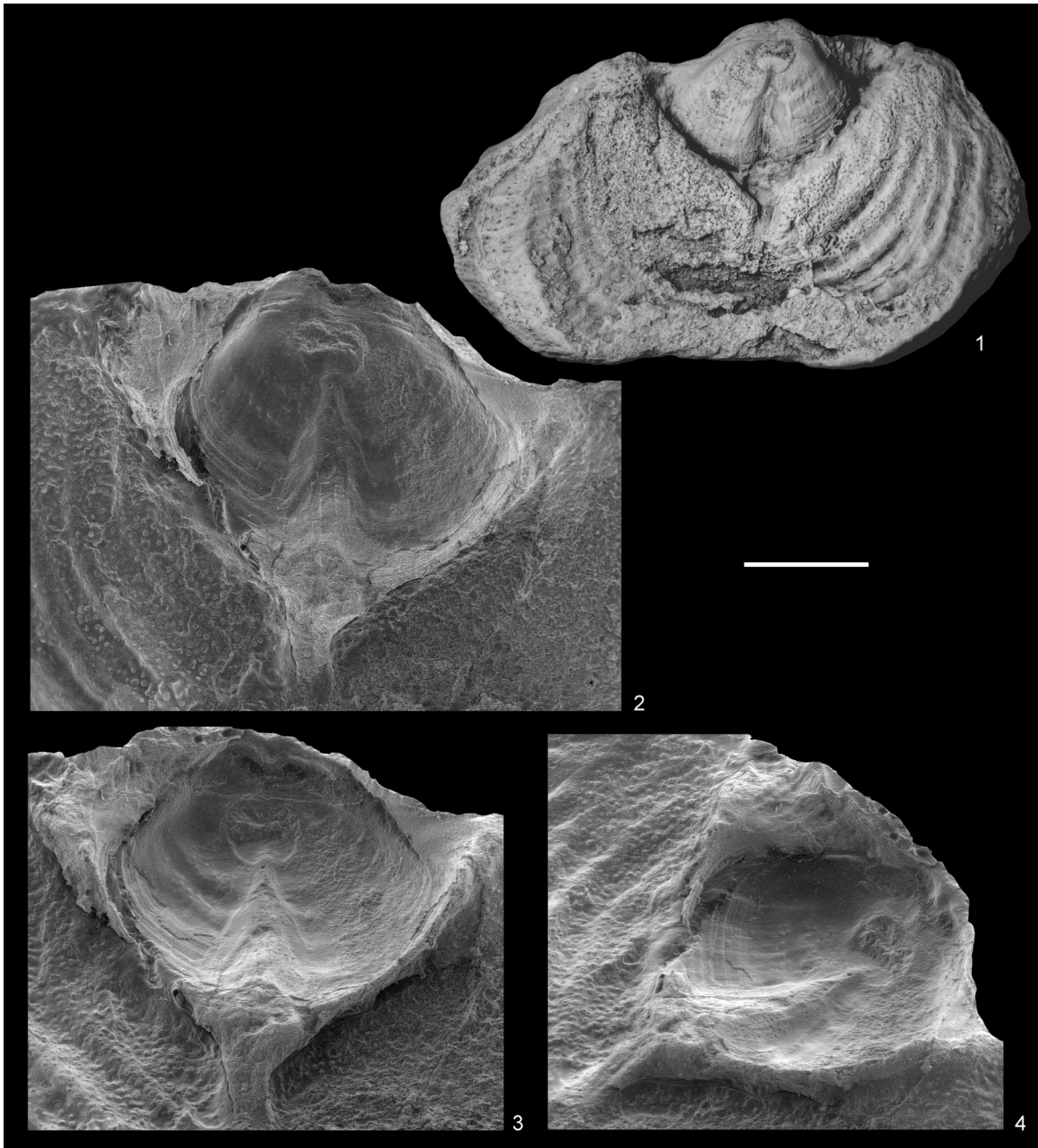
Leptagonia cf. *caledonica* Brand, 1972 from Visé, Visé Formation (Visean, Warnantian). **1-4,** ULg.PA.2016.12.25/7, distorted, articulated internal mould in ventral view and detail of the latex mould of the muscular platform in three different views. Scale bar equals 5 mm (1), 2.5 mm (2-4).

Material. RBINS: besides the specimens RBINS a5914 (Figure 9.10-14)–5915 (Figure 9.5-9) illustrated by Demanet (1934 pl. 6, figs. 6-7), the studied material includes four ventral valves and 30 articulated specimens; ULg.PA: five ventral and two dorsal valves, and 54 articulated specimens. Due to the deficient preservation (e.g., trails and cardinal extremities broken), despite the great number of specimens available, it was not possible to perform statistics.

Description. Shell medium-sized (up to ca. 38.7 mm in width), subrectangular in outline with ears developed (exceptionally preserved), wider than long, concavo-convex, resupinate; widest at hinge line; trail development unknown (exceptionally and incompletely preserved); anterior margin emarginate.

Ventral disc slightly convex in posterior and lateral view or flattened, roughly semi-circular to semi-elliptic in outline; posterior margin rectilinear, slightly broken by small umbo; sulcus round-bottomed, deep, only affecting the trail; interarea flat, low, apsacline; delthyrium closed apically by convex pseudodeltidium.

Dorsal disc convex, but with posterior part flattened in lateral view, roughly semi-circular to semi-elliptic in outline; ears flattened; in some specimens, presence of a shallow and poorly defined median depression originating in posterior part of the disc, reaching the geniculation; interarea linear, flat, catacline.

Shell parvicostellate and rugate, with 8–13 costae (n=10) in 5 mm at 10 mm from the umbones. Circa 13–16 (n=3) relatively regular rugae on ventral disc (probably a little bit more as, in most of the specimens, the umbo is blunt); rugae prominent on both discs and absent on trails.

Ventral interior (Figures 10-1-15, 11) with large, subdiamond-shaped muscle field, raised anteriorly and anterolaterally on a low pseudospondylium; teeth not observed; diductor scars large, with poorly preserved radial striation; adductor scars separating the diductors, raised on a prominent median ridge widening anteriorly; base of the adductor ridge extending slightly anteriorly to the pseudospondylium as a rounded buttress onto valve floor; numerous tubercles concentrated in posterior part of the valve floor around the pseudospondylium, and also present on the rest of the valve, although less abundantly developed; mantle canals well developed (but insufficiently preserved for complete description).

Dorsal interior (Figure 10) with stout cardinal process lobes (cardinal process pit present directly antero-medial to them); muscle platform with anterior part strongly raised above valve floor; posterior adductor scars semi-circular, separated by deep median groove from which a median septum extends anteriorly; anterior portion of muscle platform consisting of two depressions separated by the septum reaching its maximum at the junction of the lateral ridges bounding these oval depressions; numerous tubercles concentrated in posterior part of the valve floor around the muscle platform and less abundantly developed on the rest of the valve,; mantle canals well developed (but insufficiently preserved for complete description).

Remarks. Demanet (1934, pl. 6, figs. 6, 7) illustrated two specimens from the Visean of Visé, which are re-illustrated here (Figure 9.5–14), that he assigned to the productide *Sinuatella sinuata*

(de Koninck, 1851), which undoubtedly belong to *Leptagonia* by their external features (see discussion related to de Koninck's species of, e.g., Muir-Wood and Cooper [1960] and Brunton and Mundy [1988]). Brand (1972) tentatively assigned the specimen RBINS a5915 (Demanet, 1934, pl. 6, fig. 7) to his new species *Leptagonia smithi*. After examination of numerous specimens, it appears that the material from Visé cannot be assigned to *L. smithi* Brand, 1972 as it is characterized by the development of ears (rarely preserved in the investigated material), the largeness of the tuberculate areas and especially by the markedly greater development of the dorsal muscle platform (compare with Brand, 1972, text-fig. 3, pl. 11, fig. 6). From the viewpoint of the internal and external morphology, the Belgian material is comparable to *L. caledonica*, except its ornamentation, which is coarser: 8–13 versus 10–16 costae in 5 mm at 10 mm from the umbones according to Brand (1972). Nonetheless, although the available material is abundant, its relatively poor state of preservation (most of the specimens are devoid of trails and ears) does not allow a more confident identification; that is why it is doubtfully assigned to Brand's (1972) species.

Occurrence. The Belgian material originates from Visé (Visé Formation, Visean), whereas *Leptagonia caledonica* seems to be confined to the British Visean and Serpukhovian according to Brand (1972, 2011) and Brunton and Tilsley (1991).

Order ORTHOTETIDA Waagen, 1884
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily ORTHOTETOIDEA Waagen, 1884
Family PULSIIDAE Cooper and Grant, 1974
Genus SCHELLWIENELLA Thomas, 1910

Type species. *Spirifera crenistria* Phillips, 1836, from the Visean Pendleside Group of Bowland, Yorkshire, England.

Schellwienella radialiformis Demanet, 1934
Figures 4, 12-14

v*	1934	*Schellwienella aspis* mut. *radialiformis* nov. mut. Demanet, p. 85, pl. 7, figs. 6-12.
v	1934	*Schellwienella* sp.; Demanet, p. 81, text-fig. 15, pl. 7, fig. 3.
non	1954	*Schellwienella* (subgen. nov. *Carlospina*) *radialiformis* Demanet; Reed, p. 183, pl. 3, fig. 21.
v	1958	*Schellwienella aspis radialiformis* Demanet; Demanet, p. 126.
	1969	*Schellwienella aspis radialiformis* Demanet; Mortelmans, p. 31.
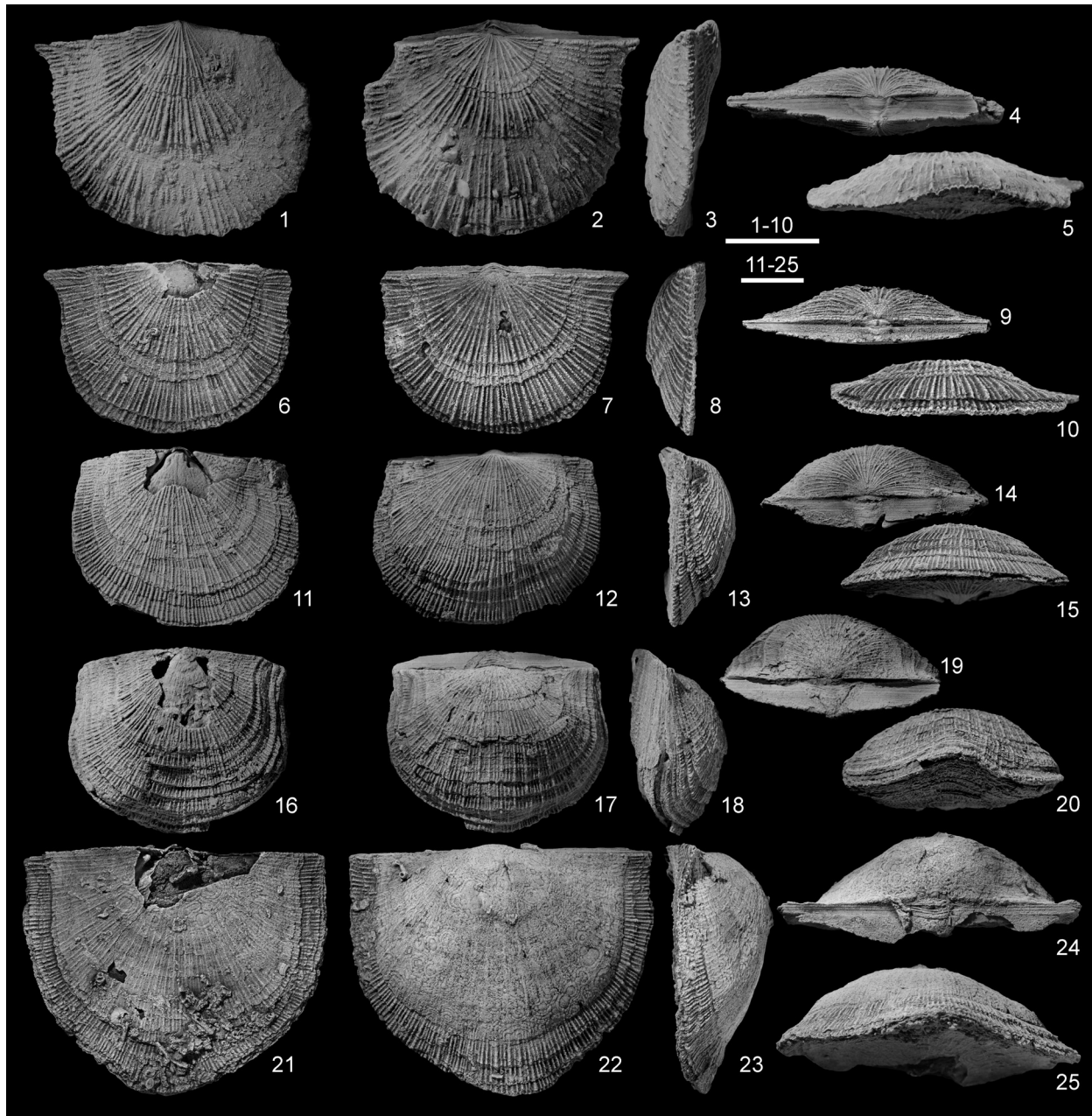
FIGURE 12. *Schellwienella radialiformis* Demanet, 1934 from the Tournai area, Tournai Formation (Tournaisian). **1-5,** RBINS a5924, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior, and anterior views. **6-10,** RBINS a5928, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior, and anterior views. **11-15,** RBINS a5929, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior and anterior views. **16-20,** RBINS a5930 (lectotype), articulated specimen, almost complete, in ventral, dorsal, lateral, posterior, and anterior views. **21-25,** RBINS a5926, almost complete articulated specimen (with a microconchid attached to the ventral valve, close to the anterior margin) in ventral, dorsal, lateral, posterior, and anterior views. Scale bars equal 10 mm.

