J. Paleont., 82(6), 2008, pp. 1052–1073
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0022-3360/08/0082-1052$03.00

LATE MIDDLE FRASNIAN TO EARLY FAMENNIAN (LATE DEVONIAN) STROPHOMENID, ORTHOTETID, AND ATHYRIDID BRACHIOPODS FROM SOUTHERN BELGIUM

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ABSTRACT—Brachiopods of the orders Strophomenida, Orthotetida, and Athyridida from the late middle Frasnian–early Famennian interval (*hassi* to *triangularis* conodont zones) in the Namur-Dinant Basin (southeastern margin of Laurussia; southern Belgium) are described. Nine genera and subgenera represented by 12 species are recognized here. One new genus, *Retrorstrophia*, and one new species, *Douvillina area*, are erected. ***Crinisarina stainbrooki*** is proposed to solve the homonymy between *C. reticulata* (Gosselet, 1877) and *Cleiothyridina reticulata* Stainbrook, 1947, the type species of *Crinisarina* Cooper and Dutro, 1982. A lectotype is selected and illustrated for *C. reticulata*. A new name is also proposed for *Athyris reticulata* Chen and Xu, 2000, which is assigned here to *Crinisarina*: *C. shashishanensis* nom. nov. In southern Belgium, the last representatives of the families Douvillinidae and Leptostrophiidae (Strophomenida) are from the Upper *rhenana* Zone (late Frasnian). Athyridid brachiopods, especially the representatives of the subfamily Cleiothyridininae constituted a significant part of the early Famennian recovery faunas with spiriferids and rhynchonellids, just after the late Frasnian mass extinction.

INTRODUCTION

DESPITE REMARKABLE interest by generations of paleontologists in Frasnian and Famennian brachiopods from southern Belgium (Namur-Dinant Basin), few studies have been dedicated to the strophomenids, orthotetids, and athyridids. The latest comprehensive list of Late Devonian species of these orders dates back to Maillieux (1941) and most of the taxa have never been illustrated.

During the Frasnian, strophomenids and orthotetids were relatively common in the Namur-Dinant Basin, but they generally constituted a minor part of the brachiopod assemblages. The late Frasnian mass extinction, notably responsible for the extinction of atrypids and pentamerids (Copper, 1986), decimated the order Strophomenida: only the Rafinesquinidae crossed the Frasnian/Famennian boundary (Rong and Cocks, 1994). Athyridids and more especially the representatives of the subfamily Cleiothyridininae played a significant role in the post-extinction brachiopod recovery together with spiriferids and rhynchonellids.

The purpose of this paper is to describe the Strophomenida and the Orthotetida from the late middle Frasnian to the early Famennian (*hassi* to *triangularis* conodont zones) as well as the Athyridida from the early Famennian (*triangularis* Zone) of the Namur-Dinant Basin, which is the historical type area of the Frasnian and Famennian stages [see overview in Coen-Aubert and Boulvain (2006) and Thorez et al. (2006)].

GEOLOGICAL SETTING

The material studied originates from 21 sections at different localities in the Namur and Dinant synclinoria, the Philippeville Anticlinorium and the Vesdre area (Fig. 1). These Variscan structural elements constituted the Namur-Dinant Basin, which developed along the southeastern margin of Laurussia during Devonian time. During the Frasnian, the facies succession reflected a ramp setting with a mixed siliciclastic-carbonate sedimentation and several breaks of slope as well as the development of carbonate mound levels in its distal part (southern flank of the Dinant Synclinorium) (Boulvain et al., 2004) (Fig. 2). The Frasnian strophomenids and orthotetids were recovered from the following lithostratigraphic units (*hassi* to Upper *rhenana* zones): Grands Breux (Boussu-en-Fagne Member only), Neuville, Aisemont, Barvaux, Les Valisettes and Lambermont (lower part) Formations. All these formations have been described in detail by Boulvain et al. (1999); they are mainly shaly with limestone beds and nodules. However, the strophomenids and orthotetids from the reddish carbonate buildups (Petit-Mont Member) occurring in the Neuville and Les Valisettes formations have not been studied because of the difficulty of extracting identifiable specimens from the limestones. The Famennian athyridids and orthotetids were recovered in the basal part of the Famenne Group ("Senzeille Formation;" *triangularis* Zone) and from the upper part of the Lambermont Formation (*triangularis* Zone) that are essentially shaly with minor sandy and carbonate beds [see Bultynck and Dejonghe (2002) and Thorez et al. (2006)].

SYSTEMATIC PALEONTOLOGY

The studied specimens are deposited in the paleontological collections of the Institut royal des Sciences naturelles de Belgique (IRScNB) (Brussels, Belgium) and in the collections of the Département de Géologie of the Université de Liège (ULg) (Liège, Belgium). Other material examined is housed at the Musée Gosselet (MGL) included presently within the Musée d'Histoire naturelle de Lille (Lille, France), at the Institut de Géologie of the Université Louis Pasteur (ULP) (Strasbourg, France), and at the United States National Museum (Smithsonian Institution) (USNM) (Washington DC, USA). Only the illustrated specimens are registered.

Abbreviations for measurements are as follows: dL, dorsal valve length; Hi, interarea height; Ht, tongue height; L, shell length; T, shell thickness; Td, dorsal valve thickness; Tv, ventral

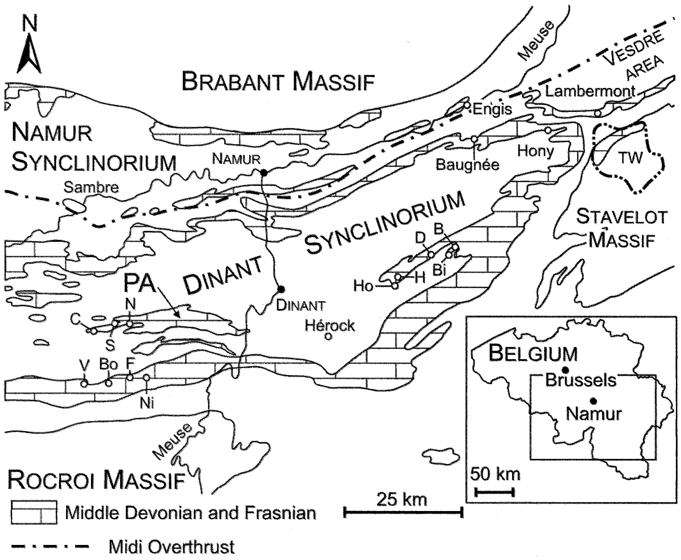

FIGURE *1*—Schematic geological map of southern Belgium. Abbreviations: B, Barvaux; Bi, Biron; Bo, Boussu-en-Fagne; C, Cerfontaine; D, Deulin; F, Frasnes; H, Heure; Ho, Hogne; N, Neuville; N, Nismes; PA, Philippeville Anticlinorium; S, Senzeille; TW, Theux Window; V, Vaulx.

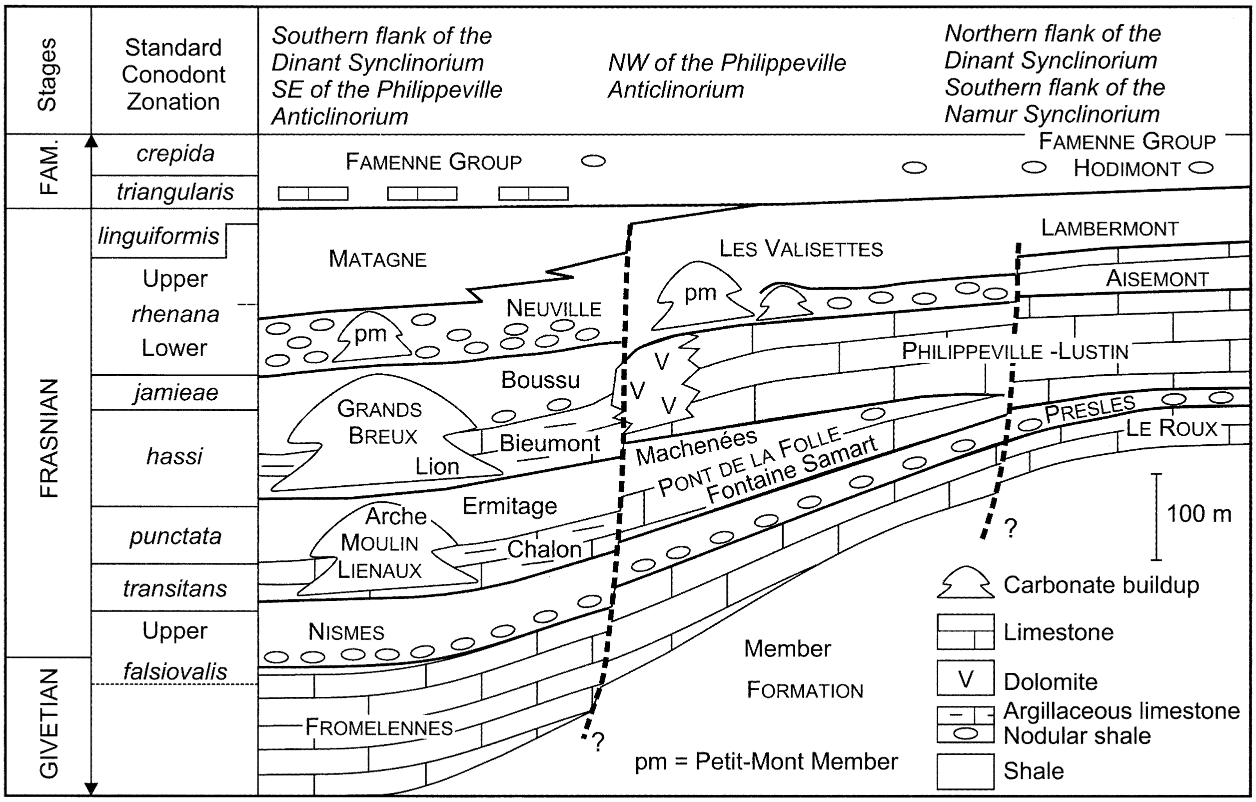

FIGURE 2—Schematic N-S cross section and main lithostratigraphic units of the Namur-Dinant Basin before the Variscan Orogeny. Modified from Boulvain et al. (2004). The Barvaux Formation is not represented here but it is a lateral equivalent of the Matagne and Les Valisettes formations and of the lower part of the Lambermont Formation. The Famenne Group includes, from base to top, the "Senzeille" and "Mariembourg" formations (see Thorez et al. (2006) for more details).

valve thickness; ULd, Unrolled length of dorsal valve; ULv, unrolled length of ventral valve; W, shell width; Wi, interarea width; Ws, sulcus width.

The name of a locality followed by a number (e.g., Durbuy 5337) corresponds to the name of an outcrop as it is recorded in the files of the IRScNB. The BM, JG, and PS prefixes indicate B. Mottequin, J. Godefroid, and P. Sartenaer's localities, respectively (see also Appendix 1).

Order STROPHOMENIDA Öpik, 1934
Superfamily STROPHOMENOIDEA King, 1846
Family DOUVILLINIDAE Caster, 1939
Subfamily DOUVILLININAE Caster, 1939
Genus DOUVILLINA Oehlert, 1887

Type species.—*Orthis Dutertrei* Murchison, 1840.

DOUVILLINA DUTERTREI (Murchison, 1840)
Figures 3.1–3.11, 4

Orthis Dutertrii MURCHISON, 1840, p. 253, pl. 2, fig. 6a–c.

Material examined.—One articulated specimen and two ventral valves from locality BM-2001-2; two ventral valves from locality BM-2002-5; three articulated specimens from locality BM-2002-7; one articulated specimen and seven ventral valves from locality BM-2002-8; 8 articulated specimens and six ventral valves from locality BM-2003-6; four articulated specimens and two ventral valves from locality BM-2003-7; five articulated specimens and three ventral valves from locality BM-2003-9; 46 articulated specimens from locality Couvin 6158p.

Measurements.—See Figure 4.

Occurrence.—In the Boulonnais region where the species was first described by Murchison (1840), Brice (2003) reported it in the Beaulieu and Ferques formations of Frasnian age. In the Namur-Dinant Basin, *D. dutertrei* occurs within the *hassi* to Upper *rhenana* zones on the basis of the current data.

Discussion.—The Belgian specimens agree with the description of Murchison's species provided by Brice (1988).

DOUVILLINA AREA new species
Figures 3.12–3.27, 4, 5

Diagnosis.—Shell large-sized (maximum W: 37.8 mm; maximum L: 29.6 mm; maximum T: 14.0 mm), wider than long (W/L: 1.03–1.39), planoconvex to concavoconvex, semi-elliptical to semicircular in outline; ventral (up to 3.25 mm) and dorsal interareas well-developed; 12–13 costae and costellae per 5 mm at front.

Description.—Shell wider than long (W/L: 1.03–1.39), planoconvex to concavoconvex, roughly semi-elliptical to semicircular in outline with straight to convex posterolateral margins and straight to rounded anterior one; maximum width between mid-length and posterior margin; anterior commissure rectimarginate, ventral interarea 1 to 3 times higher than dorsal one. Ventral valve of variable convexity (ULv/L: 1.01–1.37), maximum thickness at about midvalve; flanks sloping gently to moderately towards lateral commissure; posterior margin subrectilinear; umbo absent; posterior angle identical to apical one varying between 160°–176°; interarea high (up to 3.25 mm), flat, apsacline, vertically striated; pseudodeltidium with median part convex. Dorsal interarea flat, hypercline, vertically striated; chilidium narrow, convex. Ornamentation parvicostellate (Fig. 3.27); costellae increasing by intercalation, 12–13 costae and costellae per 5 mm at front; growth lamellae absent to rare; filae very fine.

Ventral interior (Fig. 5) with ventral process devoid of internal cavity; hinge line denticulate; muscle field relatively small, semi-elliptic, concave, elevated [width and length corresponding to 40% and 35% of W and L respectively (only one specimen)]; muscle-bounding ridges well-developed, interrupted anteriorly by a prominent myophragm extending on a low distance towards anterior margin. Dorsal interior (Fig. 5) with cardinal process composed of two posteroventrally orientated lobes uniting in anterior direction; socket ridges small, divergent; myophragm prominent but short; anderidia separated by relatively deep cavity.

Etymology.—From "*area*," Latin, a flat surface, referring to the considerable development of the ventral and dorsal interareas.

Type.—Holotype, complete specimen (IRScNB a12398) (Fig. 3.12–3.16) from the Barvaux Formation (Upper *rhenana* Zone) at locality Durbuy 5337 (=BM-2002-4).

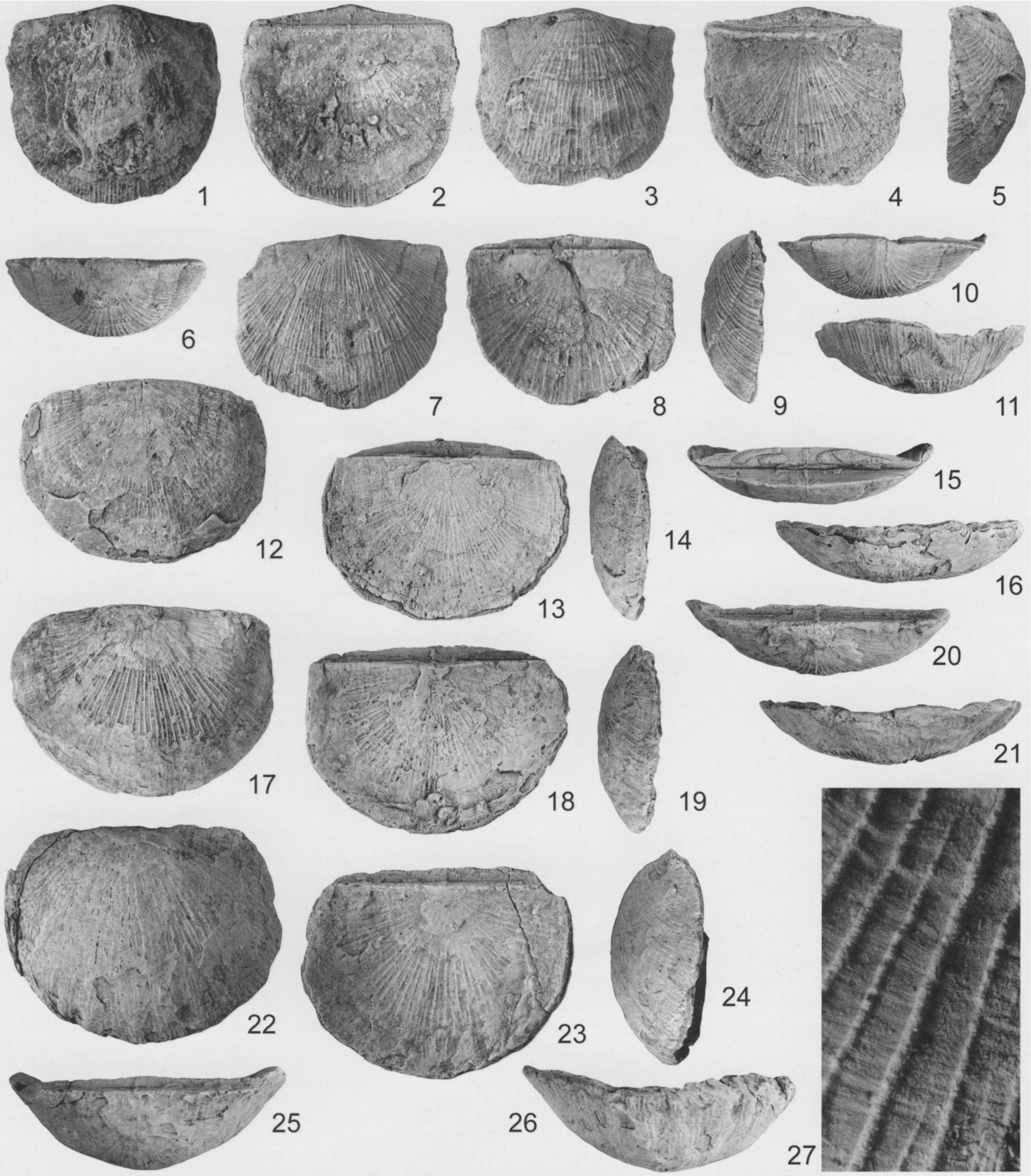

FIGURE 3—*1–11*, *Douvillina dutertrei* (Murchison 1840) from locality Couvin 6158p. (Grands Breux Formation, Boussu-en-Fagne Member): *1–2*, ventral and dorsal views of IRScNB a12395; *3–6*, ventral, dorsal, lateral, and posterior views of IRScNB a12396; *7–11*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12397. *12–27*, *Douvillina area* sp. nov. from locality Durbuy 5337 (Barvaux Formation): *12–16*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12398 (holotype); *17–21, 27*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12399 and detail of ornament on ventral valve; *22–26*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12400. *27*, ×15; others, ×1.5.

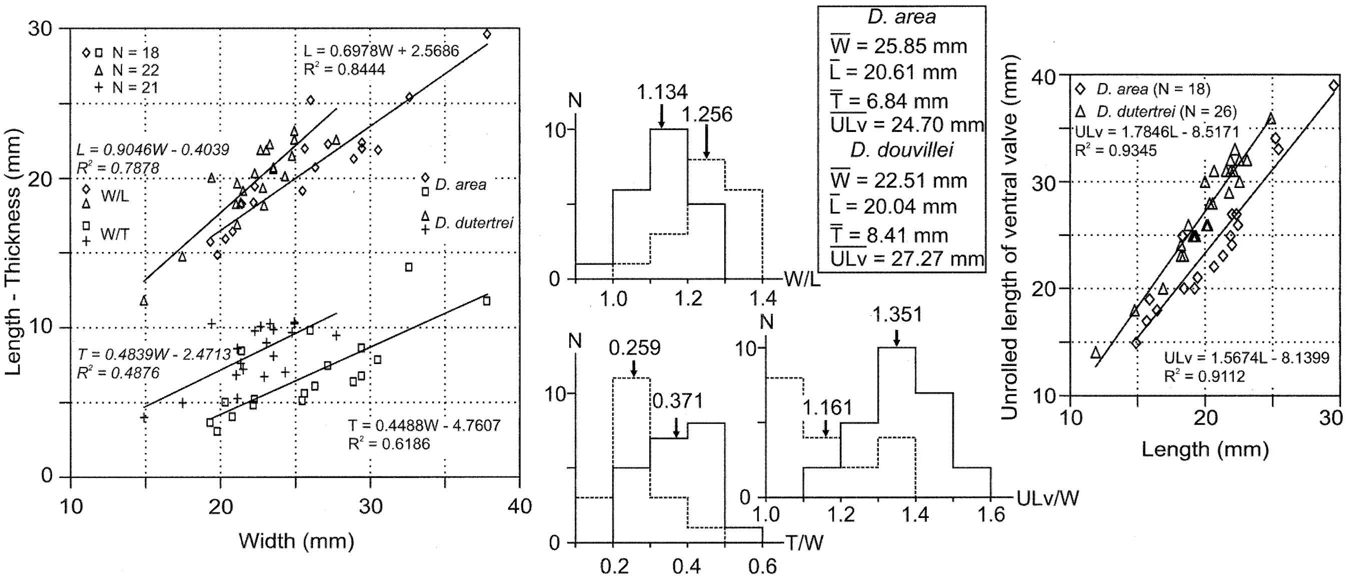

FIGURE 4—*Douvillina dutertrei* and *Douvillina area* sp. nov. Scatter diagrams of shell width to shell length, shell width to shell thickness, and shell length to dorsal valve unrolled length (ULd); frequency diagrams of W/L, T/W, and L/ULd (dotted line, *D. area*; unbroken line, *D. dutertrei*). Arrows = means. For abbreviations, see text.

Other material examined.—Two articulated specimens from locality BM-2001-2; seven articulated specimens from locality BM-2002-4; 26 articulated specimens and one ventral valve from locality Durbuy 5337.

Measurements.—See Figure 3.

Occurrence.—*Douvillina area* occurs within the Barvaux Formation (southeastern flank of the Dinant Synclinorium; Upper *rhenana* Zone) as well as in the Lambermont Formation (northern border of the Dinant Synclinorium; Upper *rhenana* Zone).

Discussion.—Pardo Alonso (2002) modified the definition of the genus *Douvillina* in order to include the species with a planoconvex profile such as *D. area*. The new species has been long included with *D. dutertrei* (Murchison, 1840) from whom it is easily distinguishable by its more developed interareas, the absence of ventral umbo and its less developed concavoconvex profile. *Douvillina area* reaches a size similar to that of *D. imitatrix* Reed, 1929, but the latter displays a thinner ornamentation and a prominent ventral umbo. *Douvillina area* is differentiated from

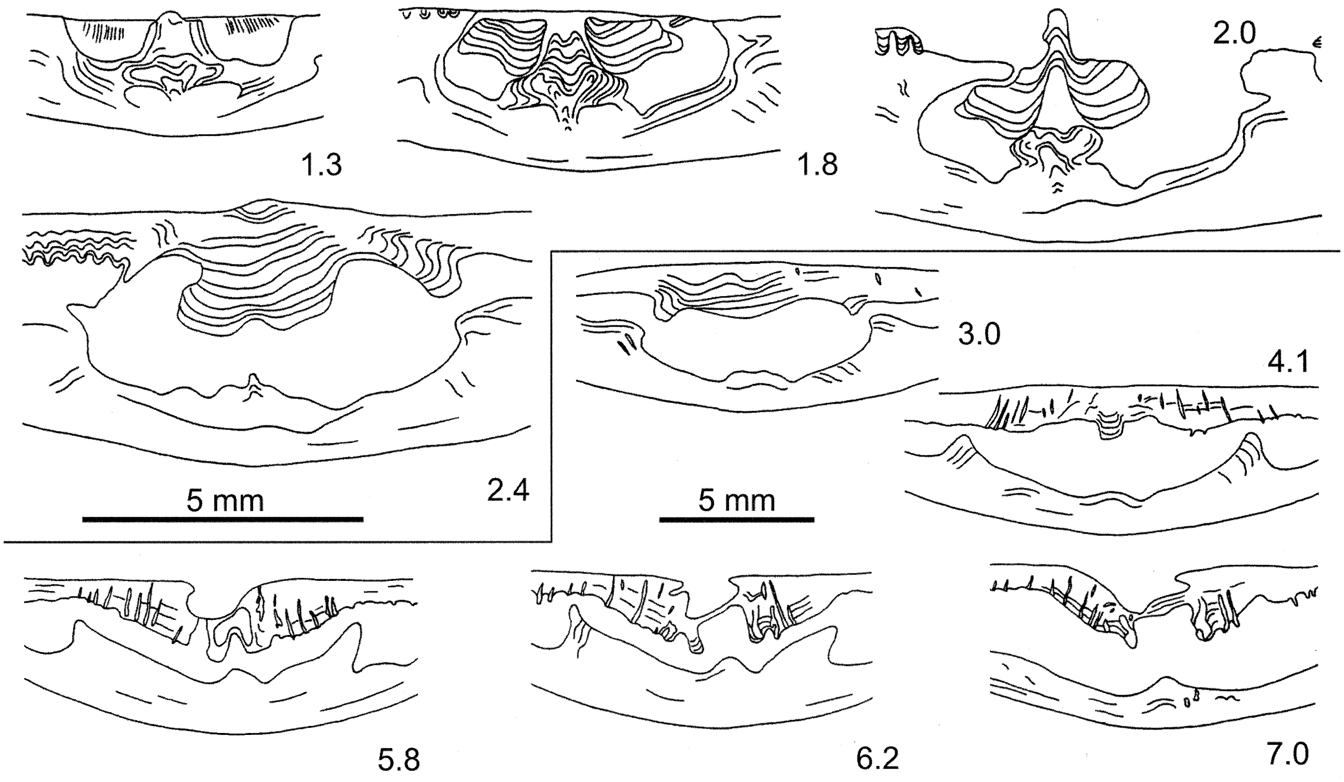

FIGURE 5—Transverse serial sections of *Douvillina area* sp. nov. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12401 from locality Durbuy 5337 (Barvaux Formation). Dimensions of specimen: width 22.3 mm; length 18 mm; thickness 6 mm.

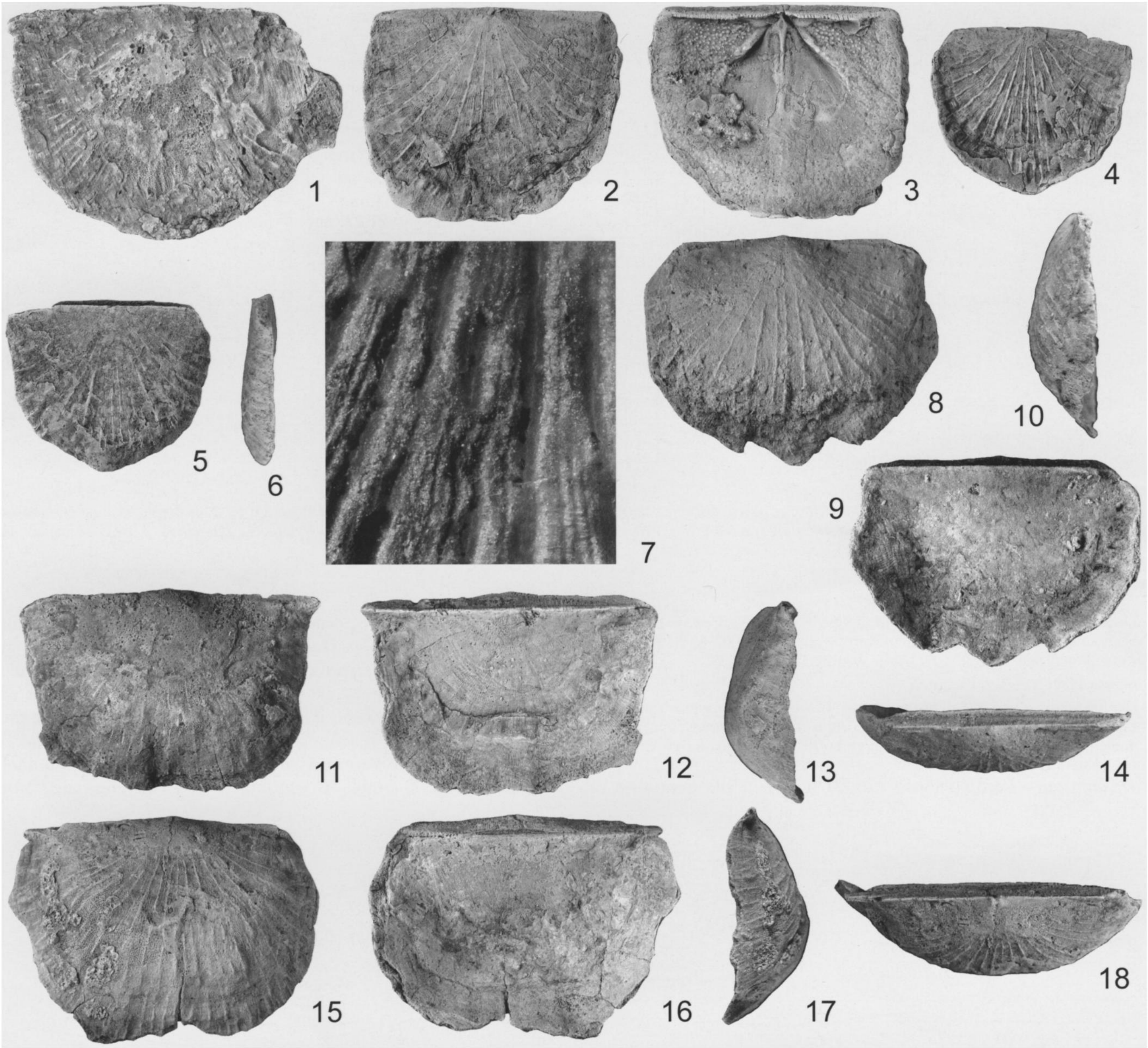

FIGURE 6—*1*, *Nervostrophia (Nervostrophia)* cf. *latissima* (Quenstedt, 1871) from locality BM-2003-8 (Neuville Formation): ventral view of IRScNB a12401. *2–7*, *Gamphalosia* sp. from locality Durbuy 5337 (Barvaux Formation): *2–3*, ventral valve (IRScNB a12402) in external and internal views; *4–7*, ventral, dorsal, and lateral views of IRScNB a12403 and detail of ornament on ventral valve. *8–18*, *Nervostrophia* (*Ailostrophia*?) sp.: *8–10*, ventral, dorsal, lateral, and posterior views of IRScNB a12404 from locality BM-2003-10 (Neuville Formation); *11–14*, ventral, dorsal, and lateral views of IRScNB a12407 from locality 6158p. (Grands Breux Formation, Boussu-en-Fagne Member); *15–18*, ventral, dorsal, lateral, and posterior views of IRScNB a12411 from locality 6158p. (Grands Breux Formation, Boussu-en-Fagne Member). *7*, ×15; others, ×2.

D. kireevae Lyashenko, 1959 by its less rounded posterolateral margins (wider hinge line), the planoconvex character of some shells, and its more developed interareas. The new species differs from *D. timanica* Alekseeva and Olenova, 2000 by its higher ventral interarea, its wider ventral muscle field, and by its less inflated ventral valve.

Family LEPTOSTROPHIIDAE Caster, 1939
Genus NERVOSTROPHIA Caster, 1939
Subgenus NERVOSTROPHIA (NERVOSTROPHIA) Caster, 1939

Type species.—*Strophomena nervosa* Hall, 1843.

NERVOSTROPHIA (NERVOSTROPHIA) cf. LATISSIMA (Quenstedt, 1871)
Figure 6.1

cf. *Leptaena latissima* QUENSTEDT, 1871, p. 598, pl. 57, figs. 59–61.

Material examined.—One articulated specimen from locality BM-2003-8.

Occurrence.—*Nervostrophia* (N.) cf. *latissima* was recovered within the Neuville Formation (southern flank of the Dinant Synclinorium; Lower *rhenana* Zone). In the Boulonnais, *N.* (*N.*) *latissima* occurs in the Ferques Formation (Brice, 2003).

Discussion.—The collections contain a single planoconvex shell whose ornamentation is poorly preserved. It displays mucronate cardinal extremities, a flat and apsacline ventral interarea. By its external characters, it is close to Quenstedt's species as reviewed by Brice (1988), but the confirmation of this identification needs better preserved specimens and the investigation of the internal morphology.

Subgenus NERVOSTROPHIA (AILOSTROPHIA) Alekseeva, 2003

Type species.—*Leptaena asella* de Verneuil, 1845.