Type material. Demanet (1934) considered all the illustrated specimens as paratypes according to the legend of his plate 7. The articulated specimen RBINS a5930 (Demanet, 1934, pl. 7, fig. 12; Figure 12.16-20) is selected here as the lectotype whereas the other RBINS specimens illustrated by Demanet (1934, pl. 7, figs. 6-11), namely a5924 (Figures 12.1-5, 13.11-12), a5925 (Figure 13.14-17), a5926 (Figure 12.21-25), a5927 (Figure 13.1-5), a5928 (Figures 12.6-10, 13.13) and a5929 (Figure 12.11-15), are considered as paralectotypes and fully illustrated herein.
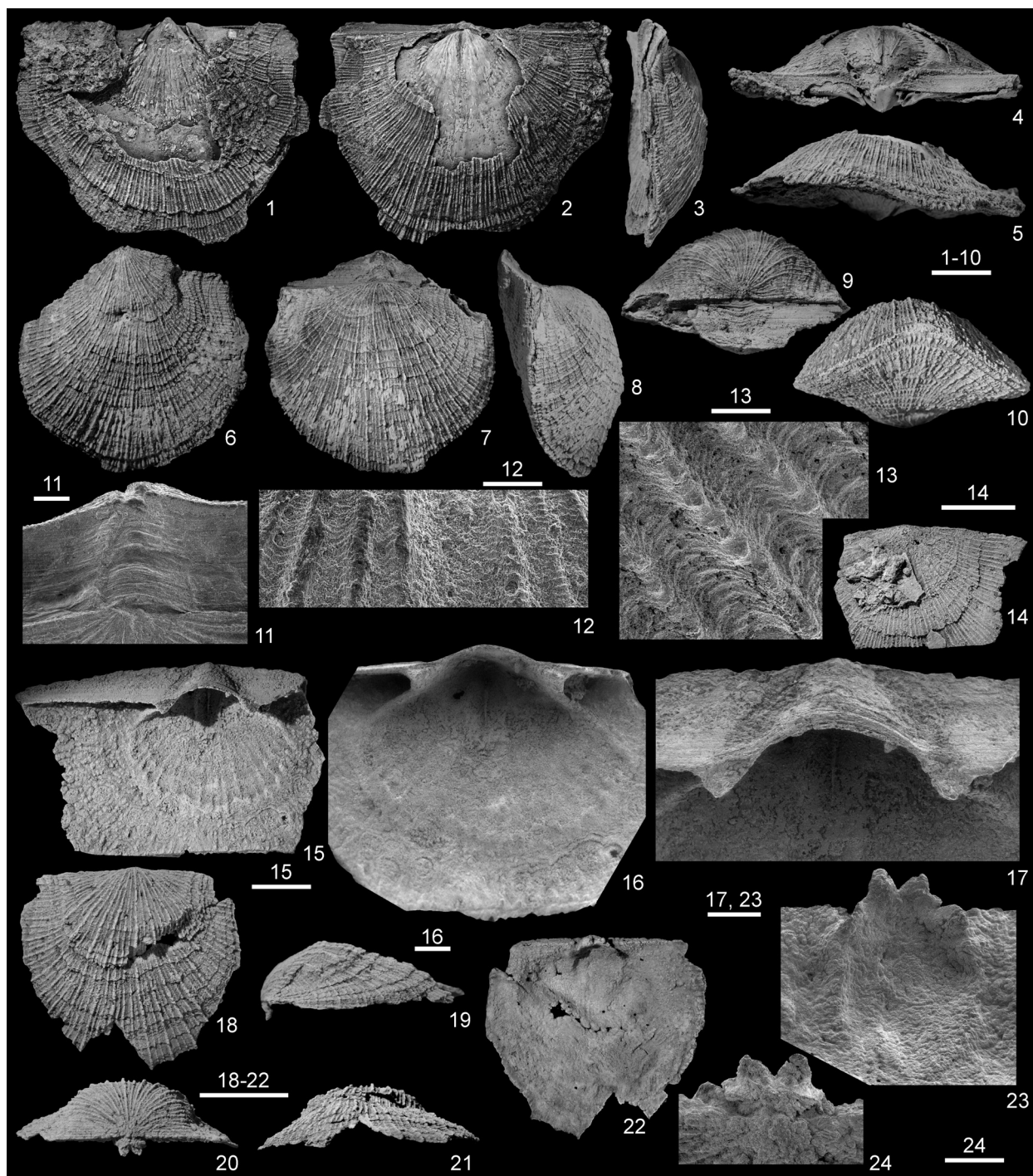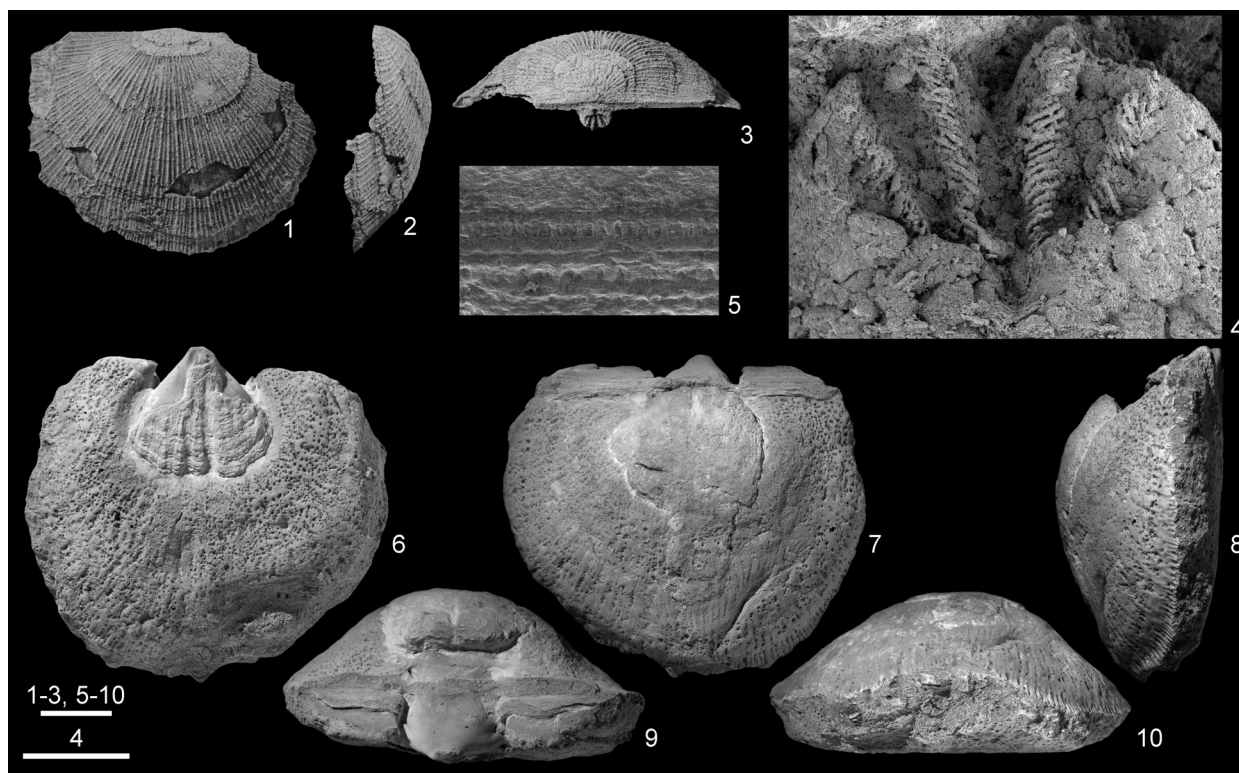
FIGURE 13. *Schellwienella radialiformis* Demanet, 1934 from the Tournai area, Tournai Formation (Tournaisian). **1-5,** RBINS a5927, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior and anterior views. **6-10,** RBINS a13105, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior, and anterior views. **11-12,** RBINS a5924, detail (SEM) of the pseudodeltidium and of the koskinoid perforations penetrating in the umbonal part of the ventral valve. **13,** RBINS a5928, detail of the microornament on dorsal valve (SEM). **14-17,** RBINS a5925, incomplete ventral valve in external and internal views and detail (SEM) of the posterior internal and external morphology. **18-24,** RBINS a13106, almost complete dorsal valve in dorsal, lateral, posterior, and internal views and detail (SEM) of the posterior morphology (cardinal process). Scale bars equal 10 mm (1-10, 14, 18-22), 1 mm (11), 0.25 mm (12), 0.5 mm (13), 2 mm (17, 23), 2.5 mm (24), 5 mm (15).

FIGURE 14. *Schellwienella radialiformis* Demanet, 1934 from the Tournai area, Tournai Formation (Tournaisian). **1-4,** RBINS a13107, almost complete dorsal valve in dorsal, lateral and posterior views and detail of the chilidium and cardinal process lobes. **5-10,** RBINS a5921, articulated internal mould with shelly remains in ventral, dorsal, lateral, posterior and anterior views and close-up of the ventral interarea (**5**). Scale bars equal 10 mm (1-2, 4-6), 1 mm (4, 5).

Additional material. Two ventral and two dorsal valves, and ten articulated specimens.

Description. Shell large-sized (up to ca. 51 mm in width), wider than long, quadrate to subquadrate in outline, slightly mucronate, strongly dorsibiconvex to resupinate, widest at hinge (juveniles) or anteriorly to it (adults); anterior margin rounded; anterior commissure rectimarginate to slightly uniplicate.

Ventral valve posteriorly convex then becoming concave anteriorly (resupinate shell) or rarely slightly convex (dorsibiconvex shell); umbo small; interarea triangular, high, flat to slightly concave, cataline to anacline; pseudodeltidium convex and perideltidium flat (Figure 13.11, 13.17); median depression rarely developed and occurring in anterior part of valve; koskinoid perforations developed in umbonal area (Figure 13.12).

Dorsal valve convex with maximum height located at midvalve or posteriorly and then decreasing rapidly towards anterior commissure; posterolateral areas flattened in posterior view; interarea linear, flat, anacline; chilidium convex.

Ornamentation parvicostellate; in some specimens, costellae can thicken so much that they become as large as the costae at the anterior margin; at front, 7–11 costae and costellae per 5 mm; growth lamellae numerous irregularly spaced, more crowded near margins in adults; filae fine, forming minute ridges across the crests of the costae and costellae (ca. 14 per 1 mm) (Figure 13.12-13).

Ventral interior (Figures 12.11, 13.1, 13.15-17) with large and deep delthyrial cavity; lateral apical cavities not filled in; dental plates strongly divergent anteriorly (78–93 degrees [n=4]), enclosing the posterior half of the muscle field; teeth large; muscle field slightly impressed, flabellate, slightly wider than long, extending up to 38 percent of the valve length; adductor muscles bounded laterally by two very low slightly curved ridges (but not fusing) and divided by a slender and low myophragm not extending beyond the distal extremities of the lateral ridges; diductor field large, flabellate, entirely enclosing the adductor field and anteriorly limited by a low ridge.

Dorsal interior (Figures 13.2, 13.20, 13.22-24, 14.3-4) with socket ridges divergent at 90 degrees (n=1!) from another and only slightly curved, fused

to cardinal process lobes; sockets deep, round-bottomed and laterally bounded by valve floor; cardinal process lobes high, posteroventrally oriented, grooved posteriorly; muscle field longer than wide, extending up to 35 percent of the unrolled length of the valve; adductor scars oval, posteriorly defined by plates extending from socket ridges, and clearly separated by a median ridge.

Remarks. Demanet (1934) considered the specimens from Tournai as a mutation of *Schellwienella aspis* Smyth (1930) from the Tournaisian Hook Head Formation of southern Ireland (see Bassett and Bryant, 2006; Mottequin, 2010). According to the article 45.6.4 of the International Code of Zoological Nomenclature (1999), the epithet *radialiformis* has to be considered as of subspecific rank in Demanet's (1934) publication. The species was promoted to a specific level by Reed (1954) and included in *Schellwienella (Carlospina)* Reed, 1954, a subgenus considered as a synonym of *Schellwienella* by Williams (1965) and Williams and Brunton (2000). *Schellwienella radialiformis* Demanet, 1934 differs from *S. radialis* (Phillips, 1836), as revised by Brunton (1968), by its less strongly parvicostellate ornamentation (the primary costae are generally less pronounced), and its ventral muscle field has a markedly different outline (compare with Davidson 1861, pl. 25, fig. 17). *Schellwienella radialiformis* differs from *S. aspis* Smyth, 1930 by its parvicostellate ornamentation and its undulose to uniplicate anterior commissure. Demanet's (1934) species is distinguished from *S. cheuma* Bassett and Bryant, 2006 notably in its parviclostellate ornamentation, its more convex pseudodeltidium, and its subrounded ventral muscle field.

Demanet (1934, text-fig. 15, pl. 7, fig. 3) illustrated the specimen RBINS a5921 that he considered as a 'forme spéciale dérivant de *Schellwienella*' as it displays some structures observed on the ventral interarea which he interpreted as hinge denticles (Figure 14.5). These structures, resulting from the intersection of the vertical and horizontal ornamentation of the ventral interarea, simply result from repetitive interruptions of the shell growth.

Occurrence. *Schellwienella radialiformis* is known from the Tournai Formation in the eponymous area.

Schellwienella ornata Demanet, 1934
Figures 4, 15

v*   1934   *Schellwienella ornata* nov. sp. Demanet, p. 83, text-fig. 16, pl. 7, figs. 4-5.

Type material. The complete internal mould (RBINS a5922) illustrated by Demanet (1934, pl. 7, fig. 4) is selected herein as the lectotype (Figure 15.1-8) whereas the specimen (RBINS a5923) figured by Demanet (1934, pl. 7, fig. 5, text-fig. 16) and of which the ventral umbo has been sectioned by him, is selected as the paralectotype (Figure 15.9-14). Both specimens were considered as paratypes by Demanet (1934). Until now, although Demanet (1934, p. 84) reported other specimens assigned to his new species, only the types have been recovered.

Description. Shell medium-sized (up to 41.8 mm in width), markedly ventribiconvex, subquadrate in outline, with maximum width near midlength; hinge line clearly shorter than maximum width; cardinal margins rounded; anterior margin straight or depressed; anterior margin rectimarginate or vaguely undulose.

Ventral valve moderately inflated, with flanks sloping moderately towards lateral commissure; umbo not prominent (at least in internal mould) beak straight; interarea irregularly triangular (deformation due to cementation on an organic or inorganic substrate), high, flat, apsacline; perideltidium flat; pseudodeltidium narrow, strongly convex; cementation cicatrix only preserved in lectotype.

Dorsal valve slightly convex, with maximum height near mid-valve then slightly decreasing towards anterior margin; interarea linear, flat, anacline; shallow median depression originating near posterior margin developed in one specimen.

Ornamentation parvicostellate (Figure 15.14); costellae increasing by intercalation, 6–7 costae per 5 mm near front separated from each other 5–6 costellae; growth varices developed; filae absent.

Ventral interior (Figure 15.1-2, 5, 7) with thin dental plates diverging at an angle of 35–37 degrees; teeth small; muscle field not excavated, obscure.

Dorsal interior (Figure 15.3, 7-8) with posteriorly grooved cardinal process lobes; socket ridges recurved, widely divergent; muscle field slightly excavated, obscure but well-defined posteriorly by lateral ridges extending from the socket ridges.

Remarks. Despite the availability of the type material illustrated by Demanet (1934), *Schellwienella ornata* remains incompletely known as its intraspecific variability cannot be investigated. Its main features are the parvicostellate ornamentation devoid of filae and the slightly divergent dental plates, which are not without evocating the genus *Pulsia* Ivanov, 1925, but the latter is characterized by parallel dental plates whereas *Schellwienella* encom-
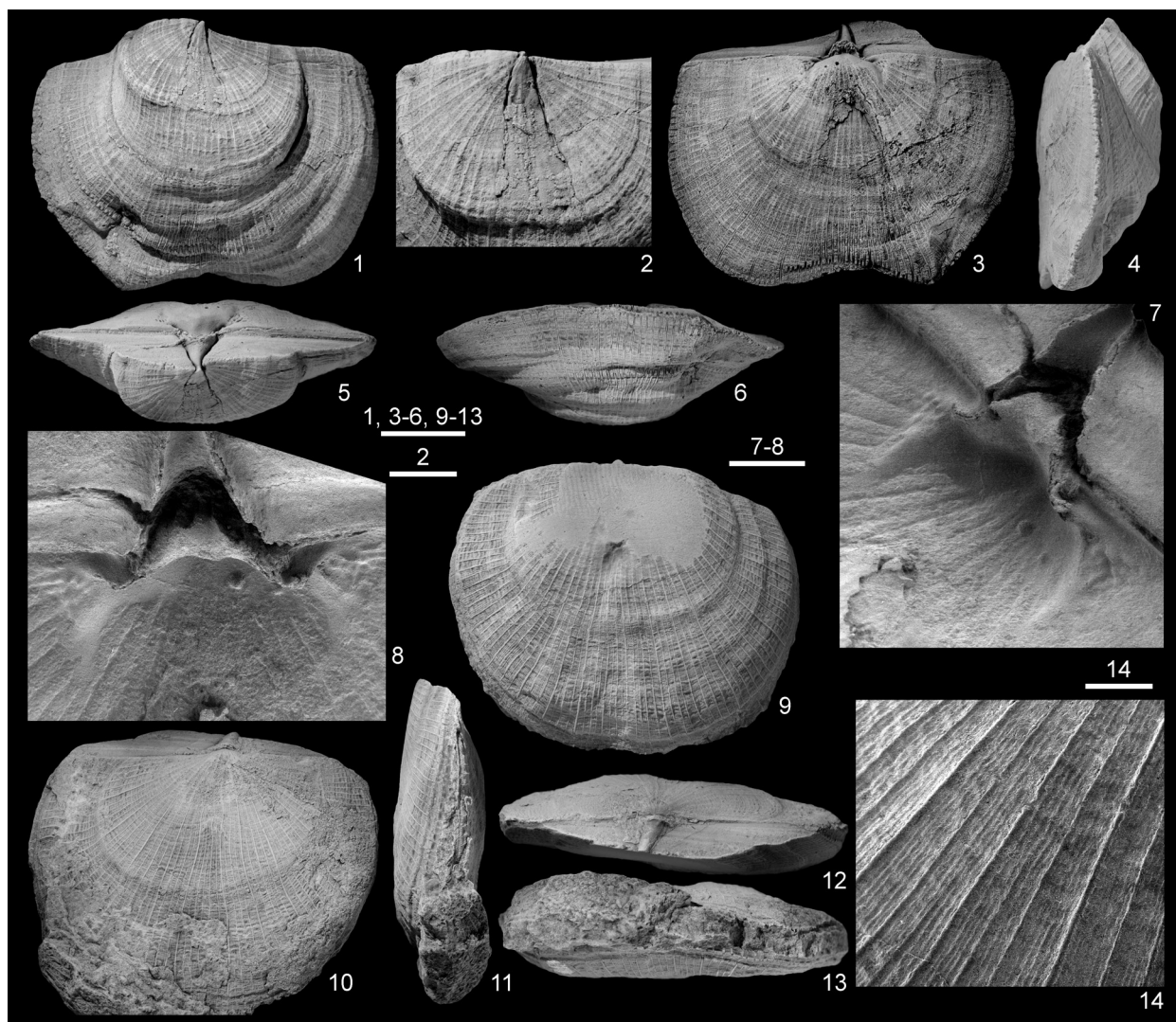
FIGURE 15. *Schellwienella ornata* Demanet, 1934 from Visé, Visé Formation (Visean, Warnantian). **1-8,** RBINS a5922 (lectotype), articulated internal mould in ventral, enlarged ventral (showing the extent of the traces left by the dissolved dental plates), dorsal, lateral, posterior, and anterior views, and internal views of a latex cast (SEM) showing the internal morphology of the posterior part of the specimen (**7-8**). **9-14,** RBINS a5923 (paralectotype), articulated specimen (partly sectioned, probably by Demanet) in ventral, dorsal, lateral, posterior, and anterior views, and close-up (SEM) of the parvicostellate ornamentation in the central part of the dorsal valve. Scale bars equal 10 mm (1, 3-6, 9-13), 5 mm (2), 2.5 mm (7-8), 1.25 mm (14).