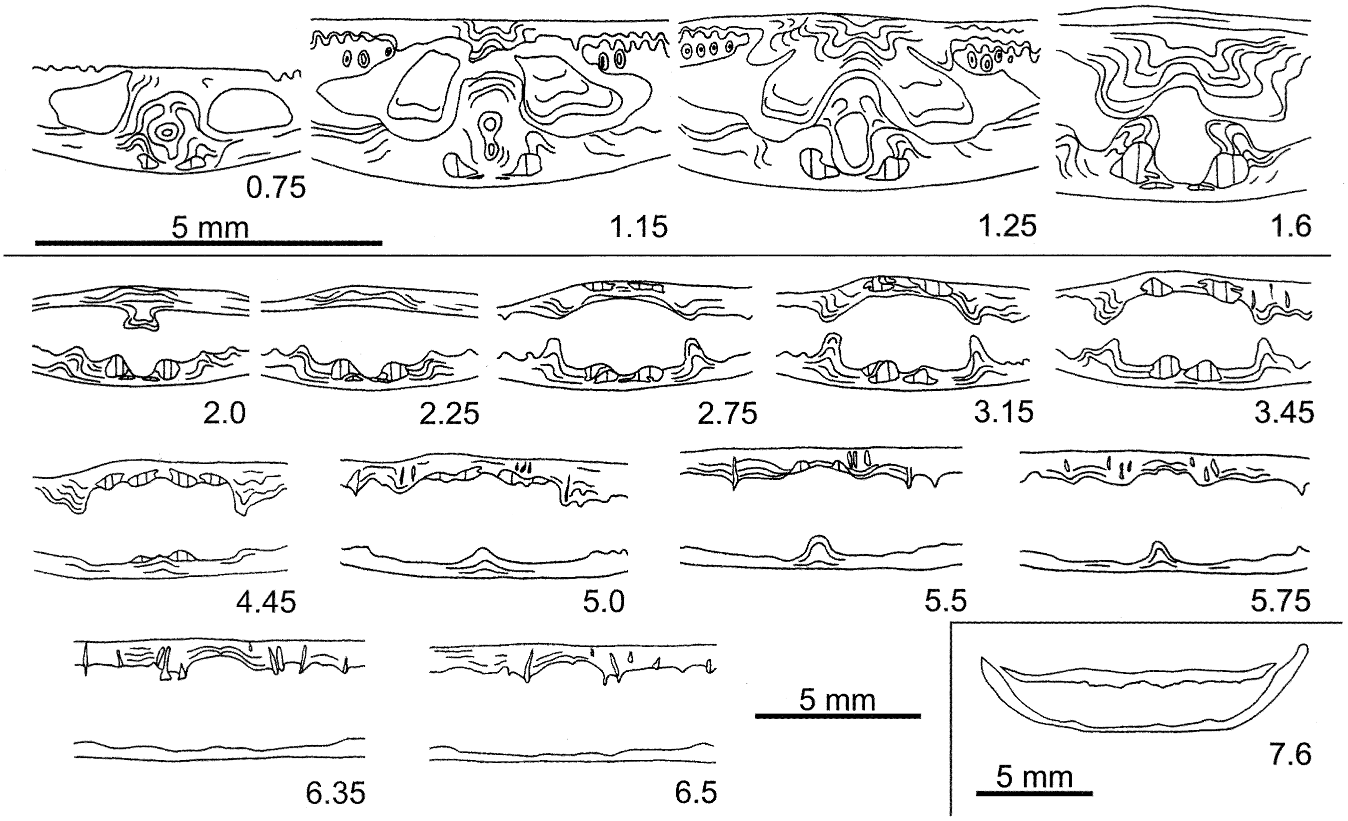

FIGURE 7—Transverse serial sections of *Nervostrophia* (*Ailostrophia*?) sp. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12412 from locality Couvin 6158p. (Grands Breux Formation, Boussu-en-Fagne Member). Dimensions of specimen: width 22.1 mm; length 16.7 mm; thickness 6.7 mm.

Nervostrophia (Ailostrophia?) sp.

Figures 6.8–6.18, 7, Table 1

Description.—Shell reaching 23.7 mm in width, wider than long (W/L: 1.23–1.49), concavoconvex, geniculate, mucronate, semi-elliptical in outline. Ventral valve of variable convexity (ULv/L: 1.19–1.38) in lateral profile, geniculate; inflexion point located at about the half of ULv or more anteriorly in the case of more flattened valves; posterior margin slightly indented by umbo; posterior angle between 169°–176°; interarea flat, low (up to 2.8 mm), apsacline, vertically striated; pseudodeltidium flat to slightly convex. Dorsal interarea flat, more or less catacline, markedly less developed than the ventral one; chilidium flat. Ornamentation unequally parvicostellate (some costae of irregular width); at front, (5?) 6–7 costae per 5 mm separated from each other by 4–7 costellae; at dorsal valve, costae less distinct from costellae.

Ventral interior (Fig. 7) with ventral process displaying internal cavity and not in continuity with relatively prominent and short myophragm; hinge line denticulate; muscle field bounded posterolaterally by prominent ridges. Dorsal interior (Fig. 7) with bilobed cardinal process; lobes posteroventrally oriented; socket ridges parallel and adjacent to cardinal process lobes; muscle field bounded by two ridges originating anteriorly to cardinal process; anderidia located in anterior part of muscle field and separate by thin median ridge.

TABLE 1—Dimensions in mm of selected specimens of *Nervostrophia (Ailostrophia*?) sp. For abbreviations, see text.

IRScNB	W	L	T	ULv
a12404	22.9	17.7	5.35	21
a12405	22.3	15.6	6.4	19
a12406	19.3	15.7	7	22
a12407	23.7	16	4.6	20
a12408	21.5	15.3	5.3	19
a12409	22.2	16	/	19
a12410	22.6	15.2	6.1	21

Material examined.—Nine articulated specimens from locality BM-2003-10; seven articulated specimens from locality JG-1995-4; 51 articulated specimens, four ventral and two dorsal valves from locality Couvin 6158p.

Measurements.—See Table 1.

Occurrence.—*Nervostrophia* (*Ailostrophia*?) sp. is recognized within the Grands Breux Formation (Boussu-en-Fagne Member; *hassi* to Lower *rhenana* zones) and in the lower part of the Neuville Formation (Lower *rhenana* Zone) at the southern border of the Dinant Synclinorium.

Discussion.—No dissociated valve of this species has been collected, so it was not possible to corroborate the observations from the transverse serial sections. It is highly probable that the internal morphology of the dorsal valve is more complex than the one described above. The clearly concavoconvex profile of numerous shells, as well as the unequally parvicostellate ornamentation, lead me to assign them to the subgenus *Ailostrophia* [considered as such by Cocks and Rong (2007)], though the internal characters of the ventral valve display more affinities with those of *Timanostrophia* Alekseeva, 2003. Further investigation is needed to resolve this problem of generic and specific assignments.

Genus Gamphalosia Stainbrook, 1945

Type species.—*Gamphalosia tenuissima* Stainbrook, 1945.

Gamphalosia sp.

Figure 6.2–6.7

Description.—Shell small-sized (up to 20 mm in width), wider than long (W/L: 1.20–1.29), slightly resupinate, semi-elliptical in outline; maximum width near posterior margin; cardinal extremities mucronate. Ventral valve

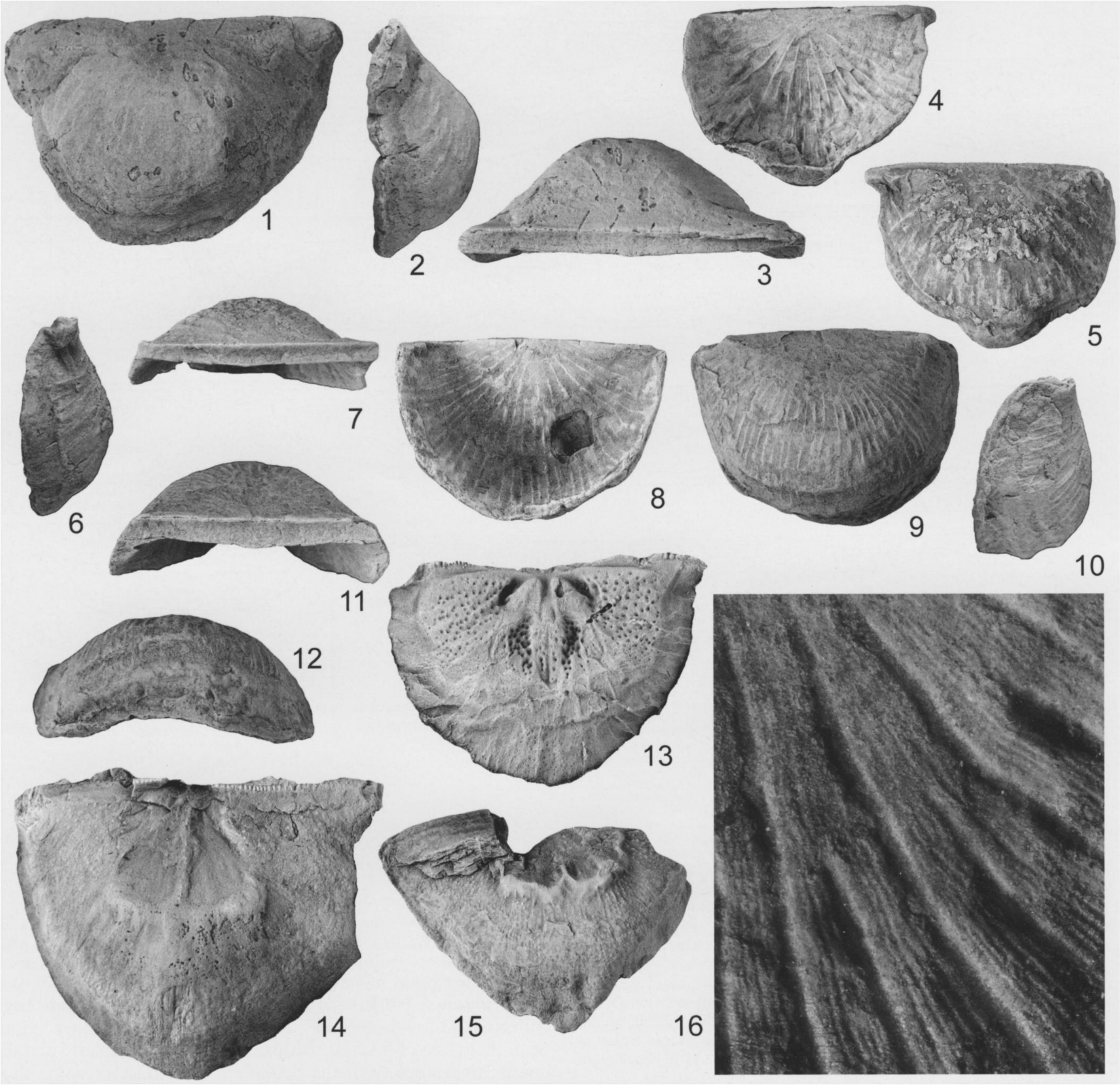

FIGURE 8—*1–16*, *Retrorstrophia retrorsa* (Kayser, 1881) from Barvaux Formation: *1–3*, dorsal, lateral, and posterior views of IRScNB a12413 (Durbuy 5337); *4–7*, ventral, dorsal, lateral, and posterior views of IRScNB a12414 (Durbuy 5337); *8–12*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12415 (Durbuy 5337); *13*, internal mould of dorsal valve IRScNB a12418 (BM-2002-4); *14*, internal view of ventral valve IRScNB a12417 (BM-2002-4); *15*, internal view of an incomplete ventral valve IRScNB a12416 (Durbuy 5337); *16*, detail of ornament on ventral valve of IRScNB a12477 (Durbuy 5337). *13, 14*, ×3; *16*, ×15; others, ×2.

with weakly convex posterocentral area on the contrary to lateral and anterior ones; sulcus weak, originating in the anterior half of the valve and producing a slight undulation of anterior commissure; posterior margin almost rectilinear; umbo hardly developed; interarea low, flat, apsacline, vertically striated; delthyrium not observed. Dorsal valve flat but convex at proximity of lateral and anterior margins; interarea low, anacline, flat, vertically striated. Ornamentation unequally parvicostellate (Fig. 6.7); rugae absent; 5 costae (sometimes of irregular width) per 5 mm separated from each other by 2–7 costellae at front; costellae more pronounced on ventral valve.

Ventral interior (Fig. 6.3) with hinge line denticulate; internal surface granulose; muscle field subtriangular, excavated, delimited in its posterior part by two short and rounded ridges; myophragm prominent whose length does not exceed the half length of the muscle field. Dorsal interior unobserved.

Material examined.—Two articulated specimens and one ventral valve from locality BM-2002-4; two articulated specimens and two ventral valves from locality Durbuy 5337.

Occurrence.—*Gamphalosia* sp. occurs in the Barvaux Formation (south-eastern flank of the Dinant Synclinorium; Upper *rhenana* Zone). Moreover, badly preserved specimens of unidentified species of *Gamphalosia* have been collected within the middle part of the Aisemont Formation (Lower *rhenana* Zone) on the southern border of the Namur Synclinorium (BM-2001-1).

Discussion.—This species displays a less nervate ornamentation than shown by North American species, which brings it closer to European taxa such as *Gamphalosia gosseleti* (Rigaux, 1873) reviewed by Brice (1988) and *G. arbizui* García-Alcalde, 1973. Its specific assignment requires additional material.

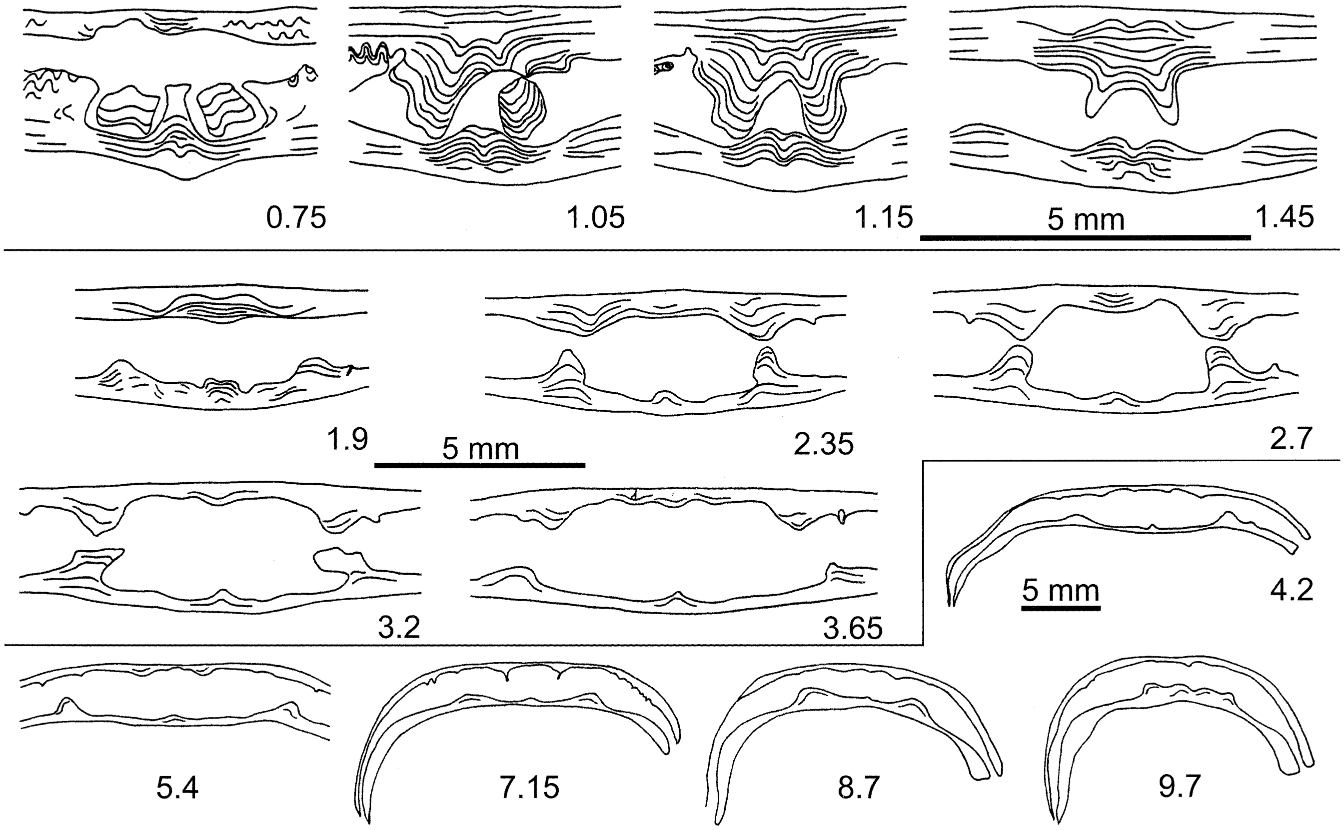

FIGURE 9—Transverse serial section of *Retrorstrophia retrorsa*. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12423 from locality Durbuy 5337 (Barvaux Formation). Dimensions of specimen: width (23.7) mm; length 16.1 mm; thickness 8.3 mm.