passes species with dental plates variably divergent from hinge line (McIntosh, 1974). *Schellwienella ornata* differs from *S. crenistria* (Phillips, 1836) by the absence of filae, its quadro-rounded outline, and its narrow hinge line (the maximum width is near midlength vs. close to the hinge). According to Demanet (1934), his species is very similar to *Orthis cylindrica* M'Coy, 1844 from the Visean (Brigantian) of Castle Espie (Comber, Co. Down, Ireland). M'Coy's (1844, pl. 22, fig. 1) original specimen was illustrated by Davidson (1861, pl. 27, fig. 9), and this species was considered as

probable *Schellwienella* representative by Thomas (1910, p. 127). Furthermore, *Orthis cylindrica* was considered as a variety of *Schellwienella crenistria* (Phillips, 1836) by Davidson (1861, p. 128; 1880, p. 290). Note that the specimens from the Serpukhovian of Scotland (base of the Millstone Grit Series) identified as *Streptorhynchus crenistria* var. *cylindrica* M'Coy and illustrated by Davidson (1880: pl. 37, figs. 6–7) have been assigned to *Schellwienella rotundata* Thomas, 1910 and *Orthothetina* cf. *thomasi* (Sokolskaya in Sarytcheva and Sokolskaya, 1952) by McIntosh (1974: 204, 209),
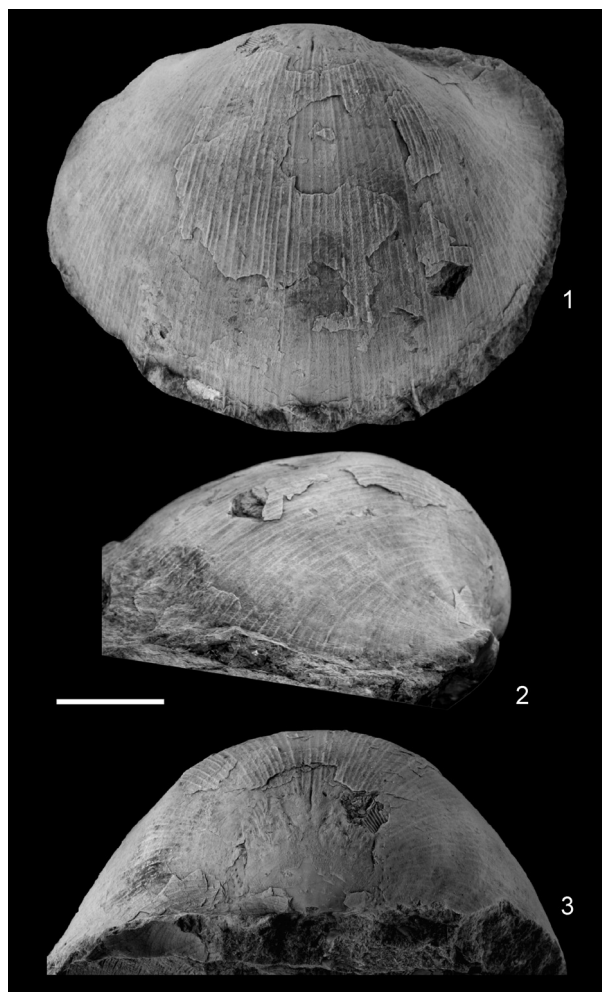
FIGURE 16. *Schellwienella cylindrica* (M'Coy, 1844), from the Visean (Brigantian) of Castle Espie (Comber, Co. Down, Ireland). **1-3,** NMING:F6267 (lectotype), almost complete dorsal valve in dorsal, lateral, and posterior views. Scale bar equals 10 mm.

respectively. The only specimen illustrated by M'Coy (1844) cannot be found in the Griffith collections curated at the National Museum of Ireland, but there is a dorsal valve (NMING:F6267) (Figure 16) from the same locality which matches M'Coy's description; thus it is herein selected as lectotype for nomenclatorial purposes. The type specimens of Demanet's (1934) species have a markedly less convex dorsal valve and a thinner radial ornamentation. Thomas (1971) noted the similarities between the ornamentation of *S. ornata* and those of *S. reprinki* Sokolskaya (in Sarytcheva and Sokolskaya, 1952) (see also Sokolskaya, 1954) and *S. weaberensis* Thomas, 1971.

Occurrence. The type specimens were recovered from the Visé Formation at Visé according to

Demanet (1934), who also reported the species in the 'calcschistes de Warnant' in the Condroz sedimentation area, corresponding now to the Upper Member of the Anhée Formation (see Poty et al., 2002) (late Warnantian; Figure 4). However, Demanet (1958) did not report this species anymore within the Anhée Formation.

Family SCHUCHERTELLIDAE Williams, 1953
Subfamily SCHUCHERTELLINAE Williams, 1953
Genus SERRATOCRISTA Brunton, 1968

Type species. *Serratocrista fistulosa* Brunton, 1968; from the Visean (Asbian) of County Fermanagh (Ireland).

Serratocrista scaldisensis sp. nov.
Figures 4, 17-19, Table 2

zoobank.org/29F8E248-E952-42A5-9307-2A3931FC86CE

Etymology. From *Scaldis* (Latin: Escaut), in reference to the Escaut river on the banks of which the town of Tournai is settled.

Holotype. RBINS a13110 (Figures 17.12-16, 18.1, 18.6).

Paratypes. RBINS: a13108 (Figure 17.1-6), a13109 (Figure 17.7-11), a13111 (Figures 17.17-21, 18.2-3, 18.19-21), a13112 (Figure 17.22-25), a13113 (Figure 18.4-5), a13114 (Figure 18.7-13), a13115 (Figure 18.14-18), and a13116 (Figure 19).

**Additional material.** RBINS: four articulated specimens.

Type locality. Tournai area (southwestern Belgium) (Figures 2-3).

Type stratum. Tournai Formation, Tournaisian (Figure 4).

Diagnosis. A small-sized (ca. 15 mm in width) *Serratocrista* species of, wider than long, planoconvex in profile and subquadrate-rounded in outline, with maximum width near midlength. Ornamentation multicostellate, 12 to15 costellae per 5 mm at anterior margin with costellae increasing essentially by intercalations. Dorsal muscle field impressed, obscure, poorly delimited anteriorly, extending up to 40 percent of the valve length; myophragm low.

Description. Shell small-sized (up to 15.6 mm in width), wider than long, subquadrate in outline, plano-convex; maximum width near midlength; hinge line shorter than maximal width; cardinal angles and anterior margin rounded; anterior commissure rectimarginate to slightly unisulcate. Shell extropunctate with extropunctae arranged radially along the axis of the costellae (Figure 18.2-3).

Ventral valve convex, with maximum height near posterior margin, then decreasing progressively towards anterior commissure; umbo small but prominent, umbonal region sometimes
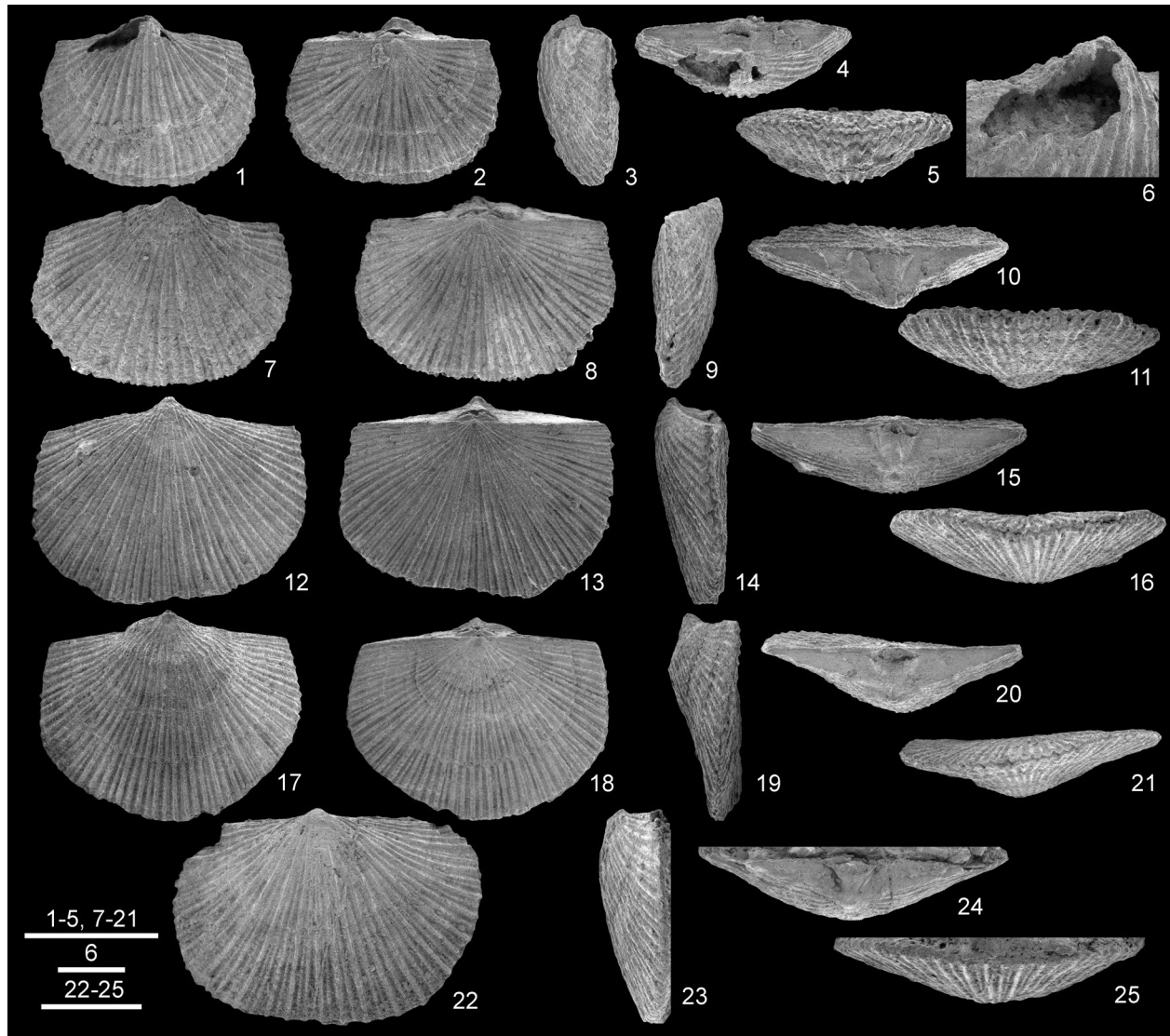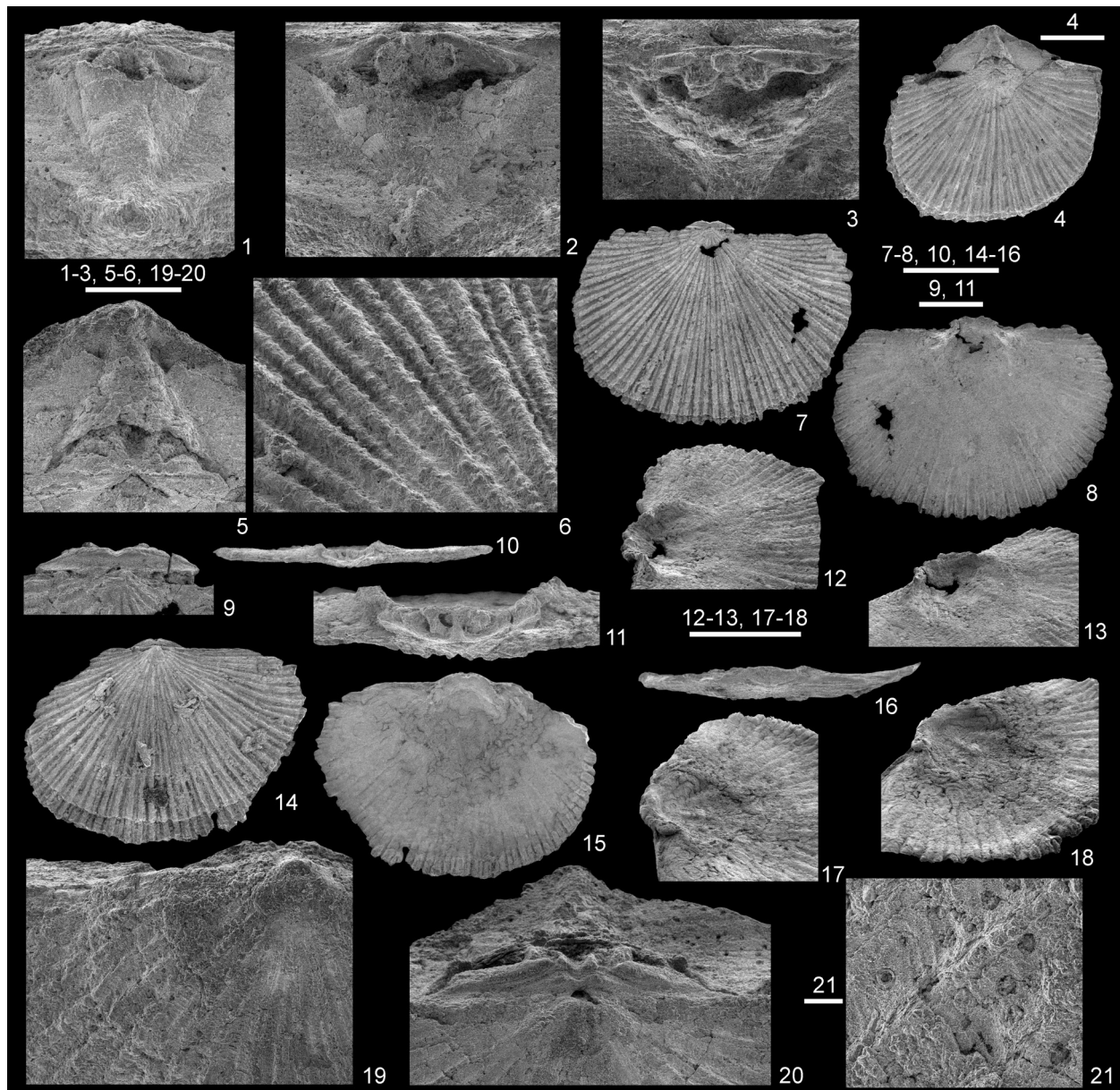
FIGURE 17. *Serratocrista scaldisensis* sp. nov. from the Tournai area, Tournai Formation (Tournaisian) (all SEM). **1-6,** RBINS a13108, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior, and anterior views, and close-up of the umbo showing the absence of dental plates. **7-11,** RBINS a13109, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **12-16,** RBINS 13110 (holotype), articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **17-21,** RBINS a13111, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **22-25,** RBINS a13112, almost complete ventral valve in ventral, lateral, posterior, and anterior views. Scale bars equal 1 mm (6), 5 mm (1-5, 7-25).

deformed (flattened) by cementation with koskinoid perforations (Figure 18.19-21), which are also present on the interarea); beak not curved; interarea triangular, low, cata-apsacline to apsacline, flat to slightly concave; pseudodeltidium strongly convex (Figure 18.1-3).

Dorsal valve flat with, in some specimens, development of a shallow median depression; chilidium small, convex, medially grooved; interarea linear, anacline, flat.

Ornamentation multicostellate (12–15 costellae per 5 mm at anterior margin) with costellae increasing essentially by intercalations, more rarely by bifurcations; ca. 10 concentric microlines per 1 mm, thickened at irregular interval (growth varices), and forming protuberances on rib crests (Figure 18.6).

Ventral interior poorly known (Figures 17.6, 19.1-4); teeth small, rounded, unsupported; muscle field not observed.

FIGURE 18. *Serratocrista scaldisensis* sp. nov. from the Tournai area, Tournai Formation (Tournaisian). **1, 6,** RBINS a13110 (holotype), close-up of the strongly convex pseudodeltidium, and detail of the microoornament (central part of the dorsal valve). **2-3, 19-21,** RBINS a13111, detail of the strongly convex pseudodeltidium and of the cardinal process, and close-up of the koskinoid perforations developed in the ventral umbonal area and on the interarea. **4-5,** RBINS a13113, incomplete articulated specimen in dorsal view and close-up of the posteriorly grooved lobes of the cardinal process. **7-13,** RBINS a13114, dorsal valve in external, internal and posterior (**10**) views, detail of the chilidium (**9**), the cardinal process (**11**), and oblique views of the internal posterior region (**12-13**). **14-18,** RBINS a13115, almost complete dorsal valve in external, internal and posterior views and oblique views of the internal posterior region. Scale bars equal 1 mm (1-3, 5-6, 9, 11, and 19-20), 2.5 mm (4), 5 mm (7-8, 10, 14-16, 12-13, and 17-18), 0.1 mm (21).

Dorsal interior (Figure 18.1-3, 8, 12-13, 15-18) with cardinal process lobes small, posteriorly grooved; muscle field impressed, obscure, poorly delimited anteriorly, extending up to 40 percent of the valve length; myophragm low (observed in one specimen); socket ridges diverging from the hinge line at an angle of 26–48 degrees (n=2).
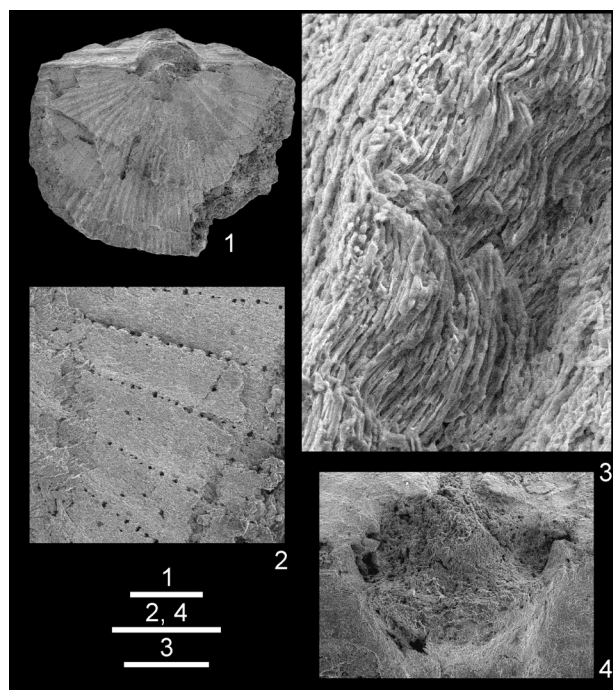
FIGURE 19. *Serratocrista scaldisensis* sp. nov. from the Tournai area, Tournai Formation (Tournaisian). **1-4,** RBINS a13116, articulated specimen, incomplete, in dorsal view (1) with detail of the extropunctae arranged radially along the axis of the costellae (**2, 3**), and of the basal part of the pseudodeltidium and of the teeth (**4**). Scale bars equal 2 mm (1), 0.5 mm (2), 0.025 mm (3), 1 mm (4).

Dimensions (Table 2)

Remarks. The ornamentation and the cardinalia of this limited material suggest an assignment to *Serratocrista*, although its type species is devoid of dorsal myophragm, which has been observed in ours. In their discussion of the original diagnosis given by Brunton (1968), Roberts (1971) and McIntosh (1974) reported the occasional occurrence of a dorsal myophragm in their material assigned to

TABLE 2. Measurements in mm of *Serratocrista scaldisensis* sp. nov. Abbreviations: see Table 1.

RBINS	W	L	T	Hi	Wi
a13108	8.1	6.5	2.9	1.2	7.2
a13109	9.8	7.1	2.4	2.2	8.8
a13110	10.4	7.7	2.7	1.8	9.6
a13111	13.1	9.8	3.3	2.2	12.1
a13112	15.6	10.8	/	2.0	/
a13117	9.4	8	3.2	2.3	7.6
a13118	7.7	6.1	2.5	1.0	5.7

Brunton's genus from Australia and Scotland, respectively. Besides the presence of a dorsal myophragm, the Belgian material is distinguished from *Serratocrista fistulosa* in its more flattened dorsal valve. Our specimens are markedly smaller than the Serpukhovian species *Serratocrista dalriensis* and *S. cylindricosta*, both described by McIntosh (1974). The Belgian species differs from *S. truyolsi* Martínez Chacón, 1979 from the Moscovian of Spain (see also Martínez Chacón, 2008) in its planoconvex shell and the not so deep dorsal median depression. The species from Tournai is relatively close to the Tournaisian (China) and Visean (Australia) *Serratocrista* sp. described by Sun and Baliński (2008) and Roberts (1971), respectively, but differs in its more divergent socket ridges.

Occurrence. *Serratocrista scaldisensis* is currently only known from the Tournai Formation in the Tournai area.

Order ATHYRIDIDA Boucot, Johnson and Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964
Superfamily ATHYRIDOIDEA Davidson, 1881
Family ATHYRIDIDAE Davidson, 1881
Subfamily ATHYRIDINAE Davidson, 1881
Genus LAMELLOSATHYRIS Jin and Fang, 1983

Type species. *Spirifer lamellosus* Léveillé, 1835, from the Tournaisian of the Tournai area, southern Belgium.

Lamellosathyris lamellosa (Léveillé, 1835)
Figures 4, 20-24, Table 3

|		
*	1835	*Spirifer lamellosus* Léveillé, p. 39, pl. 2, figs. 21-23.
	1836	*Spirifer squamosa* Phillips, p. 220, pl. 10, fig. 21.
	1843	*Terebratula lamellosa* Léveillé; de Koninck, p. 299, pl. 20, fig. 5.
	1868	*Athyris* (*Spirifer*) *lamellosa* (*sic*) Lév.; Dewalque, p. 333.
	1881	*Athyris* (*Spirifer*) *lamellosa* (*sic*) Lév.; Mourlon, p. 46.
v	1887	*Athyris lamellosa* Léveillé; de Koninck, p. 79, pl. 21, figs. 1-5.
v	1887	*Athyris vittata* de Koninck, p. 81, pl. 21, fig. 6-8.
v	1887	*Athyris squamosa* Phillips; de Koninck, p. 80, pl. 21, figs. 9-10.
	1980	*Actinoconchus lamellosus* (Léveillé); Brunton, p. 225, figs. 16-17.
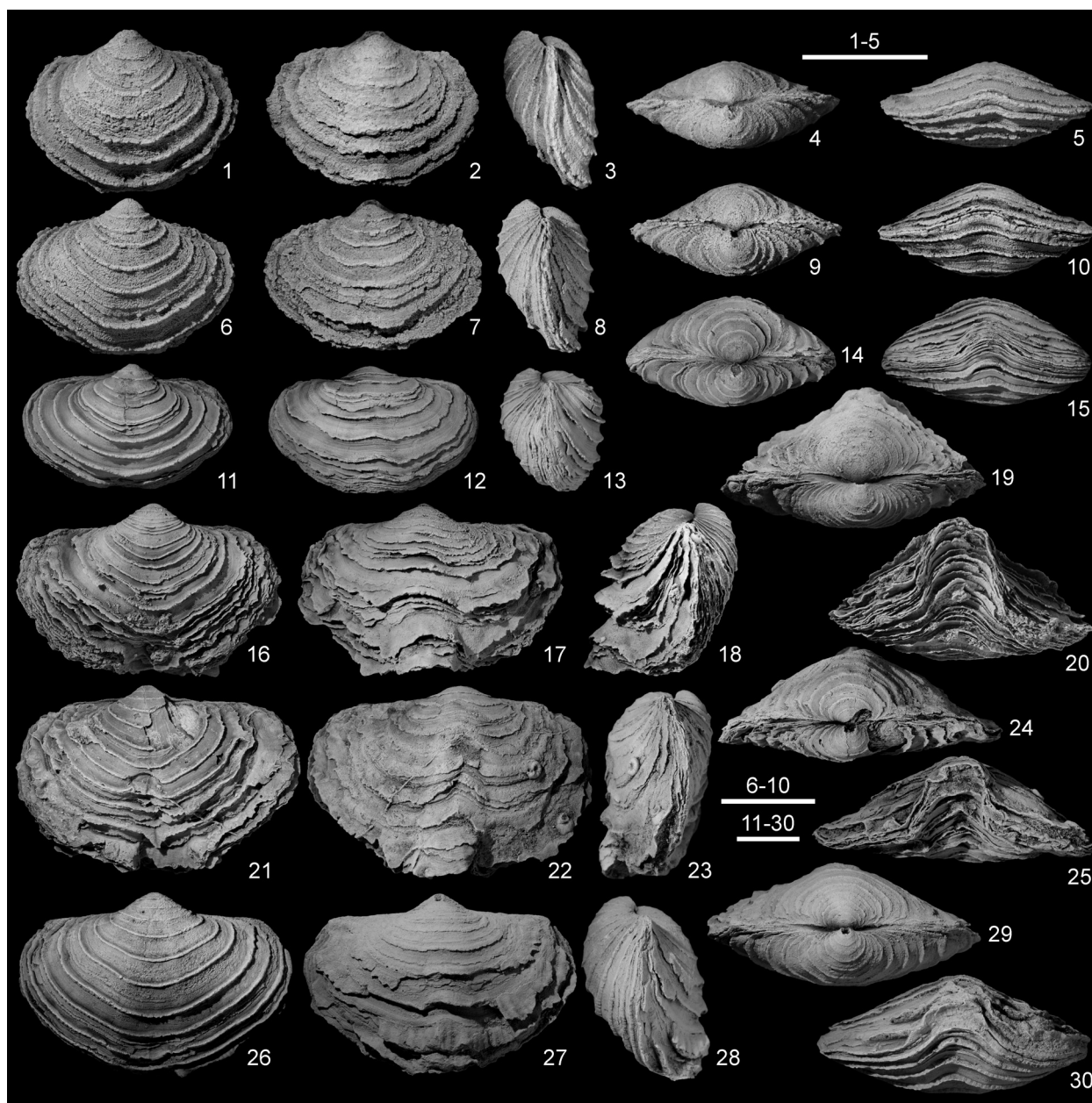
FIGURE 20. *Lamellosathyris lamellosa* (Léveillé, 1835) from the Tournai area, Tournai Formation (Tournaisian). **1-5,** RBINS a13119, juvenile articulated specimen in ventral, dorsal, lateral, posterior and anterior views. **6-10,** RBINS a13120, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **11-15,** RBINS a5468, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **16-20**, RBINS a13121, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **21-25,** RBINS a13122, articulated specimen (with two microconchids attached to the right dorsal flank) in ventral, dorsal, lateral, posterior and anterior views. **26-30,** RBINS a13123, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. Scale bars equal 10 mm.

Neotype. Specimen BMNH B20138 selected by Brunton (1980: p. 225, fig. 16).