Family ?LEPTOSTROPHIIDAE Caster, 1939
Genus RETRORSTROPHIA new genus

Type species.—*Leptaena retrorsa* Kayser, 1881 by monotypy.

Diagnosis.—Shell medium-sized, resupinate, strongly geniculate and mucronate. Ornamentation unequally parvicostellate (of similar strength in both valves), without rugae; ventral area low, flat, apsacline; pseudodeltidium flat; dorsal interarea low, flat, anacline; chilidium flat; hinge line almost entirely denticulate; ventral muscle field bilobed, divided by myophragm, generally completely bounded by ridges; dorsal muscle field laterally bounded by two prominent and divergent ridges with median ridge in its posterior part; anterior part with anderidia and thin median ridge.

Etymology.—From "*retrorsus*," Latin, meaning turned, referring to the type species.

Occurrence.—Lower and Upper *rhenana* zones (late Frasnian), Aachen area (Germany) and Namur-Dinant Basin (Belgium).

Discussion.—*Retrorstrophia* is placed tentatively in the Leptostrophiidae on the basis of its affinities with the genus *Gamphalosia* assigned to this family by Cocks and Rong (2000). The ornamentation of *Retrorstrophia* is close to that of *Gamphalosia* Strainbrook, 1945 although, in the latter, weak rugae are developed sporadically. Nevertheless, the new genus displays a strongly resupinate and geniculate shell, flat pseudodeltidium and chilidium, as well as a ventral muscle field with markedly muscle-bounding ridges. *Retrorstrophia* is reminiscent of *Strophonelloides* Caster, 1939 (Strophodontidae) of the Frasnian of North America by its resupinate shell, but this latter displays a costellate ornamentation and differs in its internal morphology.

TABLE 2—Dimensions in mm of selected specimens of *Retrorstrophia retrorsa*. For abbreviations, see text.

IRScNB	W	L	T	ULd
a12413	27.5	18	9	25
a12414	19.8	15.3	6.9	18
a12419	25	13.5	5.4	16
a12420	15.3	11.8	5.8	14
a12421	17.4	13	5.7	16
a12422	21	13.6	5.4	15

RETRORSTROPHIA RETRORSA (Kayser, 1881)
Figures 8, 9; Table 2

Leptaena retrorsa KAYSER, 1881, p. 335, pl. 19, fig. 5.

Description.—Shell reaching 27.5 mm in width, resupinate, strongly geniculate, wider than long (W/L: 1.22–1.85), semi-elliptical in outline, more or less transversally stretched; anterior margin rounded or weakly flattened; lateral margins drawing acute to right angles with the hinge line; cardinal extremities mucronate (up to 10 mm long); geniculation occurring between 35 to 63% of the ULd measured from the posterior margin. Ventral valve with almost rectilinear posterior margin; posterior margin hardly indented by the umbo; posterior angle between 169°–176°; interarea flat, apsacline, vertically striated; pseudodeltidium flat. Dorsal valve (ULd/L: 1.06–1.47) with rectilinear posterior margin; interarea flat, anacline, vertically striated, about 2 times less high than the ventral one; chilidium flat. Ornamentation unequally parvicostellate (Fig. 8.16); costellae can thicken so much that they become as large as the costae at the anterior margin (in some cases, it may be the result of the fusion of two costellae); at front, 4–8 costae per 5 mm separated from each other by 2–5 costellae; in some cases, costae get thinner anteriorly; growth lamellae rare, irregularly spaced.

Ventral interior (Figs. 8.14, 8.15, 9) with ventral process devoid of internal cavity and in continuity with the myophragm; muscular field bilobed, elevated, divided by myophragm, entirely delimited by muscle-bounding ridges. Dorsal interior (Figs. 8.13, 9) with lobes of the cardinal process posteroventrally oriented; median ridge developed in the posterior half of the muscle

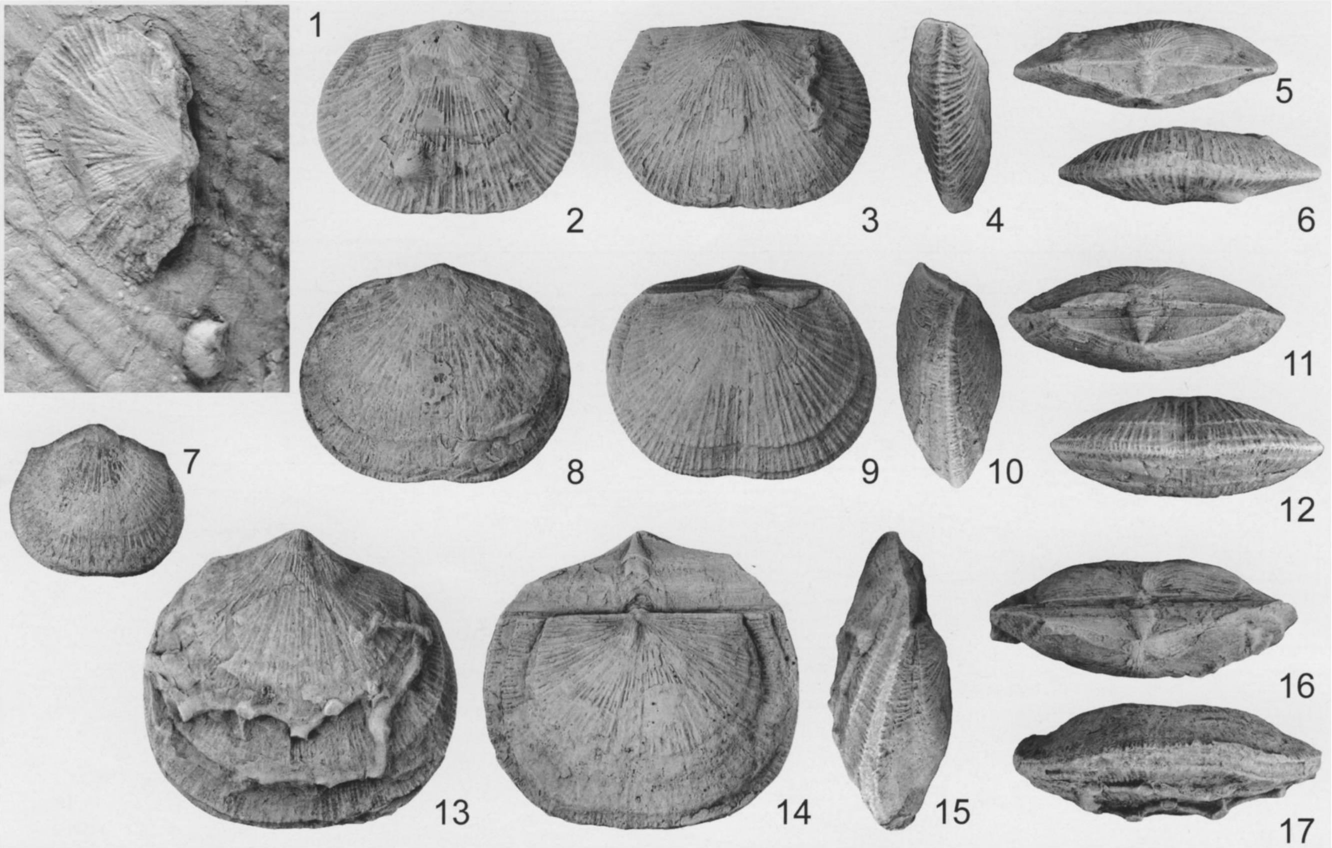

FIGURE 10—*1*, *Schuchertellopsis* (*Schuchertellopsis*) *durbutensis* Maillieux, 1939, from locality Durbuy 5337 (Barvaux Formation): dorsal view of IRScNB a12424b in sulcus of *Cyrtospirifer* sp. nov.; *2–17*, *Floweria pseudoelegans* (Gosselet, 1877) from the Famenne Group ("Senzeille Formation"): *2–6*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12426 (Senzeille 6839b); *7*, ventral view of IRScNB a12425 (Senzeille 6839b); *8–12*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12427 (Senzeille 6839b); *13–17*, ventral, dorsal, lateral, posterior, and anterior views of ULg 2007.02.04 (Senzeille 202). *1*, ×3.5; others, ×1.5.

field originating at the base of the cardinal process with its anterior extremity bifurcating; anteriorly to this median ridge, begins another one clearly thinner and dividing the anterior part of the muscle field; length of the muscle field comprised between the third and the half of the ULd; two prominent and divergent ridges originating at the base of the cardinal process delimit laterally the muscle field; anderidia developed in the anterior part of the muscular field.

Material examined.—One dorsal valve from locality BM-2001-1; 14 articulated specimens from locality BM-2001-2; one articulated specimen from locality BM-2002-1; 25 articulated specimens, two ventral and two dorsal valves from locality BM-2002-4; two articulated specimens from locality BM-2002-5; one articulated specimen from locality BM-2002-6; five articulated specimens from locality BM-2003-3; four articulated specimens from locality BM-2003-4; two articulated specimens from locality BM-2004-1; two ventral valves from locality BM-2004-4; 179 articulated specimens and one ventral valve from locality Durbuy 5337.

Measurements.—See Table 2.

Occurrence.—*Retrorstrophia retrorsa* occurs in the Frasnian of the Aachen area (Germany) where its precise stratigraphic range remains unknown. In the Namur-Dinant Basin, the species is widely distributed in the Upper *rhenana* Zone (especially within the Barvaux Formation) but it seems to appear in the Lower *rhenana* Zone (Aisemont Formation).

Discussion.—In spite of my efforts, the specimen figured by Kayser (1881, pl. 19, fig. 5) has not been found yet, but Kayser (1881, p. 336) signaled that *Leptaena retrorsa* is "Nicht selten in den schwarzen, dem älteren Oberdevon angehörigen Mergelschiefern von Stolberg bei Aachen, zusammen mit *Spirifer Verneuili*, *Rhynchonella cuboides* und *pugnus*, *Atrypa reticularis* etc. (. . .)." Klähn (1912, p. 12) mentioned that "*Str.* (=*Strophonella*) *retrorsa* ist sehr häufig in der Frasne-Schiefern und deren Kalkschiefereinlagerungen bei Schmidthof, Walheim, Hahn und Breiniger Berg;" these localities are situated in the Aachen area. The study of specimens of Holzapfel's collection mentioned by Klähn (1912) and housed at the ULP revealed that the Belgian specimens cannot be distinguished from these ones.

Order ORTHOTETIDA Waagen, 1884
Suborder ORTHOTETIDINA Waagen, 1884
Superfamily ORTHOTETOIDEA Waagen, 1884
Family SCHUCHERTELLIDAE Williams, 1953
Subfamily SCHUCHERTELLINAE Williams, 1953
Genus SCHUCHERTELLOPSIS Maillieux, 1939
Subgenus SCHUCHERTELLOPSIS (SCHUCHERTELLOPSIS) Maillieux, 1939

Type species.—*Schuchertellopsis durbutensis* Maillieux, 1939.

SCHUCHERTELLOPSIS (SCHUCHERTELLOPSIS) DURBUTENSIS Maillieux, 1939
Figure 10.1

Schuchertellopsis durbutensis MAILLIEUX, 1939, p. 5, figs. 1–6.

Schuchertellopsis (*Schuchertellopsis*) *durbutensis* WILLIAMS AND BRUNTON, 2000, p. 667, fig. 480.5a–c; LONG AND BRUNTON, 2005, figs. 1a,b, 2, 4, 5-15; BRUNTON, 2007, p. 2674, fig. 1782.a–b.

Material examined.—One articulated specimen from locality BM-2002-4.

Occurrence.—In the Namur-Dinant Basin, this rare species occurs in the Upper *rhenana* Zone (Barvaux Formation).

Discussion.—This small species, which is characterized by its ventral valve cemented almost completely to a cyrtospiriferid shell, was originally described by Maillieux (1939) on the basis of specimens from the Barvaux Formation. Its shell structure was thoroughly studied by Long and Brunton (2005).

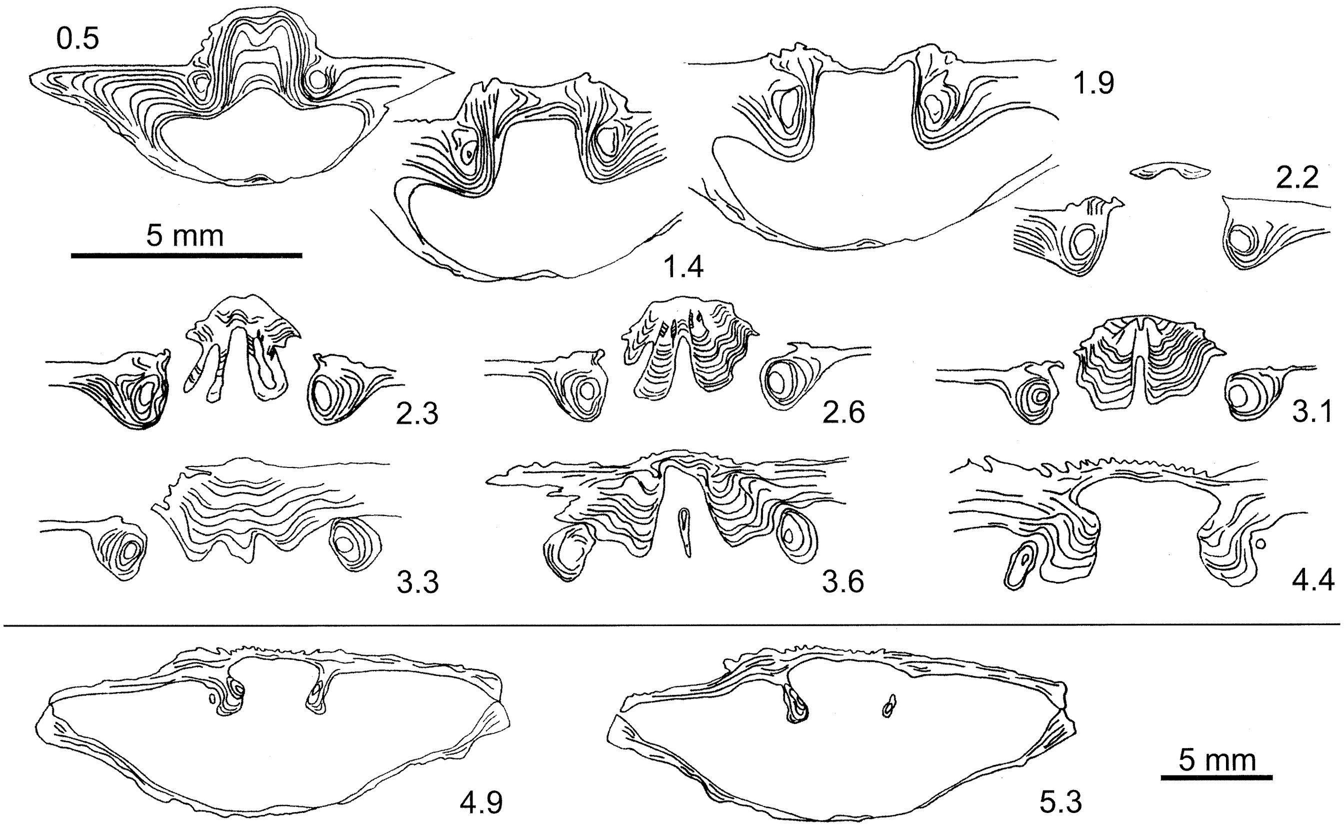

FIGURE *11*—Transverse serial sections of *Floweria pseudoelegans*. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12428 from locality Senzeille 6839b (Famenne Group: "Senzeille Formation"). Dimensions of specimen: width 27.2 mm; length 26 mm; thickness 11.4 mm.