Material. RBINS: besides the three specimens illustrated as *Athyris lamellosa* by de Koninck (1887, pl. 21, figs. 1-5), namely RBINS a5468 (pl. 21, figs. 1-3) (Figure 20.11-15), RBINS a5469 (pl. 21, fig 4), and RBINS a5470 (pl. 21, fig. 5) (Figure 21.19-23), complemented by those identified as *Athyris vittata* (de Koninck,1887, pl. 21, figs. 6-8; RBINS a5472) (Figure 23.8-12) and *Athyris squamosa* (de Koninck, 1887, pl. 21, figs. 9-10; RBINS a5471) (Figure 23.1-5), the RBINS material investi-
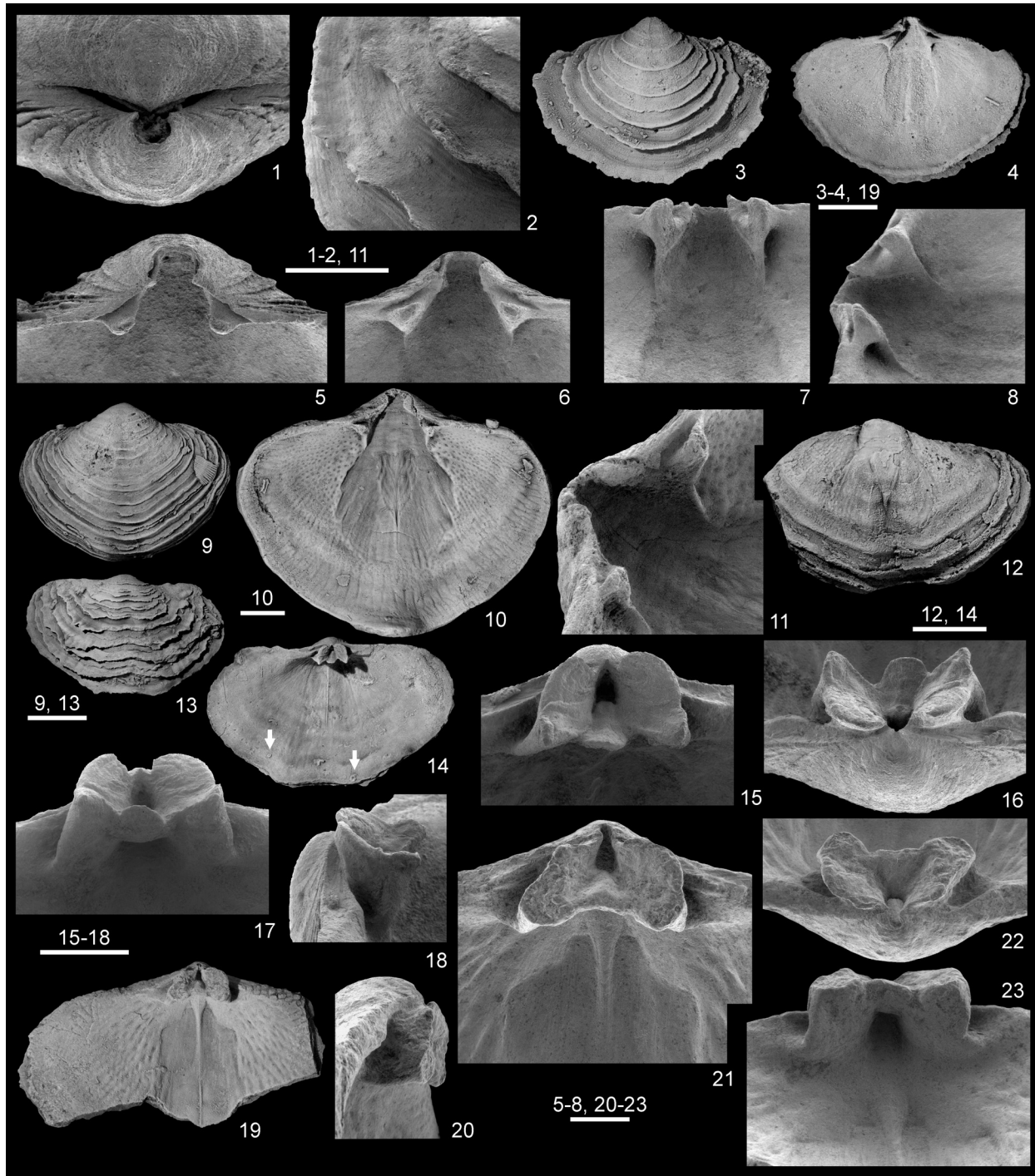
FIGURE 21. *Lamellosathyris lamellosa* (Léveillé, 1835) from the Tournai area, Tournai Formation (Tournaisian). **1-2,** RBINS a13124, partial posterior view of an articulated specimen showing the foramen and detail of the lamellose ornamentation in the anterior part of the dorsal valve. **3-8,** RBINS a13125, complete ventral valve (juvenile) in external and internal views and detail of the teeth and the dental plates. **9-11,** RBINS a13126, complete ventral valve in external and internal views and detail of teeth supported by almost vertical dental plates. **12,** RBINS a13127, incomplete internal mould of ventral valve. **13-18,** ULg.PA.2016.12.25/8, complete dorsal valve (with two microconchids attached to its internal surface (arrows), close to the anterior margin) in external and internal view and detail of the cardinalia. **19-23,** RBINS a5470, incomplete dorsal valve in internal view and detail of the cardinalia. Scale bars equal 5 mm (1-2, 3-4, 10, 11), 2 mm (5-8, 20-23), 2.5 mm (15-18), 10 mm (9, 12-14).
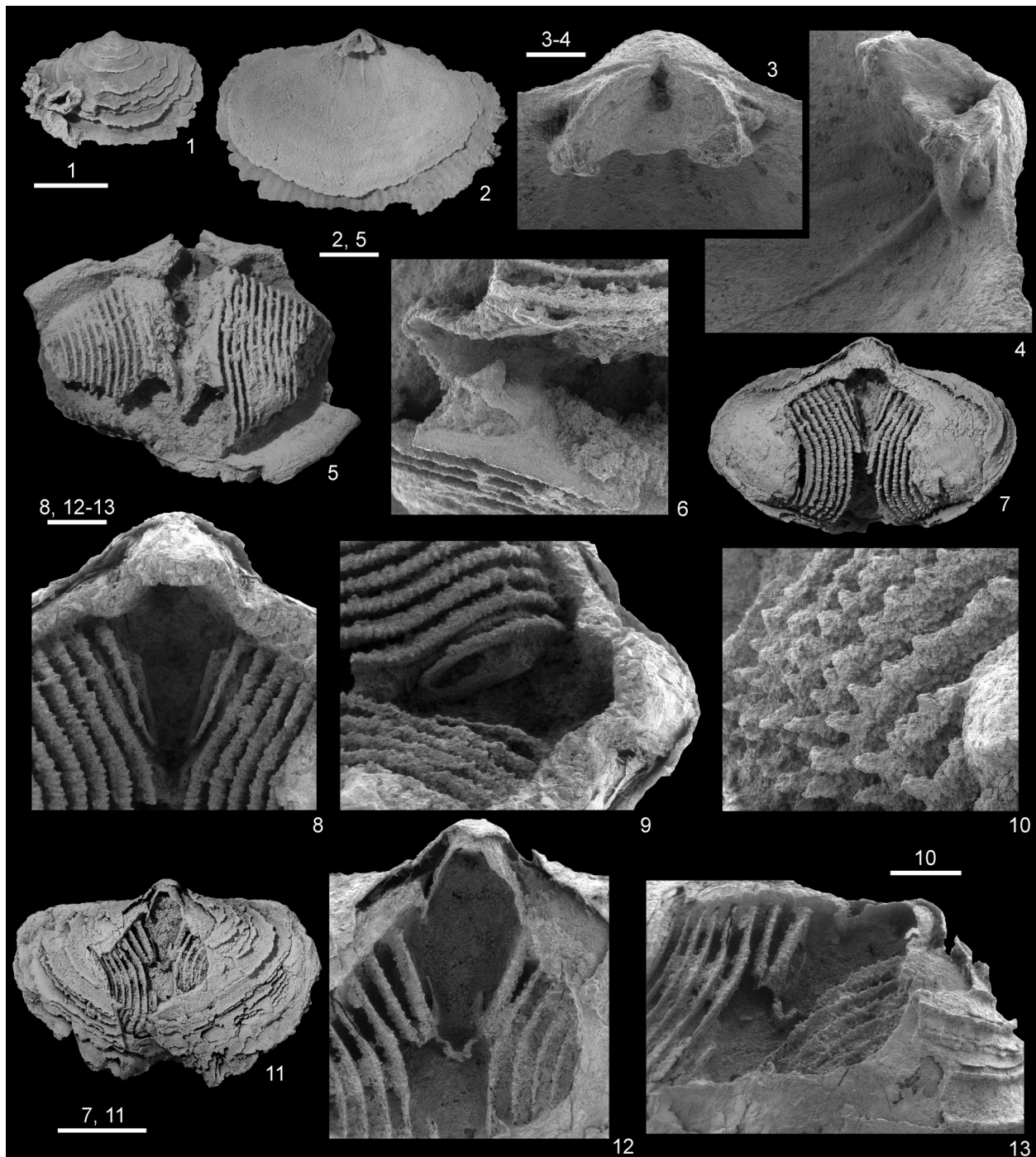
FIGURE 22. *Lamellosathyris lamellosa* (Léveillé, 1835) from the Tournai area, Tournai Formation (Tournaisian). **1-4,** RBINS a13128, almost complete dorsal valve in external and internal views, with close-up of the cardinal plate in ventral and oblique lateral views. **5-6,** RBINS a13129, incomplete ventral valve with partly preserved spiralia and detail of the jugal saddle and the primary lamella. **7-10,** RBINS a13130, articulated specimen with top of the ventral valve removed and details of the crura, spiralia and fimbria. **11-13,** ULg.PA.2016.12.25/9, articulated specimen with ventral valve partly removed in general view and details of the top of the jugal stem and the same in oblique view. Scale bars equal 10 mm (1, 7, 11), 5 mm (2, 5), 1 mm (3-4, 10), 2 mm (6, 9), 2.5 mm (8, 12-13).
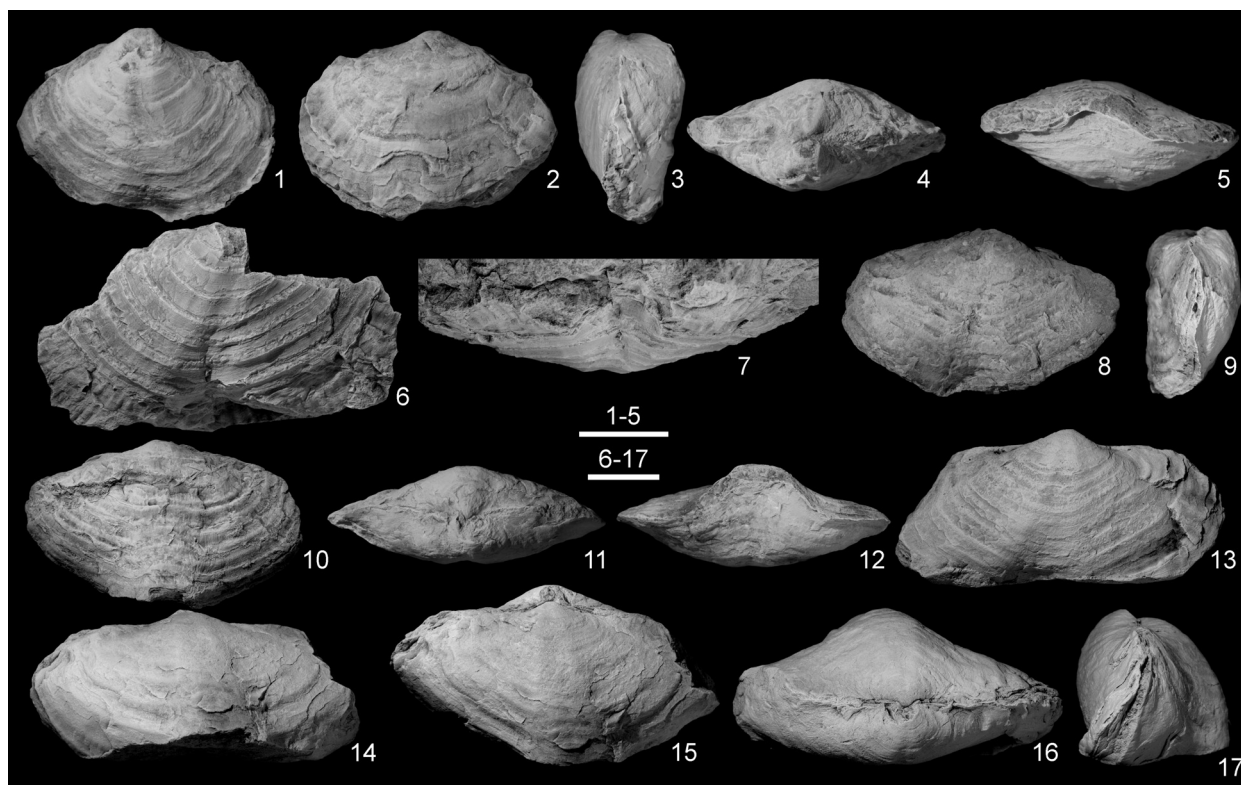
FIGURE 23. **1-7,** *Lamellosathyris lamellosa* (Lévéillé, 1835) from Visé, Visé Formation (Visean, Warnantian). **1-5,** RBINS a5471, distorted specimen in ventral, dorsal, lateral, posterior and anterior views. **6-7,** RBINS a13131, incomplete ventral valve in ventral view and anterior views. **8-17,** *Athyris vittata* de Koninck, 1887 (here placed in synonymy with *Lamellosathyris lamellosa* [Léveillé, 1835]) from Furfooz, Waulsort Formation (Tournaisian, Ivorian). **8-12,** RBINS a5472 (lectotype) distorted specimen in ventral, lateral, dorsal, posterior, and anterior views. **13-17,** RBINS a13132 (paralectotype), distorted and incomplete specimen in ventral, dorsal, posterodorsal, posterior, and lateral views. Scale bars equal 10 mm.

gated includes 126 articulated specimens, six ventral and one dorsal valves; ULg.PA: 31 articulated specimens, one ventral and one dorsal valves.

Description. Shell large-sized (up to 51 mm in width), wider than long, transversely oval in outline, generally dorsibiconvex to rarely convexo-plane; hinge line shorter than maximum width; cardinal extremities rounded; anterior margin variably emarginate; anterior commissure uniplicate (rectimarginate to vaguely undulose in juveniles).

Ventral valve with prominent umbo; beak slightly overhanging hinge line, incurved; foramen small, permesothyrid (Figure 21.1); palintropes well-developed, concave; sulcus originating inconspicuously in the posterior part of the valve, ill-defined, shallow to deep (only in largest specimens), round-bottomed at front; tongue high, round to subrectangular in outline, perpendicular to commissural plane or bent dorsally.

Dorsal valve inflated with maximum convexity at anterior margin or near midlength and then decreasing near anterior margin; fold low to high, originating near midlength, and only well perceptible near the anterior margin, exceptionally with a very shallow, median groove (Figure 21.13).

Shell covered by broad rugae, each about 3.5–4.5 mm wide at midlength (about 5–9 on 15 mm from the tip of the ventral umbo), but more crowded near the lateral and anterior commissures, and bearing thin to sometimes thickened growth lines (exact number unknown); radially corrugated shell flanges extending from rugae on both valves.

Ventral interior (Figure 21.4-8, 10-12) with thin, short dental plates converging dorsally then becoming subparallel anteriorly; teeth cyrtomatodont, stout, ovate; umbonal cavity large; lateral apical cavities poorly developed; muscle field clearly excavated posteriorly, large, subrounded in outline, with posteromedian elongate heart-shaped adductor scar enclosed laterally and anterolaterally by flabellate diductor scars extending up to 60 % of
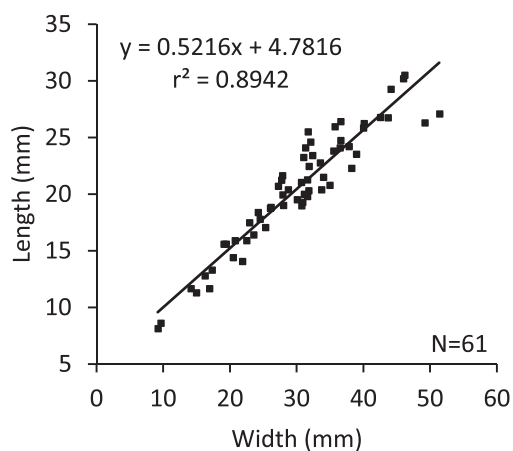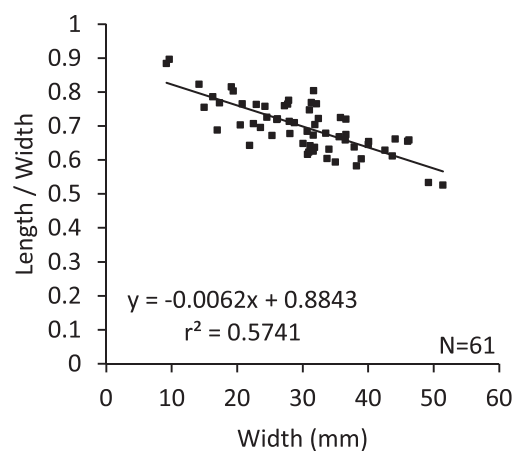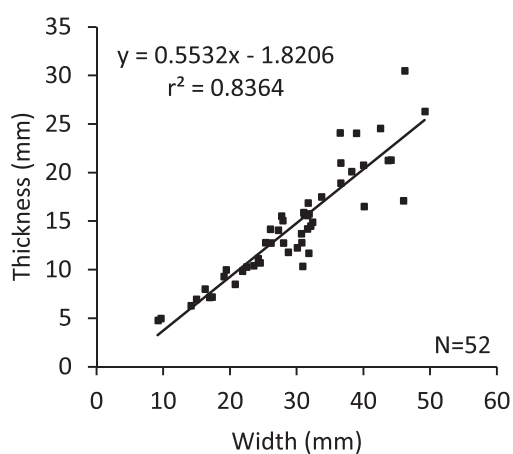
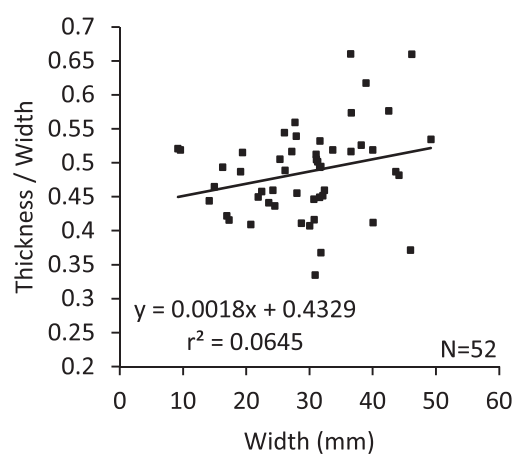**FIGURE 24.** Scatter diagrams of *Lamellosathyris lamellosa* (Léveillé, 1835). N: number of specimens measured, r^2: coefficient of linear regression. **1,** Relation between shell width and length. **2,** Relation between shell width and shell width/shell length ratio. **3,** Relation beween shell width and thickness. **4,** Relation between shell width and shell thickness/shell width ratio.

the unrolled length of the valve; posterolateral parts of the valve markedly pitted; mantle canals observed close to the anterior and lateral commissures.

Dorsal interior (Figures 21.14-23, 22.2-4) with cardinal plate extending anteriorly ca. 13% (n = 2) of the valve length, subtrapezoidal in outline, pierced apically by a foramen; inner hinge plate wide, flat to convex; crural bases well-developed; dental sockets delimited by inner socket ridges clearly more developed than outer socket ridges; posterior bilobate cardinal flanges developed; adductor muscle scars variably excavated posterolaterally according to the specimens, but more obscure anteriorly, and medially divided by a low myophragm extending to 57 % of the valve length in the largest available specimen; spiral cones with at least 16 whorls (this number is slightly underesti-

mated due to their poor preservation), with fimbriae; jugum composed anteriorly by a jugal saddle and posteroventrally by a thin jugal stem bifurcating into short accessory jugal lamellae (Figure 22.5-13).

Dimensions (Figure 24, Table 3). The increasing of the shell length is proportional to the increasing of the shell width, and these parameters are quite stable through growth. The increasing of the thickness of the shell is a more variable parameter. The length/width ratio is significantly decreasing during growth indicating that the width increases quite more than the length in this species. On the contrary, the relation thickness/width to width is not significant. The very slight increasing of this ratio is due to the variability of the thickness variation through growth.

TABLE 3. Measurements in mm of *Lamellosathyris lamellosa* (Léveillé, 1835). Abbreviations: see Table 1.

	W	L	T	L/W	T/W	T/L
N	60	60	50	60	50	50
Mean	30.1	20.5	14.5	0.70	0.49	0.70
Standard deviation	9.3122	5.1365	5.6788	0.0761	0.0667	0.1282
Standard error	±1.2021	±0.6631	±0.8031	±0.0098	±0.0094	±0.0181
MIN	9.2	8.1	4.8	0.53	0.33	0.53
MAX	51.4	30.5	30.5	0.90	0.66	1.02

Remarks. Differences between *Lamellosathyris lamellosa* and other *L.* species (see Chen et al., 2003) have been discussed in detail by Carter (1967), Brunton (1980, 1984), Chen et al. (2003), and Sour-Tovar et al. (2005). However, contrary to Brunton's opinion reported in Chen et al. (2003), *L. lamellosa* reaches a size similar to that of *L. qaidamensis* Chen et al., 2003.

Athyris vittata de Koninck, 1887 from the Tournaisian Waulsort Formation is here considered as a synonym of Léveillé's (1835) species. Only some specimens assigned to this species have been recovered from the de Koninck collection curated at the RBINS. The single specimen illustrated by de Koninck (1887, pl. 21, figs. 6-8) is here selected as the lectotype (RBINS a5472) (Figure 23.8-12). Among the four additional specimens identified as *A. vittata* by de Koninck (1887) but not illustrated by him, only two are identical to the lectotype and thus have to be considered as paralectotypes RBINS a13132 (Figure 23.13-17) and RBINS a13133 (a juvenile not illustrated herein). According to Demanet (1958), the macrofaunas from the Waulsortian mounds from southern Belgium were studied by de Koninck (e.g., 1885, 1887) at the request of the Belgian geologist Edouard Dupont, who wanted to show that the Waulsortian calcareous facies corresponded to an autonomous stage of the Dinantian as the Tournaisian and the Visean (see Lees [2006] and Groessens [2006]), and thus characterized by a distinct fauna. That is why almost all the brachiopods and bivalves recovered from these massive carbonate bodies were assigned to new species by de Koninck.

The material from Visé (Visé Formation) identified as *Athyris squamigera* (Phillips, 1836) by de Koninck (1887) is illustrated here (Figure 23.1-5) as well as another specimen (Figure 23.6-7) from the same locality. Phillips' species has been considered for a long time as a synonym of *L. lamellosa* (see Brunton, 1984).

Occurrence. Among the athyridide species recognized from the Tournaisian succession of the Tour-

nai area, *Lamellosathyris lamellosa* seems to have the most extensive distribution worldwide. It is notably known from the Mississippian succession of Western Europe (e.g., Brunton, 1980, 1984; Mottequin, 2010), North Africa (e.g., Massa et al., 1974; Havlíček and Röhlich, 1987; Mergl and Massa, 1992; Mottequin et al., 2017), Mexico (Sour-Tovar et al., 2005), the USA (Carter, 1999), and Iran (Gaetani, 1968; Bahrammanesh et al., 2011). In the Tournai area, Demanet (1958) reported *L. lamellosa* from the Orient Formation to the Vaulx Member of the Tournai Formation, i.e., from the latest Hastarian to the Ivorian. Demanet (1958) also reported its presence in various levels of the Tournaisian succession of southern Belgium, notably in the Yvoir and Waulsort formations, but the species is rare in the Visé Formation (Visean).

Superfamily NUCLEOSPIROIDEA Davidson, 1881
Family NUCLEOSPIRIDAE Davidson, 1881
Genus NUCLEOSPIRA Hall in Davidson, 1858

Type species. *Spirifer ventricosus* Hall, 1857; from the Lower Helderberg Group, Lochkovian, New York, USA.

Nucleospira hannoniae nom. nov.
Figures 4, 25-27, Table 4

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v	1887	*Athyris globulina* de Koninck, p. 78, pl. 19, figs. 42-46.
?	1893	*Athyris globulina*; Dewalque, p. 74.
	1989	*Cleiothyridina globulina* (Koninck, 1887); Grunt, p. 84.

Etymology. From *Hannonia* (Latin: Hainaut), in reference to the Hainaut Province where the town of Tournai is located.

Type specimens. Same as those of *Athyris globulina* de Koninck, 1887 that are selected herein. The specimen RBINS a5465 (de Koninck, 1887, pl. 19, figs. 42-45) is selected here as the lectotype (Figure 25.11-15) whereas the specimen RBINS a5466
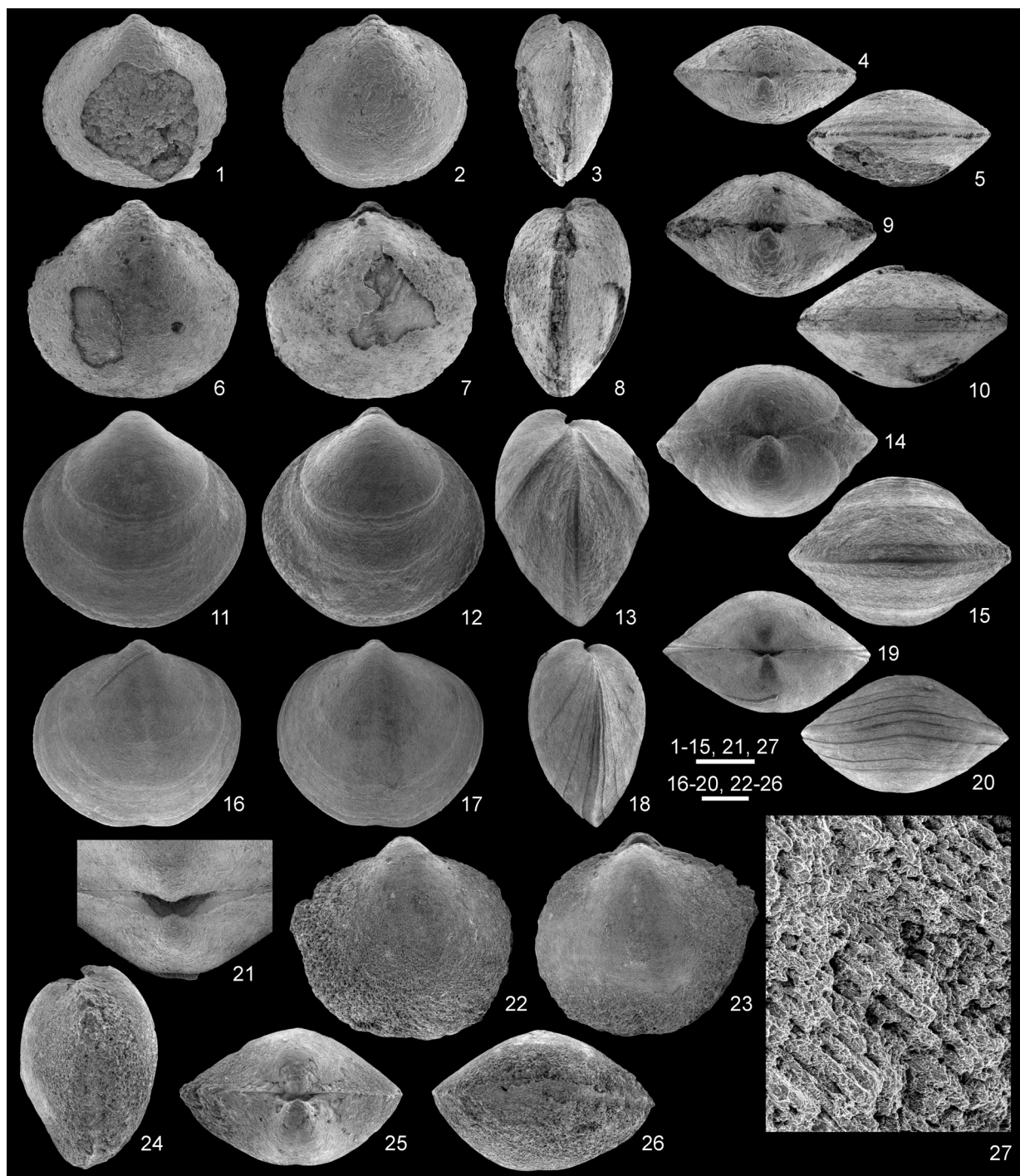
FIGURE 25. *Nucleospira hannoniae* nom. nov., from the Tournai area, Tournai Formation (Tournaisian). **1-5,** RBINS a13134, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior and anterior views. **6-10**, RBINS a5466 (paralectotype), articulated specimen, almost complete, in ventral, dorsal, lateral, posterior ,and anterior views. **11-15,** RBINS a5465 (lectotype), articulated specimen in ventral, dorsal, lateral, posterior, and anterior views. **16-21,** RBINS a13135, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views, and close-up of the interarea, Lemay quarry, Vaulx Member. **22-27**, RBINS a13136, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views, and close-up of the solid spines (right flank of the dorsal valve). Scale bars equal 2 mm (1-20, 22-26), 1 mm (21), 0.2 mm (21, 27).
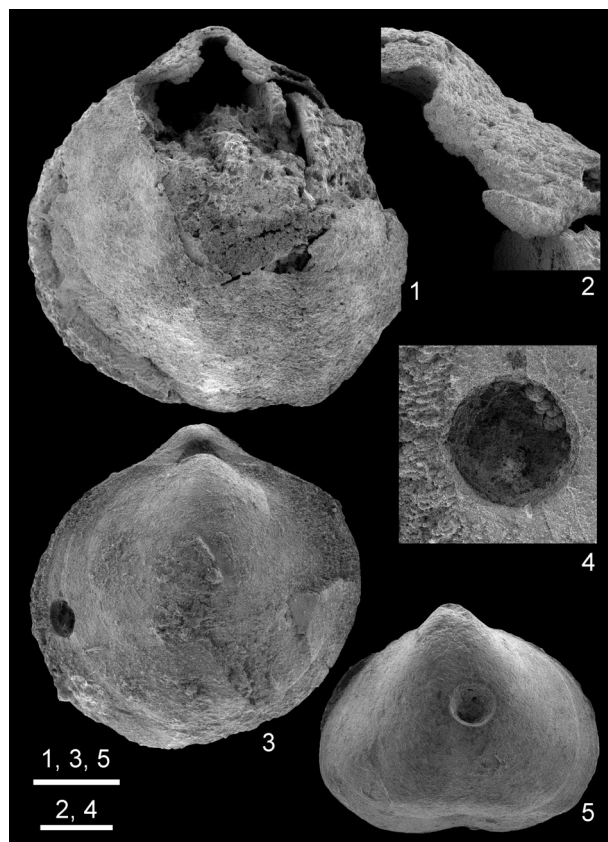
FIGURE 26. *Nucleospira hannoniae* nom. nov., from the Tournai area, Tournai Formation (Tournaisian). **1-2,** RBINS a13137, distorted and incomplete specimen in dorsal view showing two whorls of the spiralium and detail of one of the cyrtomatodont teeth. **3-4,** RBINS a13138, distorted articulated specimen in dorsal view displaying a circular drill hole and detail of the latter. **5,** RBINS a13139, distorted articulated specimen with a circular drill hole in ventral view. Scale bars equal 2 mm (1, 3, 5), 0.5 mm (2, 4).

(de Koninck, 1887, pl. 19, fig. 46) is a paralectotype (Figure 25.6-10).

Additional material. RBINS: 13 articulated specimens; ULg.PA: 8 articulated specimens.

Description. Shell small-sized (up to 10 mm in width), biconvex, slightly wider than long, subcircular in outline; hinge line clearly shorter than maximum width; anterior margin rounded to very slightly emarginate; anterior commissure rectimarginate to slightly undulose.

Ventral valve with flanks moderately sloping towards lateral commissures; umbo small but prominent; beak curved, not in contact with dorsal umbo; interarea low, triangular, apsacline, concave; delthyrium large, open (no deltidial plates observed due to deficient preservation [?]); shallow

median depression occasionally developed and originating inconspicuously near umbo; no tongue.

Dorsal valve highest posteriorly to midvalve then decreasing progressively towards anterior margin; flanks sloping gently to moderately towards lateral commissures; no fold.

Shell smooth with only some irregularly spaced and thickened growth lines; spines solid, densely crowded, long (rarely preserved) (Figure 25.27).

Ventral interior poorly known (Figure 26.1-2); teeth cyrtomatodont, small.

Dorsal interior unknown; only some whorls observed (Figure 26.1).

Dimensions (Figure 27, Table 4). An insufficient number of specimens have been measured. The scatter diagrams just indicate that relations between width and length of the shell or between the width and the thickness of the shell seem not affected by a large variability. The length/width or thickness/width ratios seem stable during the growth.

Remarks. The presence of solid spines covering the shell surface and the apsacline ventral interarea are characteristic of the genus *Nucleospira*, but their internal morphology was not investigated. *Athyris globulina* Waagen, 1883 (now included in *Cleiothyridina* Buckman, 1906; see Angiolini, 1995) and *A. globulina* de Koninck, 1887 are primary homonyms as rightly stressed by Grunt (1989), who included the latter species in *Cleiothyridina*. De Koninck's species is a junior primary homonym and must be renamed: *Nucleospira hannoniae*. The name-bearing type of *Nucleospira hannoniae* remains that of *Athyris globulina* de Koninck, 1887 (not Waagen, 1883) (see above).