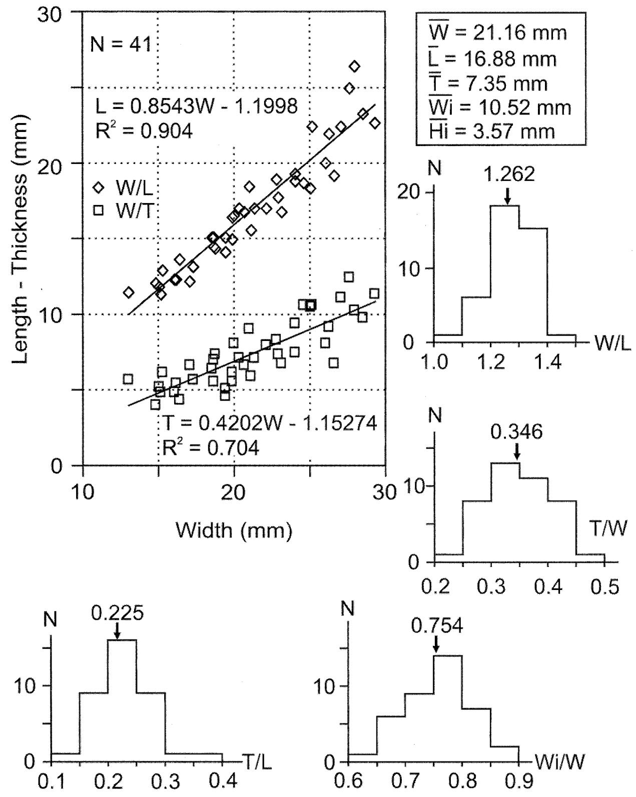

FIGURE *12*—*Floweria pseudoelegans*. Scatter diagrams of shell width to shell length, shell width to shell thickness; frequency diagrams of W/L, T/W, T/L, and Wi/W. Arrows = means.

Superfamily CHILIDIOPSOIDEA Boucot, 1959
Family AREOSTROPHIIDAE Manankov, 1979
Subfamily ADECTORHYNCHINAE Henry and Gordon, 1985
Genus FLOWERIA Cooper and Dutro, 1982

Type species.—*Orthis prava* Hall, 1858.

FLOWERIA PSEUDOELEGANS (Gosselet, 1877)
Figures 10.2–10.17, 11, 12

Orthis pseudo-elegans GOSSELET, 1877, p. 319, pl. 4, fig. 10a,b.

Description.—Shell reaching 29.3 mm in width, wider than long (W/L: 1.06–1.40), ventribiconvex, oval to subquadrate in outline (Wi/W: 0.64–0.89); lateral margins rounded; anterior border straight; maximum width at about mid-length; cardinal angles generally rounded, but some specimens with poorly developed ears; anterior commissure rectimarginate or slightly undulose. Ventral valve regularly convex in lateral profile; in some cases, its anterior part is flattened while its posterior one is convex (however, profile not resupinate); very slight median depression sometimes developed close to anterior margin; umbonal area frequently distorted, with cementation traces and koskinoid perforations; posterior margin indented; posterior and apical angles varying between 132°–165° and 107°–121° respectively; interarea triangular, variably high (Hi/Wi: 0.14–0.35), apsacline, flat but curved at its top due to the beak curve; pseudodeltidium convex. Dorsal valve wider than long (W/dL: 1.3–1.5), almost flat or convex (posterolateral extremities generally flat), roughly semi-elliptical in outline; slight median depression occurring sometimes in the anterior part of the valve and extending towards the front; interarea linear; chilidium sometimes with a slight median groove. Ornamentation parvicostellate; 3–4 costae and costellae per mm at anterior margin (curved close the posterolateral extremities); filae very fine (± 31/mm), some thickened at irregular intervals.

Ventral interior (Fig. 11) with teeth rounded in section, unsupported by dental plates; muscle field poorly defined and divided by a myophragm. Dorsal interior (Fig. 11) with cardinal process lobes low, grooved medially; socket ridges recurved; muscle field badly defined in its anterior part, divided by myophragm extending up to the half of ULd.

Material examined.—Two articulated specimens from locality BM-2001-3; one ventral valve from locality BM-2001-5; one dorsal valve from locality BM-2002-1; three ventral valves from locality BM-2002-6; 10 articulated

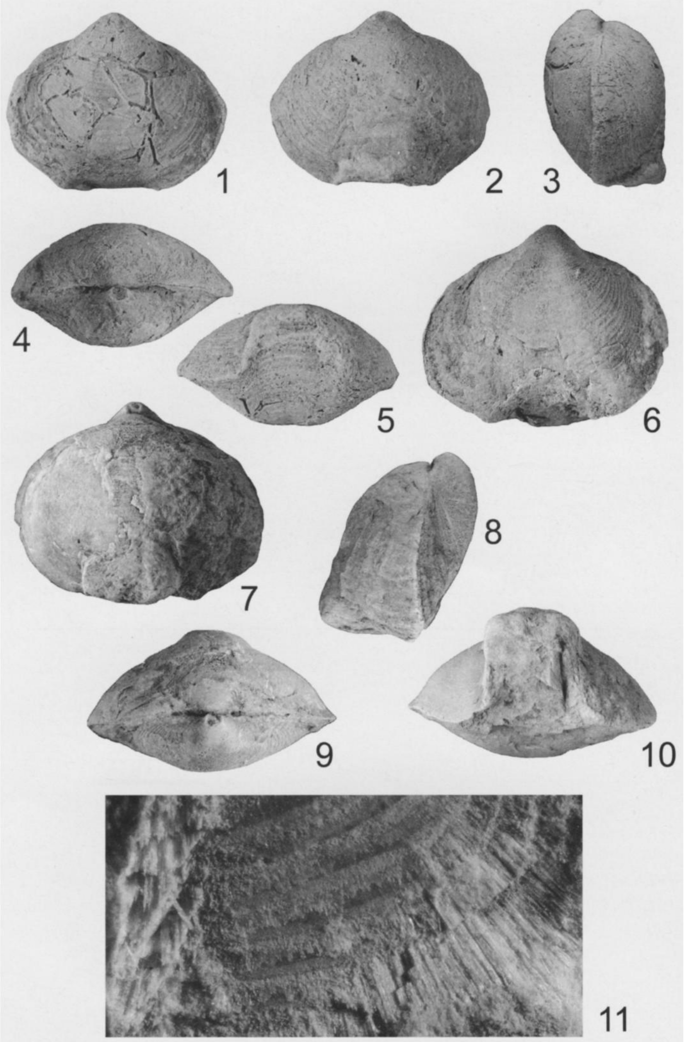

FIGURE 13—*1–11*, *Cleiothyridina davidsoni* (Rigaux, 1873) from locality BM-2003-2 (Famenne Group: "Senzeille Formation"): *1–5*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12265; *6–10*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12266; *11*, detail of ornament on dorsal valve of IRScNB a12478. *11*, ×15; others, ×2.

specimens and two dorsal valves from locality BM-2003-2; 45 articulated specimens from locality, one ventral and one dorsal valves from locality Senzeille 6839; 11 articulated specimens from locality Senzeille (ULg).

Measurements.—See Figure 12.

Occurrence.—In the Namur-Dinant Basin, the species occurs within the lower part of the Famenne Group ("Senzeille Formation") as within the Famennian part of the Lambermont Formation, i.e., in the Lower (?)/Middle *triangularis* Zone.

Discussion.—This species is referred to *Floweria* rather than to the related genus *Eoschuchertella* Gratsianova, 1974 for the following reasons: general look, shell rarely strongly ventribiconvex, thin costae increasing by bifurcation, cementation cicatrix, and lobes of the cardinal process grooved posteriorly. Koskinoid perforations have been observed in the specimens of *F. prava* (Hall, 1858), *F. magnacicatrix* Cooper and Dutro, 1982, and *F. transversalis* Cooper and Dutro, 1982 which have been figured by Cooper and Dutro (1982) and housed at the USNM. Till now, the types of *F. pseudoelegans* have not been found in the collections of the MGL. *F. pseudoelegans* has been misidentified with *Orthotetes consimilis* de Koninck, 1882 of uncertain generic position by Maillieux (1941, p. 6) and Bultynck and Martin (1995, p. 9) but it differs from it in its smaller size, its more inflated shell and its well-developed triangular interarea.

Order ATHYRIDIDA Boucot, Johnson, and Staton, 1964
Suborder ATHYRIDIDINA Boucot, Johnson, and Staton, 1964
Superfamily ATHYRIDOIDEA Davidson, 1881
Family ATHYRIDIDAE Davidson, 1881
Subfamily CLEIOTHYRIDININAE
Alvarez, Rong, and Boucot, 1998
Genus CLEIOTHYRIDINA Buckman, 1906

Type species.—*Atrypa pectinifera* J. de C. Sowerby, 1840 *in* 1840–1846.

CLEIOTHYRIDINA DAVIDSONI (Rigaux, 1873)
Figures 13, 14

Spirigera Davidsoni RIGAUX, 1873, p. 48, fig. 10a–c.
e.p. *Athyris Davidsoni* RIGAUX, 1908, p. 13, non pl. 1, fig. 3 (=*Athyris oehlerti* Rigaux, 1908); BRICE, 1988, p. 352, pl. 43, figs. 1, 3, 4, non pl. 43, fig. 2 (=*A. oehlerti*) (complete synonymy from the Boulonnais region (northern France) up to 1988).

Description.—Shell small-sized for the genus (up to 16.4 mm wide), rounded to elliptic in outline, generally wider than long (W/L: 0.92–1.38), dorsibiconvex; in ventral view, anterior margin rounded to slightly emarginate; anterior commissure uniplicate to parasulcate; anterolateral commissures sometimes slightly ventrally deflected. Ventral valve with flanks sloping gently towards the lateral commissures; anterolateral part of the valve flattened in some specimens; umbo prominent; beak slightly curved; small permesothyrid foramen; sulcus wide at front (Ws/W: 0.37–0.62), originating at about midvalve or more posteriorly, with a flattened bottom, sometimes delimited anteriorly by rounded crests; tongue 0.98–1.55 times wider than high, U-shaped, perpendicular or nearly perpendicular to the commissural plane; posterior and apical angles between 111°–129° and 80°–105° respectively; palintropes small and poorly defined. Dorsal valve highest at the front or about midvalve from where it curves progressively or maintains its height towards the anterior margin (sometimes its upper surface curves before standing up again sharply near the front); fold originating at about midvalve, with a relatively flat top, moderately high. In the plane of symmetry of adult specimens, the distance between two successive growth lamellae is about 0.5 mm. They are more closely spaced anteriorly and anterolaterally. Growth lamellae projecting anteriorly and anterolaterally as flat, solid spine-like outgrowths (rarely observed) (Fig. 13.11).

Ventral interior (Fig. 14) with dental plates converging dorsally, short, somewhat thickened in their posterior part and supporting small and subrectangular teeth in transverse section; apical cavities relatively wide; thin lens of prismatic calcite occurring within the fibrous shell, in the median part of the valve. Dorsal interior (Fig. 14) with cardinal plate pierced apically by a dorsal foramen; inner hinge plates ventrally concave, conjunct, with a low median ridge, projecting anteriorly further than reduced outer hinge plates; cardinal flanges developed; dental sockets shallow; myophragm short; brachidium not preserved in the sectioned specimen.

Material examined.—Seventy complete specimens from locality BM-2003-2.

Measurements (in mm).—Width range 7.8–16.4, average 11.7 (N = 51); length range 7.2–13.1, average 9.8 (N = 51); thickness range 4.0–9.4, average 6.7 (N = 51); width of sulcus range 4.7–8.5, average 6.3 (N = 34).

Occurrence.—*Cleiothyridina davidsoni* has been recovered from the basal part of the Famenne Group (Lower (?)/Middle *triangularis* zones) at Senzeille, but it occurs also in the Neuville Formation (Lower *rhenana* Zone) at the southern border of the Dinant Synclinorium (Mottequin, 2005). No specimen has been collected within the Matagne and the Les Valisettes formations of late Frasnian age (Upper *rhenana* and *linguiformis* zones). The species was originally described in the Boulonnais region (northern France). According to Brice (1988), the range of this taxon in the latter, in terms of conodont zones, spans the interval of the Middle/Upper *varcus* zones to the *Ancyrognathus triangularis* Zone.

Discussion.—The presence of thin spine-like outgrowths projecting from the growth lamellae and the type of cardinalia led me to assign *Spirigera davidsoni* Rigaux, 1873 to *Cleiothyridina* rather than to *Athyris* M'Coy, 1844. Brice (1988) also reported that the growth lamellae bear numerous thin spines at their distal extremity in topotypical material of Rigaux's species but assigned it to *Athyris*. The specimen identified as *Athyris davidsoni* by Rigaux (1908, pl. 1, fig. 3) and designated as a paralectotype by Brice (1988) displays widely spaced growth lamellae; that leads me to assign it rather to *A. oehlerti* Rigaux, 1908. Moreover, Brice (1988) considered this specimen as exceptional because of the unusual development of its sulcus ridges. The specimens presently

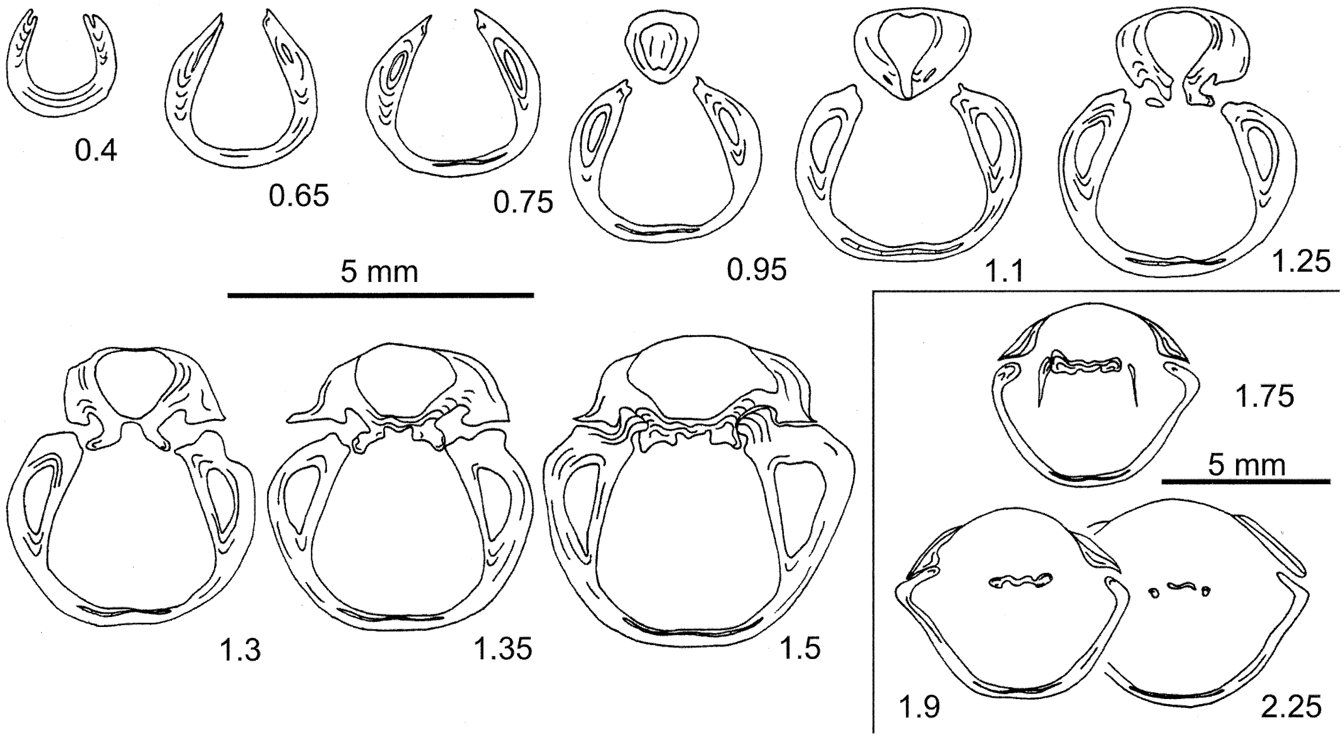

FIGURE *14*—Transverse serial sections of *Cleiothyridina davidsoni.* Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12267 from locality BM-2003-2 (Famenne Group: "Senzeille Formation"). Dimensions of specimen: width (12.9) mm; length 10.9 mm; thickness 7.3 mm.

studied may correspond to those reported by Gosselet (1877) as *Spirigera concentrica* var. *sparsilamella.*

Genus CRINISARINA Cooper and Dutro, 1982

Type species.—*Crinisarina stainbrooki* new name pro *Cleiothyridina reticulata* Stainbrook, 1947 (see below).