There are few reports of the genus *Nucleospira* in the Mississippian of Western Europe (Brunton, 1984; Mottequin et al., 2015); this is most probably related to the small size of its representatives. Several species were described in the Mississippian of North America (see Weller, 1914, and Carter and Carter, 1970), while Pennsylvanian representatives of the genus are very rare according to Carter and Poletaev (1998). Externally, *N. hannoniae* is very close to *N. carlukensis* (Davidson, 1859) but according to Brunton (1984), the anterior commissure of the latter is commonly weakly uniplicate due to the presence of a sulcus whereas, in our very restricted material, it is generally rectimarginate (sulcus generally absent). Only the observation of the internal morphology of the material from Tournai will permit to better discriminate (or otherwise) both species. *N. hannoniae* differs from *N.*
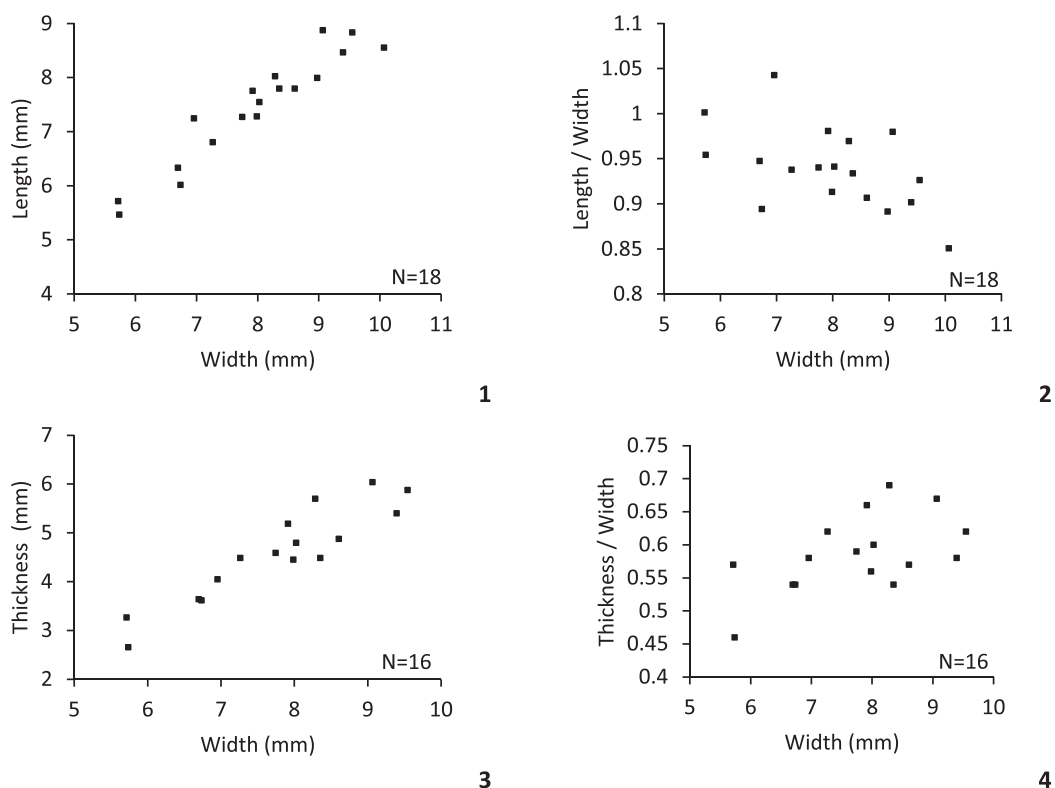
FIGURE 27. Scatter diagrams of *Nucleospira hannoniae* nom. nov. N: number of specimens measured. **1,** Relation between shell width and length. **2,** Relation between width and shell length/shell width ratio. **3,** Relation beween shell width and thickness. **4,** Relation between shell width and shell thickness/shell width ratio.

barrisi White, 1860 by the absence of a tongue (rectimarginate vs. uniplicate anterior commissure). On the basis of its external features, *Nucle-*

TABLE 4. Measurements in mm of *Nucleospira hannoniae* nom. nov. Abbreviations: see Table 1.

	W	**L**	**T**	**L/W**	**T/W**
N	18	19	16	18	16
Mean	7.9	7.5	4.6	0.94	0.59
MIN	5.7	5.5	2.7	0.85	0.46
MAX	10.1	9.5	6.0	1.04	0.69

ospira hannoniae is close to *N. obesa* Rowley, 1900 but can be distinguished from the latter by its larger size and the usual absence of a ventral median depression.

Occurrence. *Nucleospira hannoniae* is presently known only from the Tournai Formation (at least in the Vaulx Member) of the Tournai area. Dewalque (1893) reported *Athyris globulina* de Koninck, 1887 (not Waagen, 1883) within the Ourthe Formation (Figure 4), but the conspecificity with the species from Tournai has to be confirmed.

Suborder RETZIIDINA Boucot, Johnson, and Staton, 1964
Superfamily RETZIOIDEA Waagen, 1883
Family NEORETZIIDAE Dagys, 1972
Subfamily HUSTEDIINAE Grunt, 1986
Genus COVEENIA Alvarez and Brunton, 2000

Type species. *Retzia ulothrix* de Koninck, 1843; from the Tournaisian of Tournai, Belgium.

Coveenia ulothrix (de Koninck, 1843)
Figures 4, 28

	1843	*Terebratula crispata* de Koninck, p. 292, pl. 19, fig. 5a-c.
*	1843	*Terebratula ulothrix* de Koninck, p. 635 (replacement name).
	1868	*Retzia (Terebratula) ulothrix,* de Kon.; Dewalque, p. 332.
	1881	*Retzia (Terebratula) ulothrix,* de Kon.; Mourlon, p. 46.
v	1887	*Retzia ulothrix* de Koninck; de Koninck, p. 92, pl. 22, figs. 1-4.
?	1958	*Retzia ulotrix* (*sic*) de Koninck; Demanet, p. 121.
?	1969	*Retzia ulotrix (sic)* de Kon.; Mortelmans, p. 33.

33
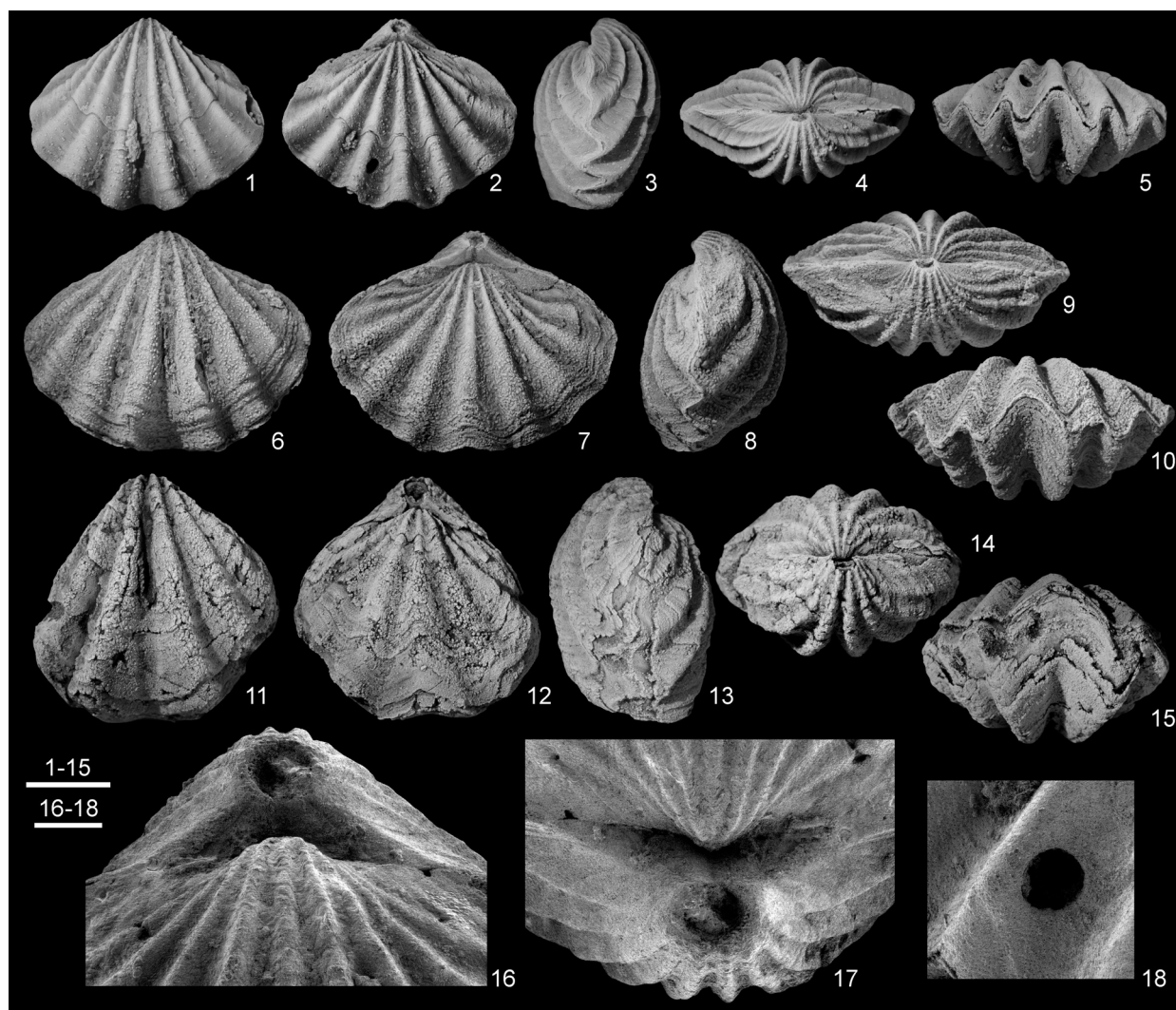
FIGURE 28. *Coveenia ulothrix* (de Koninck, 1843) from the Tournai area, Tournai Formation (Tournaisian). **1-5, 16-18,** ULg.PA.2016.12.25/10, articulated specimen in ventral, dorsal, lateral, posterior and anterior views, and detail (SEM) of the foramen and the symphytium, and of circular drill hole developed close to the dorsal anterior margin. **6-10,** RBINS a13140, articulated specimen in ventral, dorsal, lateral, posterior, and anterior views, Dutoit quarry, Pont-à-Rieu. **11-15,** RBINS a13141, articulated specimen, almost complete, in ventral, dorsal, lateral, posterior and anterior views, Dutoit quarry, Pont-à-Rieu. Scale bar equals 10 mm (1-15), 1 mm (16-18).

v   2000   *Coveenia ulothrix* (de Koninck, 1843); Alvarez and Brunton, p. 822, pl. 1, figs. 1-10, text-fig. 1-2, 5 (see for a more complete synonymy).

v   2007   *Coveenia ulothrix* (de Koninck, 1843); Alvarez, p. 2769, figs. 1851-1852 (copy of Alavarez and Brunton, 2000, pl. 1, figs. 1-4, 6, text-fig. 2 (*pro parte*).

Material. Besides the material from the RBINS used by Alvarez and Brunton (2000), 18 additional articulated specimens; ULg.PA: four articulated specimens.

Remarks. Although this species has been re-described thoroughly by Alvarez and Brunton (2000) on the basis of material from Tournai, three additional specimens are illustrated here (Figure 28.1-18) in order to provide the posterior views missing in Alvarez and Brunton's (2000) publication, and details of the permesothyrid foramen and the symphytium (Figure 28.16-17).

Occurrence. In Belgium, *Coveenia ulothrix* is known with certainty only from the Tournai area (Tournai Formation; Figure 4). Few specimens belonging to the genus *Coveenia* (*C.* sp. indet. in Figure 4) have been collected in the contempora-

neous Yvoir Formation in the Dinant Synclinorium, but further material is required to reach a better identification. Two other *Coveenia* species are also recognized in Belgium (Figure 4): *C. davidsoni* (de Koninck, 1887) (see below) from the Waulsort Formation and *C. buchiana* (de Koninck, 1843) from the Visé Formation. The genus *Coveenia* is known from the Tournaisian–Visean of Western Europe, including British Isles (Alvarez and Brunton, 2000; Alvarez, 2007) but has also been doubtfully reported in the Tournaisian of Algeria by Mottequin and Legrand-Blain (2010).

<div align="center">

Coveenia davidsoni (de Koninck, 1887)
Figures 4, 29.1-4
</div>

v*	1887	*Retzia davidsoni* de Koninck, p. 92, pl. 22, fig. 10.
?	1923	*Retzia davidsoni* de Koninck; Demanet, p. 189, pl. 11, fig. 87.

Holotype. De Koninck (1887, p. 92) stressed on the fact that this species is based on a single poorly preserved specimen of the Dupont collection (RBINS a5508; Figure 29.1-4) from Dréhance (Waulsort Formation, Ivorian), which has to be considered as the holotype by monotypy.

Remarks. The limited material available for study cannot permit to fully describe this species, which is currently only represented by the holotype and assigned to *Coveenia* on the basis of its external features. This incomplete specimen is small (ca. 11 mm in width), wider than long, biconvex, and bears height high, rounded costae on the dorsal valve, which are separated by similar grooves. De Koninck (1887) presumably assumed that the holotype was identical to the two specimens from England identified as *Retzia ulothrix* by Davidson (1861, pl. 18, figs. 14-15). Alvarez and Brunton (2000) assigned the first specimen illustrated by Davidson (1861, pl. 18, fig. 14) to their new species *Coveenia tilsleia* whereas the second (Davidson, 1861, pl. 18, fig. 15) may belong to another species (see Alvarez and Brunton's (2000) synonymy list of *C. tilsleia*). However, de Koninck's (1887) species is less rostrate than *C. tilsleia*, but further material is required to provide a full description of this poorly known species and a detailed comparison with *C. ulothrix*. The specimen identified as *Retzia davidsoni* by Demanet (1923), originating from Sosoye (Waulsort Formation) has not been traced.

Occurrence. *Coveenia davidsoni* is only known from the Waulsortian mud mounds (Waulsort Formation, Tournaisian) in southern Belgium (Dinant sedimentation area).
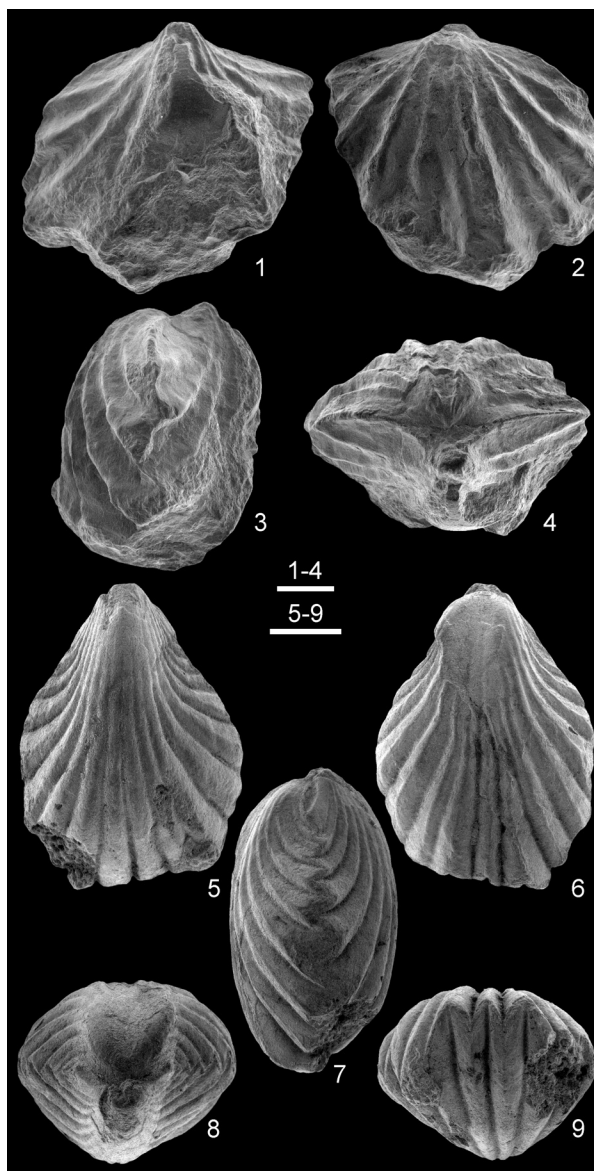
FIGURE 29. 1-4, *Coveenia davidsoni* (de Koninck, 1887), RBINS a5508 (holotype), articulated specimen in ventral, dorsal, lateral and posterior views, from Dréhance, Waulsort Formation (Tournaisian, Ivorian). **5-9,** '*Retzia' intermedia* de Koninck, 1887 (here considered as a rhynchonellide species), RBINS a5510 (lectotype), articulated specimen in ventral, dorsal, lateral, posterior and anterior views, from Furfooz, Waulsort Formation (Tournaisian, Ivorian). Scale bars equal 2 mm.