Discussion.—Gosselet (1877) described *Spirigera reticulata* based on specimens from the former Senzeille railway section, which is now filled in (Sartenaer, 1960; Bultynck and Martin, 1995). He defined three varieties within the species: *Spirigera reticulata* var. *depressa*, *S. reticulata* var. *gibbosa*, and *S. reticulata* var. *carinata*. Only *S. reticulata* var. *carinata* was figured by Gosselet (1877, pl. 3, fig. 3, 1880, pl. 5, fig. 6) and later by Asselberghs (1912, pl. 1, fig. 15). According to the ICZN (4th edition, art. 45.6.1), Gosselet's varieties have only an infrasubspecific rank because he did not define a type variety. If he had clearly indicated a type variety (e.g., *Spirigera reticulata* typus), his varieties would have been considered as subspecies.

Asselberghs (1912), because he did not consider the presence of "ornements radiaires (sic)" (i.e., the spines) as a specific character, transferred the variety *depressa* as well as several of the specimens identified as *Spirigera reticulata* var. *gibbosa* to *Athyris concentrica* (Murchison, 1840) non Von Buch, 1834 (=*A. murchisoni* Brice, 1988). The others were placed in *A. davidsoni* (Rigaux, 1873). He maintained the variety *carinata* and promoted it to specific rank. Asselberghs' position is unacceptable because he discarded Gosselet's species, whereas it is possible to define it on the basis of the lectotype indicated hereafter.

Study of the lectotype and identical specimens shows that *Spirigera reticulata* Gosselet, 1877 belongs to *Crinisarina*, as previously suggested by Baliński (2002). Therefore, *C. reticulata* (Stainbrook, 1947) is a secondary homonym for which a new name must be proposed, namely *Crinisarina stainbrooki* nom. nov. A new name is also proposed for *Athyris reticulata* Chen and Xu, 2000, which is assigned here to *Crinisarina*: *Crinisarina shashishanensis* nom. nov. Re-examination of *C. reticulata* (Gosselet, 1877) led to the recognition of the additional taxa *C. angelicoides* (Merriam, 1940) and *C. stainbrooki* nom. nov. within the early Famennian succession of the Namur-Dinant Basin.

In the case of well-preserved specimens of *Crinisarina* (e.g., *C. angelicoides*, Fig. 18.6–18.15), the radially-aligned spines give the shell a reticulate appearance. *Athrythyris* Struve, 1965 also displays a similar appearance resulting from radial ornamentation close to that observed in some atrypids (Alvarez and Rong, 2002) and not from spines, which are absent in the latter.

CRINISARINA RETICULATA (Gosselet, 1877) emend.
Figures 15, 16, 17

Spirigera reticulata nov. sp. var. *Carinata* GOSSELET, 1877, p. 312, pl. 3, fig. 3.
Spirigera reticulata GOSSELET, 1880, pl. 5, fig. 6, 6a,b.
Athyris carinata ASSELBERGHS, 1912, p. 16, pl. 1, fig. 15.

Description.—Shell of normal size for the genus, reaching about 22 mm in width, wider than long (W/L: 1.02–1.54) and dorsibiconvex (Tv/Td: 0.67–0.91), rounded subpentagonal in outline (more or less transversally stretched with the anterior margin deeply excavated; accentuated bilobed outline), widest about midvalve or more anteriorly; anterior commissure uniplicate to parasulcate. Ventral valve with upper surface corresponding to the upper part of a trapezium whose median part is more or less excavated by the sulcus in posterior view; upper surface of the flanks plane to convex; umbo prominent, beak curved; foramen permesothyrid; sulcus wide at front (Ws/W: 0.53–0.74), originating close to the umbo, subangular, clearly defined, deep to very deep; subtriangular tongue 0.72–2.76 times wider than high, perpendicular to the commissural plane, indeed bent dorsally; posterior and apical angles between 85°–135° and 72°–118°, respectively; palintropes concave and little high. Dorsal valve elliptical to subpentagonal in outline; upper surface of the flanks plane to convex, flanks sloping moderately towards the lateral commissure; fold usually high, originating at about midvalve, like the upper part of a hull; mostly, maximal height at or close to the anterior margin. Shell covered by imbricate, very close growth lines projecting anteriorly and anterolaterally as flattened, radially-aligned solid spines (Fig. 15.16).

Ventral interior (Fig.16) with thin, short dental plates more or less arched depending on specimens, supporting cyrtomatodont teeth that are subrectangular in transverse section; lateral apical cavities moderately developed. Dorsal interior (Fig. 16) with conjunct, ventrally concave inner hinge plates; outer

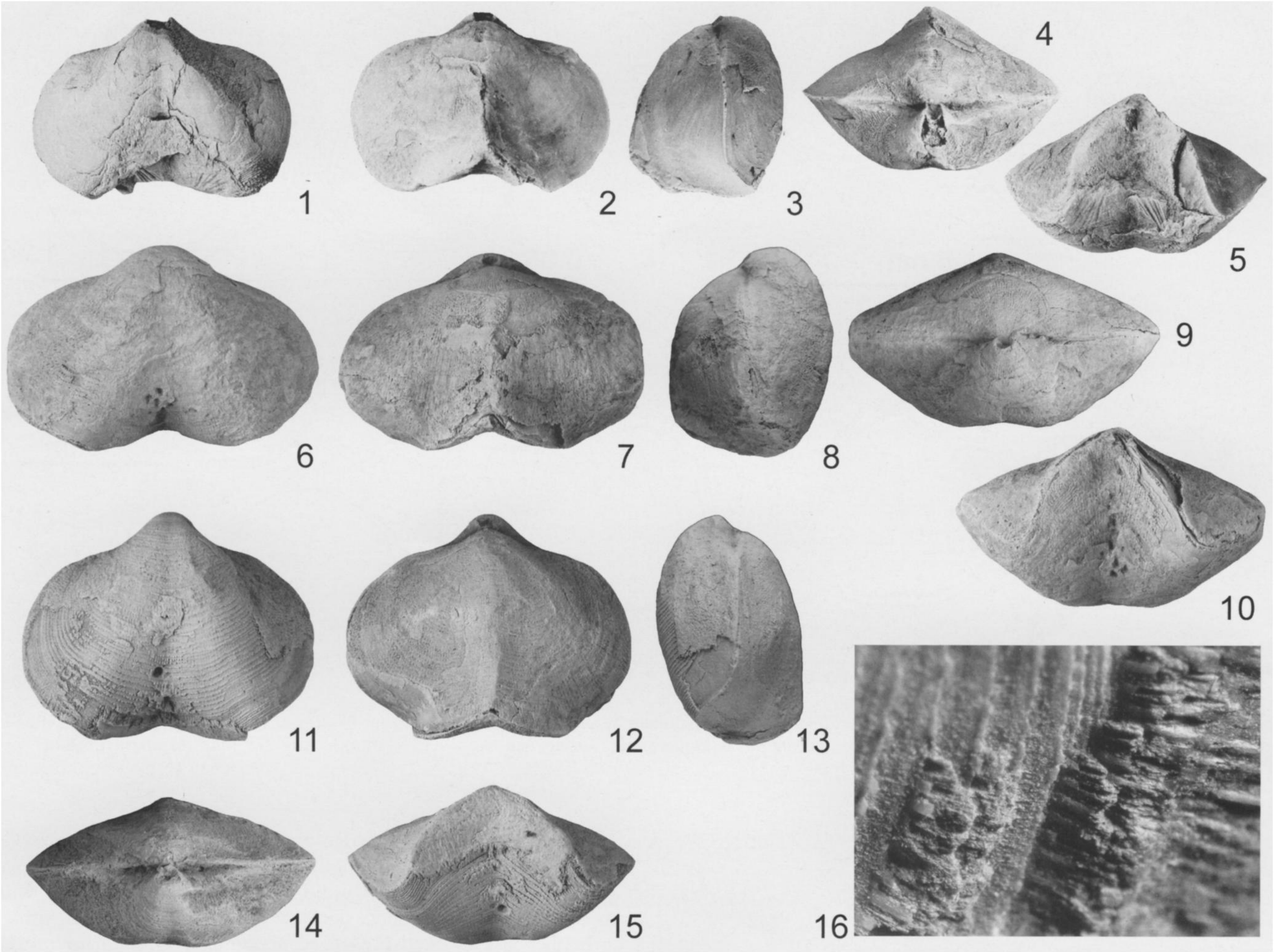

FIGURE *15*—*1–16*, *Crinisarina reticulata* (Gosselet, 1877) from Famenne Group ("Senzeille Formation"): *1–5*, ventral, dorsal, lateral, posterior, and anterior views of MGL 29165 (lectotype) from the old Senzeille railway section; *6–10*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12268 (BM-2003-2); *11–16*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12269 (BM-2003-2) and detail of ornament on ventral valve. *16*, ×15; others, ×2.

hinge plates ventrally concave; cardinal flanges developed; dorsal foramen not observed; internal crests of the dental sockets moderately developed; myophragm very short; spiral cones with at least 11 whorls (they rotated inside the shell due to the break of the crura).

Type.—The specimen figured by Gosselet (1877) originates from the former Charleroi-Vireux railroad cut situated south of Senzeille which is now filled in. It is designated here as the lectotype and is housed at the Musée d'Histoire naturelle de Lille where it bears the number MGL 29165 (Fig. 13.1–13.5). According to Gosselet (1877), the type horizon would correspond to his "Couches K" consisting of black shales with or without nodules. According to Sartenaer (1960, fig. 1), who revised the Senzeille section, the layers K (*Tenuisinurostrum crenulatum*, *Eoparaphorhynchus lentiformis* and *Ptychomaletoechia omaliusi* rhynchonellid zones) are comprised between 220–355 m measured from the SE flank of the "pont rouge." Nevertheless, after the examination of the material collected by P. Sartenaer in this outcrop, it appears that the species is absent in these layers (see also Occurrence, below).

Material examined.—Nine articulated specimens from locality BM-2001-5; three articulated specimens from locality BM-2002-1; 98 articulated specimens and two ventral valves from locality BM-2003-2.

TABLE *3*—Dimensions in mm of selected specimens of *Crinisarina angelicoides*. For abbreviations, see text.

IRScNB	W	L	T	Ws	Ht
a12271	22.6	17.9	18.8	10.35	8
a12272	22	18	17.9	10.8	10.3
a12273	21.9	18.7	15.8	11.4	6.6
a12274	16.6	15.3	14.2	8.4	7.7
a12275	20.9	15.6	13.5	9.2	8.1

Measurements.—See Figure 17.

Occurrence.—*Crinisarina reticulata* is recognized in the lower part of the Famenne Group as well as in the Famennian part of the Lambermont Formation. The species is abundant on the southern flank of the Dinant Synclinorium (Senzeille), but it is clearly less frequent on its southeastern flank and in the Vesdre area. The specimen figured by Asselberghs (1912) would have been collected within the Frasnian of the Sautour area (Philippeville Anticlinorium) with "*Rhynchonella cuboides*, *Spirifer Verneuili*, *Atrypa aspera*." This aberrant assemblage results certainly from a mixing of Frasnian and Famennian specimens from various localities.

Discussion.—*Crinisarina reticulata* differs externally from all other species included presently in the genus *Crinisarina* in its bilobed outline in ventral view, its subtriangular tongue and its hull-shaped fold.

CRINISARINA ANGELICOIDES (Merriam, 1940)
Figures 18, 19, Table 3

Athyris angelicoides MERRIAM, 1940, p. 84, pl. 10, figs. 1–4.

Description.—Shell of normal size for the genus, reaching 22.6 mm in width, generally wider than long (W/L: 0.96–1.31), dorsibiconvex to ventribiconvex (Tv/Td: 0.89–1.21), very globose, rounded subpentagonal in outline with anterior margin moderately to strongly emarginate; anterior commissure sharply parasulcate. Ventral valve with upper surface drawing the upper part of a trapezium whose top is excavated by the sulcus (in posterior view); flanks plane to moderately convex and sloping moderately to sharply towards the

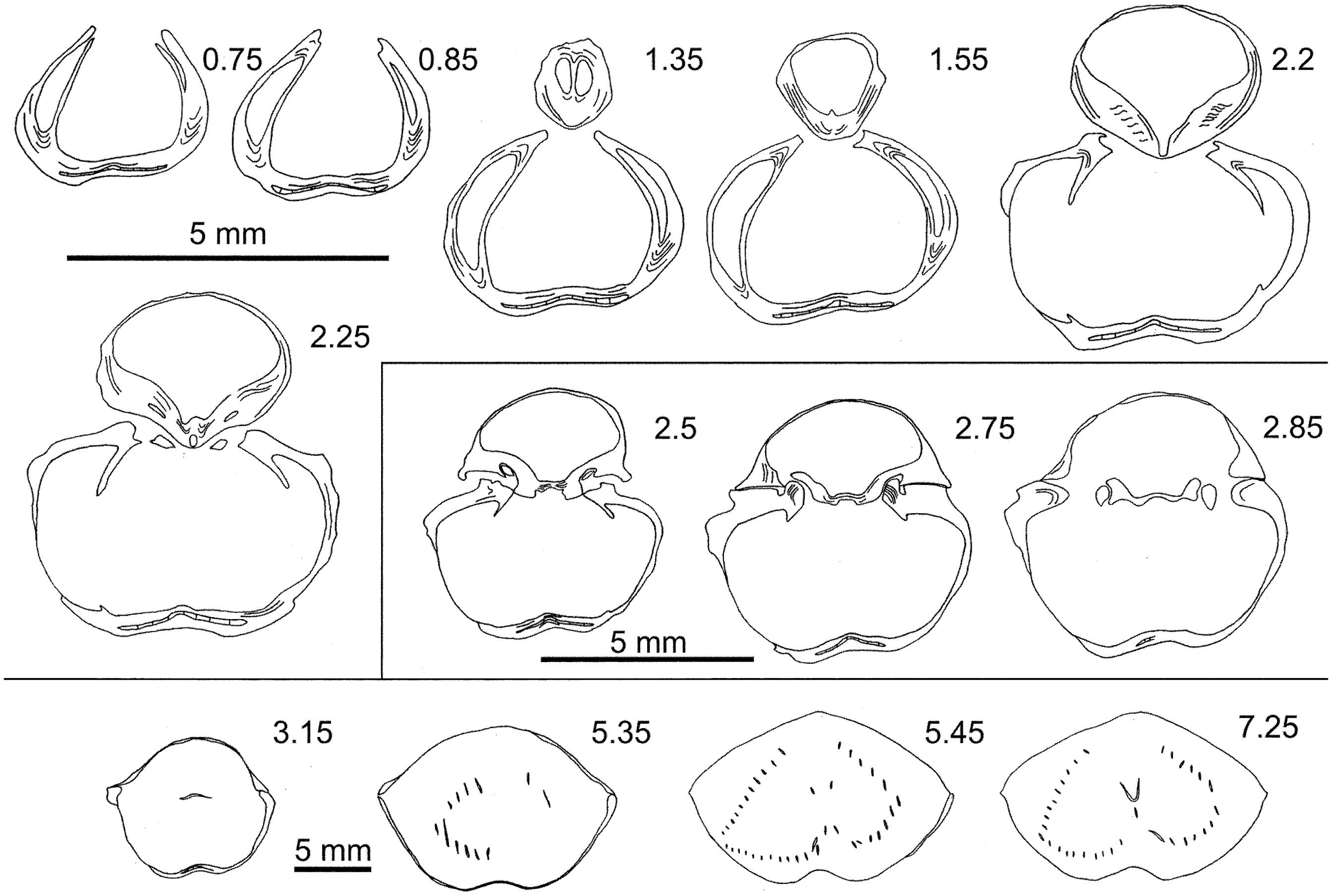

FIGURE *16*—Transverse serial sections of *Crinisarina reticulata*. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12270 from locality Senzeille 6839b (Famenne Group: "Senzeille Formation"). Dimensions of specimen: width 18.0 mm; length 13.8 mm; thickness 11.7 mm.

lateral commissures; umbo prominent; beak curved, pierced by a permesothyrid to epithyrid (?) foramen; sulcus wide at front (Ws/W: 0.42–0.59), originating imperceptibly in the posterior part of the valve, close to the umbo, deepening rapidly, with flat to rounded bottom at the front and sharply defined by more or less strong bounding ribs; tongue 1.05–1.73 times wider than high, subtrapezoidal to semioval in outline, perpendicular to the commissural plane, bent dorsally; posterior and apical angles between 109°–122° and 98°–111°, respectively; palintropes well-defined. Dorsal valve with its upper surface defining a coarse semi-ellipse or semicircle whose median part is raised by the fold; fold of variable height, rounded to flattened at the front, originating at about midvalve or posteriorly to this, generally well-defined and, in some specimens, sharply defined by two lateral grooves; maximal height anterior to mid-length. Ornamentation similar to that of *Crinisarina reticulata* (see above; Fig. 18.19).

Ventral interior (Fig. 19) with short and thickened dental plates supporting cyrtomatodont teeth; lateral apical cavities strongly filled in; thin lens of prismatic calcite developed in the median part of the valve. Dorsal interior (Fig. 19) with nearly flat cardinal plate (it is difficult to differentiate inner and outer hinge plates); cardinal flanges developed; dorsal foramen not observed; internal crests of the dental sockets little, high; spiral cones with at least 7 whorls (not illustrated in Fig. 19).

Material examined.—Forty-nine articulated specimens from locality BM-2001-3; 11 articulated specimens from locality BM-2001-5; 82 articulated specimens from locality BM-2002-6.

Measurements.—See Table 3.

Occurrence.—According to Merriam (1940), *Crinisarina angelicoides* occurs within the *Cyrtospirifer* Zone of the Upper Devils Gate Formation (Nevada). In southern Belgium, *C. angelicoides* is confined to the base of the Famenne Group (south and south-eastern borders of the Dinant Synclinorium). In Poland, Baliński (2002) reported the species within the early Famennian from the Cracow area (lower part of the Lower *triangularis* Zone) and from the Holy Cross Mountains. In Alberta (Rocky Mountains), Day (in Whalen et al., 2002) mentioned *C.* cf. *C. angelicoides* in the basal Famennian (Sassenach Formation). More recently, Baliński (in Gischler et al., 2004) cited its presence in the Famennian (*triangularis* and *marginifera* zones) from the Harz Mountains (Germany). However, some specimens such as that figured (Baliński in Gischler et al., 2004, pl. 1, fig. 6) are sharply dorsibiconvex, which brings them to the forms placed in *Athyris*; moreover, the typical ornamentation of *Crinisarina* is not observable.

Discussion.—Most of the specimens identified by Gosselet (1877) as *Spirigera reticulata* var. *gibbosa* are placed in *C. angelicoides* in this paper. The latter differs from *C. reticulata* by the outline of its tongue and its globose appearance.

CRINISARINA STAINBROOKI new name
Figures 20, 21, 22

Cleiothyridina reticulata Stainbrook, 1947, p. 326, pl. 45, figs. 31–35; Johnson, Reso, and Stephens, 1969, p. 1362, text-fig. 5, pl. 159, figs. 1–26.

Crinisarina reticulata Cooper and Dutro, 1982, p. 92, pl. 26, figs. 31–51, pl. 45, figs. 1–15; Alvarez and Rong, 2002, p. 1510, pl. 1025, fig. 4a–k [copy of Cooper and Dutro (1982, pl. 26, figs. 42–45, pl. 45, figs. 4, 5, 7, 8, 15)].

Description.—Shell of normal size for the genus, reaching 23.9 mm in width, generally wider than long (W/L: 0.98–1.33), dorsibiconvex to ventribiconvex (Tv/Td: 0.84–1.30), rounded subpentagonal in outline; anterior margin variably emarginate; anterior commissure uniplicate to slightly parasulcate. Ventral valve regularly convex in lateral profile; in posterior view, upper surface draws the upper part of a trapezium whose flanks slope moderately towards lateral commissures; umbo prominent; beak curved; foramen permesothyrid; sulcus wide at front (Ws/W: 0.40–0.69), shallow to moderately deep, originating in the posterior half of the valve, never defined by crests (its lateral boundaries are generally vague, except in the case of slightly parasulcate shells, bottom flattened to rounded at the front; tongue moderately high to high; posterior and apical angles between 102°–114° and 95°–105°, respectively; palintropes well-developed and concave. Dorsal valve with upper surface dome-shaped (median part sometimes raised by the fold); flanks sloping moderately towards lateral commissures; maximal height at about midvalve and then decreasing progressively towards the front; fold originating

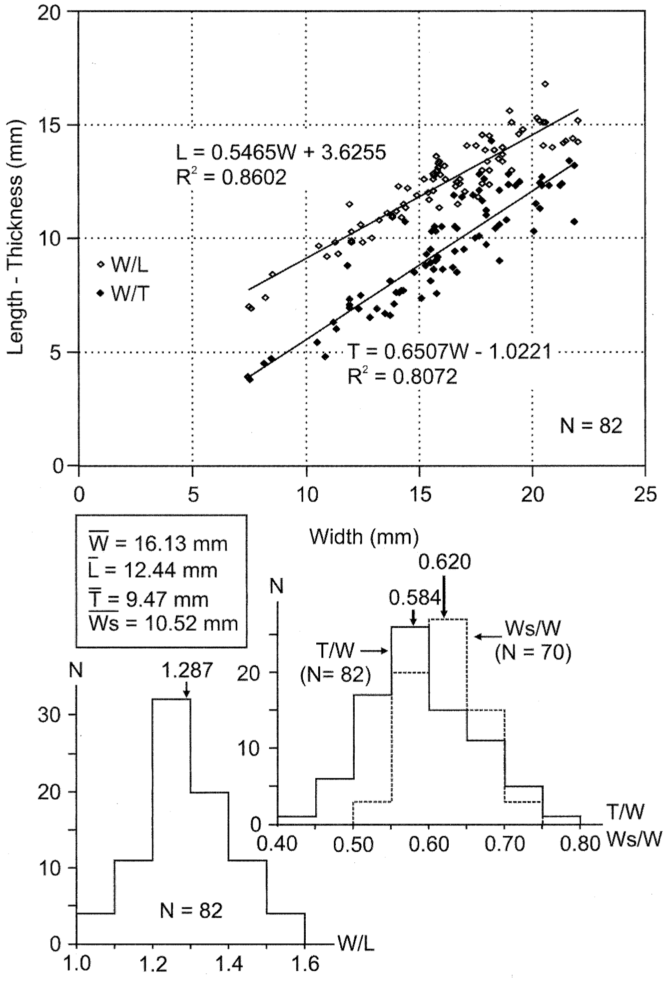

FIGURE 17—*Crinisarina reticulata*. Scatter diagrams of shell width to shell length, shell width to shell thickness; frequency diagrams of W/L, Ws/W, and T/W. Arrows = means. For abbreviations, see text.

a little behind the midvalve and never bounded by lateral grooves, low to moderately high, with its top rounded to flattened at the front. Ornamentation similar to that of *Crinisarina reticulata* (see above; Fig. 20.11).

Ventral interior (Fig. 21) with thin, short dental plates converging dorsally and supporting cyrtomatodont teeth; small lateral apical cavities slightly filled. Dorsal interior (Fig. 21) with conjunct, weakly concave ventrally to nearly flat inner hinge plates; outer hinge plates flat; cardinal flanges developed; internal crests of the dental sockets well-developed; myophragm very short (only seen in the section taken at 1.5 mm taken from the ventral umbo); only some fragments of spiral cones observed.

Etymology.—In honor of Dr. Merrill A. Stainbrook (1897–1956).

Types.—Same as those of *Cleiothyridina reticulata* Stainbrook, 1947; holotype: USNM 135248 [in Stainbrook (1947, pl. 45, figs. 31, 32, 35)]; figured paratype: USNM 135249 [in Stainbrook (1947, pl. 45, figs. 33, 34)], plus the unillustrated paratypes and labelled M.A.S. 1588 which are housed also at the USNM.

The type horizon and type locality are the "Percha shale" and the "South of east entrance of Rhodes' Pass, San Andres Mts, New Mexico," respectively (Stainbrook, 1947, p. 327). According to Johnson et al. (1969), the brachiopod fauna from the lithostratigraphic level identified as the Percha Shale by Stainbrook (1947) has nothing in common with the one occurring in the locality of Hillsboro which characterizes the Box Member of the Percha Shale and would indicate an older age. According to Cooper and Dutro (1982), Stainbrook's specimens originate from the Rhodes Canyon Formation and not from the Percha Shale, which was not identified in this area of New Mexico (see below).

Other material examined.—Sixteen articulated specimens from locality BM-2001-2; 30 articulated specimens from locality BM-2001-3; 63 articulated specimens from locality BM-2001-5; 102 articulated specimens from locality BM-2002-1; 107 articulated specimens from locality BM-2002-6; 52 articulated specimens from locality BM-2003-2.

Measurements.—See Figure 22.

Occurrence.—In southern Belgium, *C. stainbrooki* occurs at the base of the Famenne Group (south and southeastern borders of the Dinant Synclinorium) as well as in the Famennian part of the Lambermont Formation (northern border of the Dinant Synclinorium and Vesdre area). *Crinisarina stainbrooki* is reported in New Mexico within the Thoroughgood and Rhodes Canyon formations by Cooper and Dutro (1982). Following the revision by Sorauf (1984), both formations are considered as the middle and upper members of the Contadero Formation and have been named the Thurgood Sandstone Member and the Rhodes Canyon Member respectively [see also Day (1998)]; these latter are placed in the *triangularis* Zone. Johnson et al. (1969) reported the species within the West Range Limestone (Nevada).

Discussion.—As discussed previously in the paragraph related to the taxonomic position and the content of *Spirigera reticulata* Gosselet, 1877, *Crinisarina reticulata* (Stainbrook, 1947) is a secondary homonym of Gosselet's species as revised earlier. So, a new name is proposed, namely *Crinisarina stainbrooki* nom. nov. It turns out that the species defined by Stainbrook is also present in the Famennian of southern Belgium. There are no significant differences between the North American and Belgian specimens which would justify the erection of several subspecies. The Belgian material identified as *C. stainbrooki* includes the specimens assigned to *Spirigera reticulata* var. *depressa* by Gosselet (1877) as well as some of those included in the variety *gibbosa*.

The characters that distinguish *C. stainbrooki* from *C. reticulata* have been stated previously (see the discussion concerning *C. reticulata*). *Crinisarina stainbrooki* differs from *C. angelicoides* by its less globular appearance, its less developed tongue, and its uniplicate to slightly parasulcate anterior commissure.

DISCUSSION

Ecology.—The strophomenids studied in this paper are characteristic of an environment with relatively low water energy (essentially argillaceous) and low- to moderate-diversity faunas (e.g., brachiopods, corals). The external shape of their shell is conspicuously variable: planoconvex to concavoconvex (*Douvillina area*), planoconvex but almost flat (*Nervostrophia* (*N.*) cf. *latissima*), concavoconvex (*D. dutertrei*), geniculate and strongly resupinate (*Retrorstrophia retrorsa*), slightly resupinate (*Gamphalosia* sp.). All these morphologies are well-adapted to soft fine-grained substrates. Thayer (1974) compared this morphology with snowshoes that prevented the shell from sinking into the sediment. According to Rudwick (1970), they would have been able to lift back if they were too deeply buried by a snapping action of the valves. Their shells are generally mucronate; these mucrons (up to 10 mm in *R. retrorsa*) may have provided an additional support. Bassett (1984) suggested that genera characterized by strongly geniculate shells would have lived entirely within the sediment with no need to snap to the surface periodically; a similar mode of life probably applied to *R. retrorsa* and to *Nervostrophia* (*Ailostrophia*?) sp. The encrusting species *Schuchertellopsis* (*S.*) *durbutensis* ranks among the epizoans of the large cyrtospiriferid brachiopods occurring in the Barvaux Formation with *Petrocrania*, *Aulopora*, and spiral worm tubes. It lived attached ventrally, close to the anterior margins on either the dorsal or ventral valve of its host (Long and Brunton, 2005) but without simulating the ornamentation of the latter. The presence of a small cementation cicatrix and koskinoid perforations in the ventral umbo of *Floweria pseudoelegans* attest to at least temporary fixation to a hard substrate. The koskinoid structure as defined by Jux and Strauch (1966) has been generally interpreted as the trace of a fixation system (Schumann, 1969; Martínez-Chacón and García-Alcalde, 1978; Grant, 1980), although Williams and Brunton (1993), after careful examination using scanning microscopy of the shell structure of the ventral valve of some orthotetidine brachiopods, suggested a parasitic nature for these perforations. The small size of the cicatrix seen in *F. pseudoelegans* may indicate that the shell was cemented only during

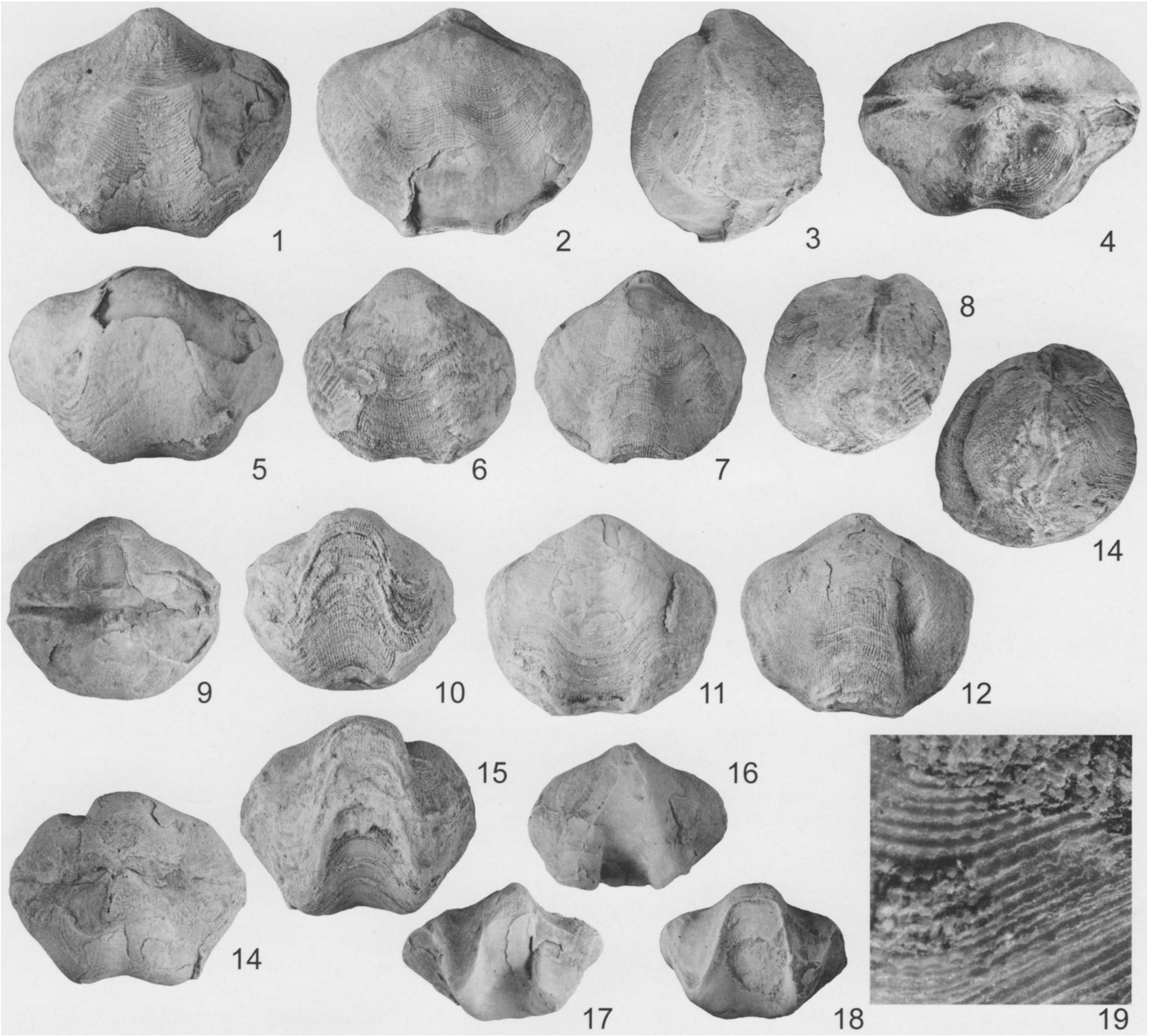

FIGURE *18—1–19*, *Crinisarina angelicoides* from Famenne Group ("Senzeille Formation"): *1–5*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12273 (Senzeille 6839b/PS); *6–10, 19*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12274 (Senzeille 6839b/PS) and detail of ornament (spines are broken) on dorsal valve; *11–15*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12276 (Senzeille 6839b/PS); *16–17*, ventral and anterior views of IRScNB (BM-2001-3); *18*, anterior view of IRScNB a12279 (BM-2001-3). *16–17, 18*, ×1.5; *19*, ×15; others, ×2.

early stages, as supposed by Bassett (1984) for some Silurian strophomenids. Muir-Wood and Cooper (1960) suggested that some Productidina with a cicatrix of attachment were attached only in youthful stages until the weight of the growing shell or the currents prevented the spat from clinging to the hard substrate. An alternative hypothesis is that the fibrils passing through the perforations were strong enough to maintain the shell in a stable position throughout the life of the animal, as suggested by Grant (1980, fig. 4) for *Derbya*. Some species of *Floweria* such as *F. magnacicatrix* may have lived fixed for a long time, based on the evidence of the large size of the cicatrix with koskinoid perforations seen in its holotype (USNM 200855), unless it is an exceptional case. The athyridids described herein were pedunculate and attached to the substrate by a thin pedicle which possibly rooted into argillaceous sediment, as suggested for Carboniferous Cleiothyridininae (Brunton, 1984).