Systematic position of *Retzia intermedia* de Koninck, 1887

Among the three new species briefly described by de Koninck (1887) and assigned to *Retzia* King, 1850 (*R. davidsoni* (= *Coveenia davidsoni,* see above), *R. multiplicata* (= *Hustedia multiplicata*, see Mottequin et al., 2015), and *R.*

intermedia), the third is definitely not an athyridide, but a rhynchonellide on the basis of its external morphology. For purposes of nomenclatorial formality, the only specimen (RBINS a5510) illustrated by de Koninck (1887, pl. 22, figs. 11-15) from Furfooz (Figures 2-3) is selected herein as the lectotype of *Retzia intermedia* de Koninck, 1887 (Figure 29.5-9). The other specimens cited by de Koninck (1887) were not traced in the RBINS collections. The lectotype could be a juvenile, likely of one of the numerous costate rhynchonellide species occurring within the Waulsortian mudmounds from Belgium and illustrated by de Koninck (1887), Fraipont (1908), and Demanet (1923), but its precise identification requires their revision, which is well beyond the scope of this paper.

DISCUSSION

Stratigraphic summary

The stratigraphic range and the geographic distribution of the athyridides, orthotetides and strophomenides investigated in this study across the Namur–Dinant Basin are presented in Figure 4. Those of the representatives of the abovementioned orders were indicated by Demanet (1958) and Mortelmans (1969), but need to be revised.

Some comments on the athyridide, orthotetide, and strophomenide diversity during the Devonian and the Mississippian in southern Belgium

Strophomenides. One of the striking features of the Tournaisian–Visean brachiopod assemblage of the Namur–Dinant Basin is the re-occurrence of Leptaeninae (Rafinesquinidae) representatives both in mixed siliciclastic-carbonate ramp and buildup environments, after their absence during almost, if not, all of the Late Devonian in this area. The Family Rafinesquinidae, which first appeared during the Ordovician (Rong and Cocks, 1994), is the only strophomenide family to cross the Frasnian–Famennian (late Frasnian Crisis) and the Devonian–Carboniferous (Hangenberg Crisis at the end of the Famennian) boundaries, and become extinct by the Bashkirian according to Curry and Brunton (2007). No modern study of Devonian Leptaeninae representatives from Belgium is available.

In southern Belgium, the first Devonian Leptaeninae are known from the Pragian (Godefroid in Godefroid et al., 1994), although they occur in this area at the top of the Silurian (Pridolian) (e.g., Boucot, 1960; Godefroid and Cravatte, 1999). Their

last Middle Devonian occurrence is recorded within the late Eifelian (Maillieux, 1938; Godefroid, 1968; Bultynck, 1970). Maillieux (e.g., 1940a, 1940b, 1941) and Mottequin (2008a) did not mention rafinesquinids in the Givetian–Frasnian succession of southern Belgium, a time span during which Strophomenida are represented by douvillinids and leptostrophiids in this area, and maybe strophodontids, but further investigations are needed. The presence of Leptaeninae in the early Famennian of the Namur–Dinant Basin is doubtful according to Maillieux (1941). They were reported within the uppermost Famennian (Strunian) by Demanet (1958), but this report has to be revised. In north-western France, namely in the Avesnois area (Figure 2) which corresponds to the western prolongation of the Namur–Dinant Basin, Leptaeninae were reported in the uppermost Famennian by Dehée (1929) and Brice et al. (2013), but this occurrence has been challenged by Mottequin and Brice (2016). Elsewhere in the world, several authors reported their occurrence in Frasnian and Famennian deposits (e.g., Karapetov, 1971; Xu (in Xu and Yao, 1988), Mergl and Massa, 1992; Brice in Brice et al., 2005; Alekseeva, 2011; Popov in Ghobadi Pour et al., 2013; Baranov et al., 2016; Zong et al., 2016). The absence of Leptaeninae from the Givetian–Famennian interval in southern Belgium is quite strange as, during the same time, the long-ranging orthide genus *Schizophoria*, which was already associated to the last Eifelian Leptaeninae, did not temporarily disappear and is even one of the first to recover after the Frasnian–Famennian Crisis in Belgium (Mottequin, 2008b; Mottequin and Poty, 2016), and persisted after the Hangenberg Crisis. They flourished again during the Tournaisian–Visean, notably in Europe (e.g., Demanet, 1934; Pocock, 1968; Żakowa, 1989).

After the Hangenberg Crisis, Leptaeninae proliferated in some argillaceous and carbonate environments of Tournaisian age, a time interval marked by the transition between the Devonian greenhouse and the Carboniferous icehouse climates (e.g., Bruckschen et al., 1999; Buggisch et al., 2008), notably in Western Europe (e.g., Demanet, 1934; Bassett and Bryant, 2006; Mottequin, 2010), North America (e.g., Carter, 1968, 1987, 1988, 1999), Australia (Cvancara,1958; Thomas, 1971), Russia (Sokolskaya in Sarytcheva et al., 1963; Gretchischnikova, 1966), Iran (Bahrammanesh et al., 2011), and China (Shi et al., 2005; Sun and Baliński, 2008). The range of leptaenines (identified as *Leptaena analoga*) within the Hastarian and Ivorian of southern Belgium has

been indicated by Demanet (1934, 1958). According to his data, they are clearly more abundant in the argillaceous and mixed carbonate-argillaceous environments than in more carbonate ones, such as the encrinitic facies that prevailed during the Ivorian. Until now, their only Visean occurrence is reported in the upper Visean buildup of Visé, where they seem to be confined (Demanet, 1934). At Visé, besides *Leptagonia* cf. *caledonica*, de Koninck (1843) and Demanet (1934) reported the presence of *Leptaena distorta* Sowerby, 1840, which is the type species of *Pseudoleptaena* Miloradovich, 1947, a genus which is generally considered as a synonym of *Leptagonia* (e.g., Williams, 1965; Cocks and Rong, 2000), although the general shape of Sowerby's species is markedly different of the type species of *Leptagonia*. The revision of this material from Visé has still to be carried out, but it is included in Figure 4 as *L.? distorta*. The recurrence of siliciclastic environments at the onset of the Serpukhovian in relation with the glaciations did not favour their return in southern Belgium as they are absent at the end-Mississippian (Demanet, 1941). In contrast, Brand (1972, 2011) recorded leptaenines in the Arnsbergian (Serpukhovian) of Scotland and Northern Ireland whereas Carter et al. (2014) stressed on the fact the genus *Leptagonia* first appeared within the basal Tournaisian and temporarily disappeared at the end of this stage before reappearing in North America during the late Serpukhovian.

Orthotetides. Representatives of this order were common within the Devonian–Mississippian succession of southern Belgium but were generally not abundant, except in some Visean horizons (Demanet, 1934). There, Devonian species remain relatively poorly documented (e.g., de Koninck, 1882; Maillieux, 1909, 1939; Boucot, 1960; Long and Brunton, 2005; Mottequin, 2008a), whereas their Carboniferous counterparts have never been revised since Demanet's (1934, 1938, 1941, 1943) monographs, except the partial revision herein. It is currently not possible to discuss precisely the consequences of the Hangenberg Crisis on the representatives of this order as the most recent data (lists of species) date back to Demanet (1958). Further work is thus needed to better assess the diversity of the Tournaisian and Viséan orthotetides, although a large a part of them was previously described by Demanet (1934). As is the case for many of the brachiopod orders (e.g., productides, spiriferides), their specific diversity unsurprisingly reaches a zenith within the Visean (Warnantian) buildups composed of massive algal

and bioclastic boundstones similar to the English Cracoean facies (Mundy, 1994) and some of these Warnantian species reach a very large size (more than 100 mm in width) in comparison with their Tournaisian counterparts. Note that numerous orthotetide species were described within the Mississippian succession of Western Europe, especially in Great Britain and Ireland, notably by Phillips (1836), M'Coy (1844), Thomas (1910), Smyth (1930), and Reed (1954), but despite some partial revisions of these pioneering works by Brunton (1968), McIntosh (1974), and Bassett and Bryant (2006), many of them are still poorly known.

Athyridides. In spite of their great abundance in diverse environments, our knowledge of the Devonian athyridides from Belgium is still strongly lacunar despite some recent contributions on their Middle and Late Devonian representatives (Godefroid and Mottequin, 2005; Mottequin, 2004, 2008a, 2008b; Mottequin et al., 2016). Known since the Lochkovian (Asselberghs, 1930; Boucot, 1960; Godefroid and Cravatte, 1999), most of the Lower and Middle Devonian athyridides are only known by lists of species or brief descriptions generally devoid of illustrations (e.g., Asselberghs, 1923; Maillieux, 1931, 1932, 1941) and thus insufficient to provide a detailed analysis of their change in diversity through Devonian time in this part Laurussia.

During the Tournaisian and Visean, these spire-bearers seem to rank among the most diverse brachiopod orders from the specific viewpoint along with the productides and spiriferides in the Namur–Dinant Basin, as for the Devonian counterparts, only their thorough revision will permit to assess their real diversity. Athyridida were described by Léveillé (1835) and de Koninck (1843, 1851, 1887), especially from Tournai and Visé, but most of them have never been revised and are still only known by embellished drawings, except those discussed and re-illustrated by Brunton (1980, 1984), Alvarez and Brunton (2000), Mottequin et al. (2015), Mottequin and Simon (2015, 2017), and the present paper.

Among the Tournaisian Athyridoidea, the Subfamily Cleiothyridininae includes the genera *Carteridina* and *Cleiothyridina* represented by several species previously described by Léveillé (1835) and de Koninck (1843, 1851, 1887), whose revision is in progress. In northern France and southern Belgium, cleiothyridinines (*Cleiothyridina*) are firstly recorded in the Frasnian (Mottequin, 2008b; Brice et al., 2008), but this subfamily encountered there a great development during the Famennian

with other undescribed *Cleiothyridina* species and more particularly with several *Crinisarina* ones (Mottequin, 2008a, 2008b). Thus, cleiothyridinines took part to post-Kellwasser brachiopod recovery, a phenomenon well-known elsewhere in the world (e.g., Baliński, 2002), but also after the Hangenberg Crisis. In contrast, Tournaisian athyridines (*Lamellosathyris*) and spirigerellines (*Composita*) are less diverse specifically. However, it is important to stress on the fact that in some Viséan reef facies of the Namur–Basin, *Composita* representatives (or at least identified as such) are so locally abundant that they provided substantial firm ground for reef builder encrustation (e.g., Chevalier and Aretz, 2005). Moreover, representatives of the superfamilies Retzioidea *(Coveenia, Hustedia)* and Nucleospiroidea (*Nucleospira*) were generally minor components of the brachiopod assemblages from the Tournaisian and Visean successions of the Namur–Dinant Basin, even if *Hustedia* and *Nucleospira* seem to be more abundant in Warnantian carbonate buildup environment, such at the top of the Visé Formation, but this needs to be confirmed.

Palaeobiology

Life position. The largest specimens of *Leptagonia franca* are characterized by the great development of shelly expansions both laterally and postero-anteriorly, which induces the formation of a kind of flattened ledge by the lateral parts of the trail as observed by Hoel (2005, 2014) in Silurian Leptaeninae. In relation with the development of such shelly structures, the supra-apical foramen disappears through ontogeny reflecting the loss of utility of the functional pedicle. These observations reflect an early anchored lifestyle followed by an ambitopic one (e.g., Jaanusson, 1979; Bassett, 1984; Rachebœuf, 1991; Hoel, 2014), lying on its ventral valve and floating in a soft substrate thanks to its long trail, very wide and flattened alae. However, the position of the epizoans (craniide brachiopods and microconchids) may also indicate that the shell lived in vertical position (e.g., Spjeldnaes, 1984; Hoel, 2014) with the umbo pointing downwards, during a significant part of the ontogeny as reflected by the presence of the supra-apical foramen. Note that the life orientation of concavo-convex brachiopods is still hotly disputed (e.g., Lescinsky, 1995; Leighton, 1998, 2005; Baliński, 2010; Mergl and Nolčová, 2016). The specimen RBINS a5895 (Figure 6.7-12) displays two epibionts on its ventral valve, namely a microconchid on the trail (but very close to the geniculation) and a

craniide specimen sitting astride the disc and the trail (Figure 6.7-9). If this *L. franca* shell was resting on its ventral valve during its life, the growth of both epibionts was impossible as they were buried in the sediment. One can argue that the shell would have been exposed in a convex-up, hydrodynamically stable position after its death during a time interval sufficient to allow its colonization by epibionts. Nonetheless, this is unlikely, according to Hoel (2014), as the deltidiodont dentition of Leptaeninae is not strong enough to maintain the valves in close connection during a long time. In this case, and thus probably for most of the specimens (except the largest), the vertical position of life is the most probable. Another shell of similar size (RBINS a5829, Figure 6.1-6) displays craniide brachiopods attached to both the dorsal disc (Figure 6.3) and to the ventral trail (Figure 6.1, 6.4, 6.6). The state of preservation of *L. caledonica* did not permit to observe the presence of a supra-apical foramen.

The Tournaisian orthotetides *Schellwienella radialiformis* and *Serratocrista scaldisensis* display a small cementation cicatrix at the top of the ventral umbo with koskinoid perforations (Jux and Strauch, 1966) (Figures 13.12, 18.19-21), of which the origin is still controversial: drilling by organisms (Thomas, 1958; Williams and Brunton, 1993) or resulting from the development of an attachment organ (e.g., Schumann, 1969, Grant, 1976, 1980; Martínez Chacón and García-Alcalde, 1978). The reduced size of the cementation cicatrix may indicate that the fixation to a hard substrate was only effective during the early growth stages of these brachiopods (Bassett, 1984). In contrast, in the lectotype of *Schellwienella ornata*, a large part of the ventral umbonal area is flattened (Figure 15.1).

The morphology and mode of life of athyridide brachiopods was discussed in great detail by Alvarez (1990).

Predation. One articulated shell of *Schellwienella radialiformis* (Figure 13.6-10) displays damage probably resulting from the bite of a predator (fish?) in the centre of the posterior half of the ventral valve and at close to the right posterior margin (the interarea is also affected). It took place during a relatively early stage of the growth of the brachiopod and was not lethal as reflected by the deviation of the radial ornamentation and the distortion of the shell outline. Similar phenomena, which were observed recently in spiriferides from the Tournai Formation by Mottequin and Simon (2017), were discussed notably by Baliński (1993) and Sun and Baliński (2011). Circular drill holes perpendicular to

shell surface similar to those described by Mottequin and Sevastopulo (2009) on *Crurithyris goldfussiana* and Mottequin and Simon (2017) on other spiriferide species were observed rarely in *Serratocrista scaldisensis* (Figure 17.12), *Nucleospira hannoniae* (Figure 26.3-5), and *Coveenia ulothrix* (Figure 28.2, 28.18).

Epizoans. Brachiopods from the Tournai Formation are commonly encrusted by different kinds of epizoans according to the nicely preserved material curated at the RBINS and the ULg (Mottequin and Simon, 2017). The most common epizoans are the tentaculitoid tubeworms (microconchids) (Figures 6.7-12, 12.21-25, 20.21-25, 21.14), auloporides (Figure 5.13-18), and craniide brachiopods (Figure 6.1-12). Some of these epibionts clearly colonized brachiopods that were already dead before encrustation; this is particularly evident with an isolated dorsal valve of *Lamellosathyris lamellosa* (ULg.PA.2016.12.25/8) bearing two microconchids on its internal surface (Figure 21.14). The case of the craniides attached to *Leptagonia franca* are discussed above.

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