Biogeography.—Reconstructions of Late Devonian paleogeography (Scotese and McKerrow, 1990; Golonka, 2000) place Belgium in a subtropical position on the southeastern margin of Laurussia. The mid- and late Frasnian as well as the early Famennian were intervals of prolonged cosmopolitanism due to the connections between the different basins brought about by high sea-levels (Johnson et al., 1985). However, on the basis of the available data, *Schuchertellopsis* (S.) and *Retrorstrophia* seem to be restricted to Western Europe, although Williams and Brunton (2000) reported, with some doubts, the presence of the former in southern North America. Until recently, *Crinisarina* was only reported within the Famennian of North America. Species of *Crinisarina* have been reported in Iowa (Stainbrook, 1950), Montana (Raymond, 1909), Nevada (Merriam, 1940; Johnson et al., 1969), New Mexico (Stainbrook, 1947), Alberta (Day in Whalen et al., 2002), and Alaska (Savage et al., 1978; Dutro et al., 1994). In

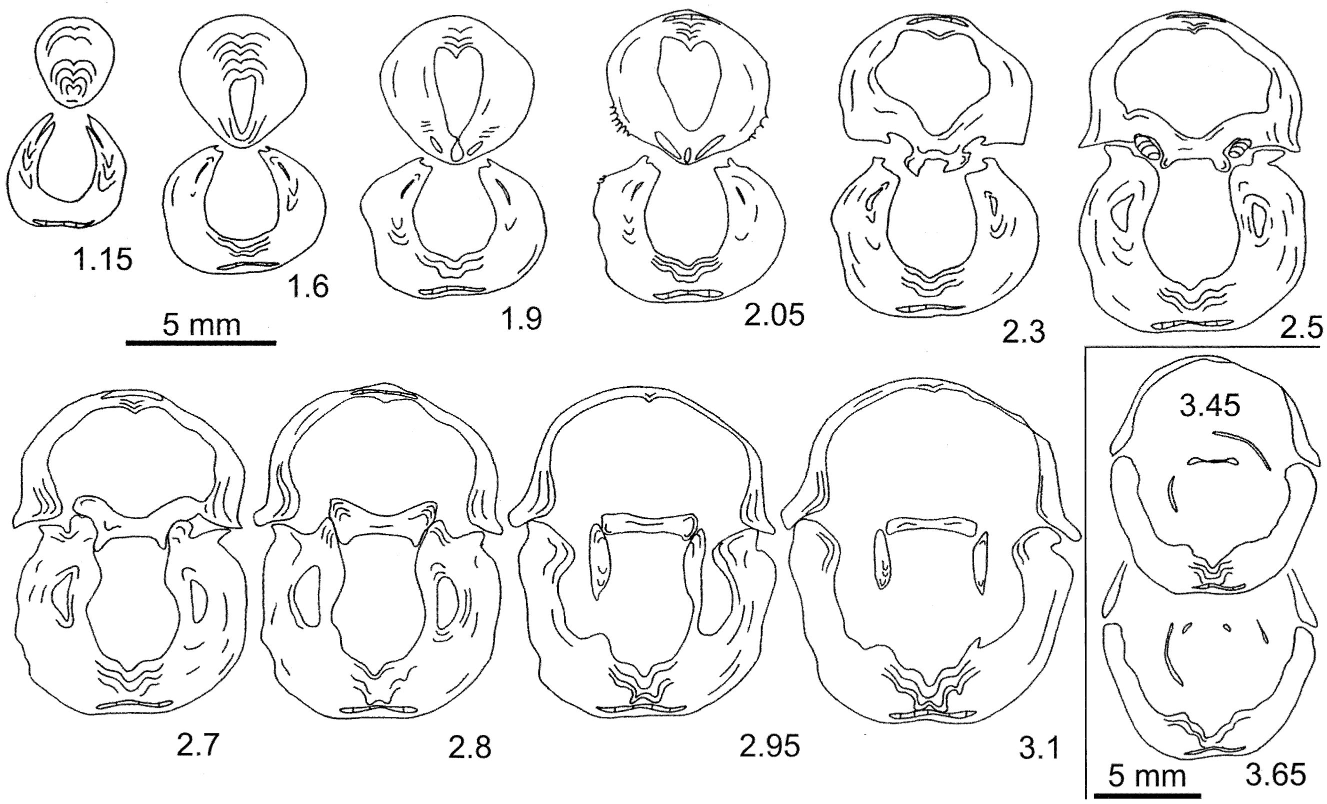

FIGURE *19*—Transverse serial sections of *Crinisarina angelicoides*. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12277 from locality Senzeille 6839b (Famenne Group: "Senzeille Formation"). Dimensions of specimen: width 14.2 mm; length 14.3 mm; thickness 13.4 mm.

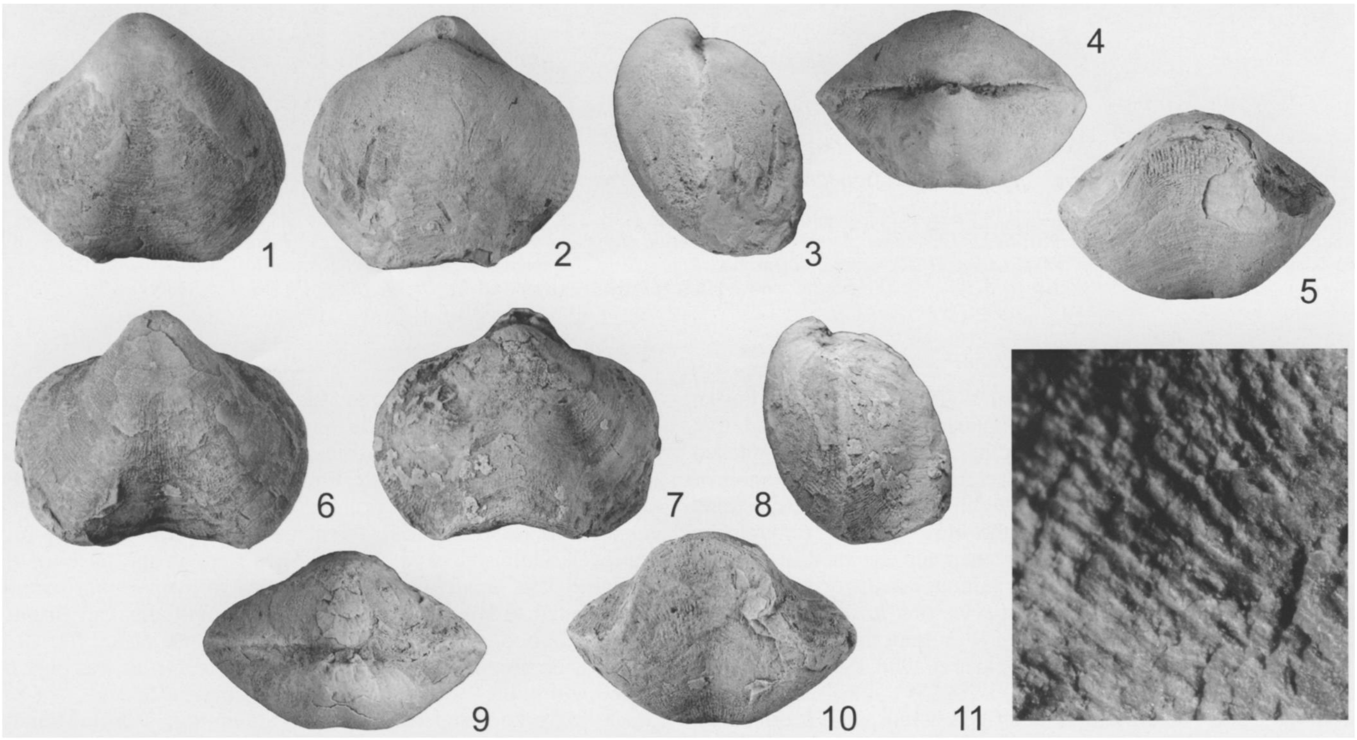

FIGURE *20*—*1–11*, *Crinisarina stainbrooki* new name from Famenne Group ("Senzeille Formation"): *1–5*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12278 (BM-2001-5); *6–11*, ventral, dorsal, lateral, posterior, and anterior views of IRScNB a12279 (BM-2003-2) and detail of ornament on ventral valve. *11*, ×15; others, ×2.

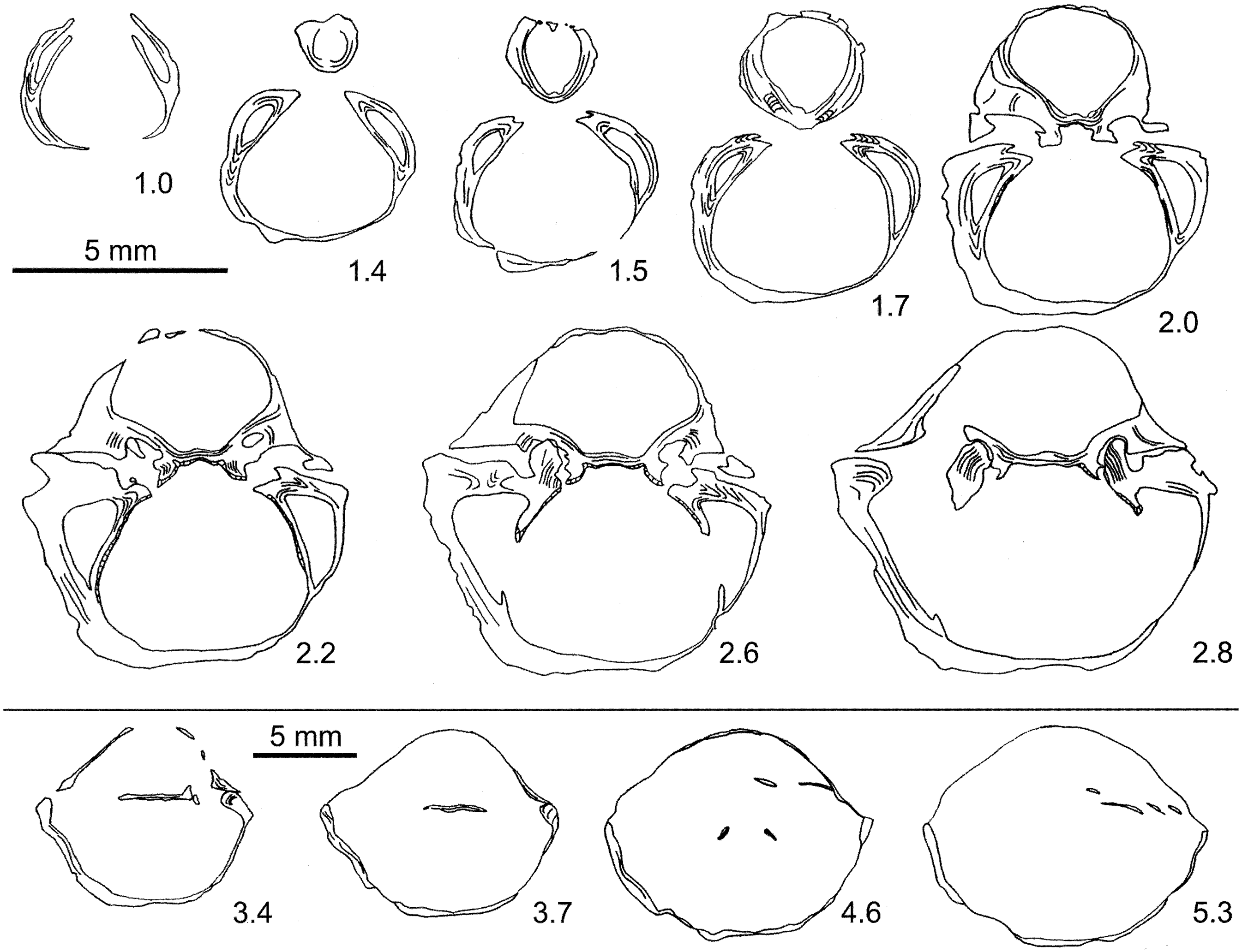

FIGURE *21*—Transverse serial sections of *Crinisarina stainbrooki*. Numbers refer to distances in mm from the top of the ventral umbo; IRScNB a12282 from locality BM-2001-3 (Famenne Group: "Senzeille Formation"). Dimensions of specimen: width 19.9 mm; length 17.5 mm; thickness 12.4 mm.

Europe, species of *Crinisarina* have been mentioned in Poland by Baliński (1995a, 2002), and in Germany (Wulff, 1923; Baliński in Gischler et al., 2004), as well as in Belgium and northern France (Gosselet, 1888). The genus is present in South Tianshan (China) (Chen and Xu, 2000) and maybe in Kerman province (Iran), where Dastanpour and Aftabi (2002) mentioned the genus *Cleiothyridina* (perhaps *Crinisarina*) in the early Famennian. In southern Belgium, available data suggest that *C. angelicoides* and *C. stainbrooki* appear nearly at the same time; both species precede *C. reticulata*, all three occurring in the *triangularis* Zone, i.e., in the lower part of the Famenne Group ("Senzeille Formation"). Nevertheless, accurate conodont biostratigraphy is lacking for most of the sampled Famennian sections. Linkages of the genera recognized in the Namur-Dinant Basin with faunas from other areas are discussed below.

Aftermath of the Frasnian-Famennian mass extinction on the orders investigated in southern Belgium.—The late Frasnian mass extinction, whose causes are still hotly disputed (e.g., McGhee, 1996; Racki, 2005), strongly affected the tropical marine faunas (e.g., corals, stromatoporoids, conodonts). Of the four families (Rafinesquinidae, Leptostrophiidae, Strophodontidae, Douvillinidae) included in the superfamily Strophomenoidea, and still flourishing during the Early and Middle Devonian, only the rafinesquinids persisted into the Famennian, where they were represented by the Leptaeninae known from the Ordovician (Llanvirn) to the Carboniferous ("Namurian") according to Rong and Cocks (1994). In the Namur-Dinant Basin, the last Douvillinidae (*Douvillina area*) and Leptostrophiidae (fragmental valves which are tentatively assigned to *Nervostrophia* from the Les Valisettes Formation) disappeared in the Upper *rhenana* Zone (Fig. 23). Maillieux (1940, 1941) did not mention rafinesquinids in the Frasnian of southern Belgium; their presence in the early Famennian is doubtful according to him. Up to now, no strophomenid has been recovered in the blackish shales of the highly diachronous Matagne Formation (Upper *rhenana* to *linguiformis* zones) developed on the southern flank of the Dinant Synclinorium and in the Philippeville Anticlinorium or within the similar facies developed in the Barvaux and Lambermont formations, just below the Frasnian/Famennian boundary (Fig. 23).

Among the Orthotetida, Cocks and García-Alcalde (in Brice et al., 2000) reported that the Chilidiopsiidae (sic) became extinct near the end of the Frasnian, but according to Williams and Brunton (2000), this family had already disappeared during the Middle Devonian. The orthotetids are poorly represented in the Frasnian formations that have been investigated, and only *Schuchertellopsis* (*S.*) *durbutensis* is definitely identified. Some badly preserved and unidentified orthotetids were recovered in the Upper *rhenana*

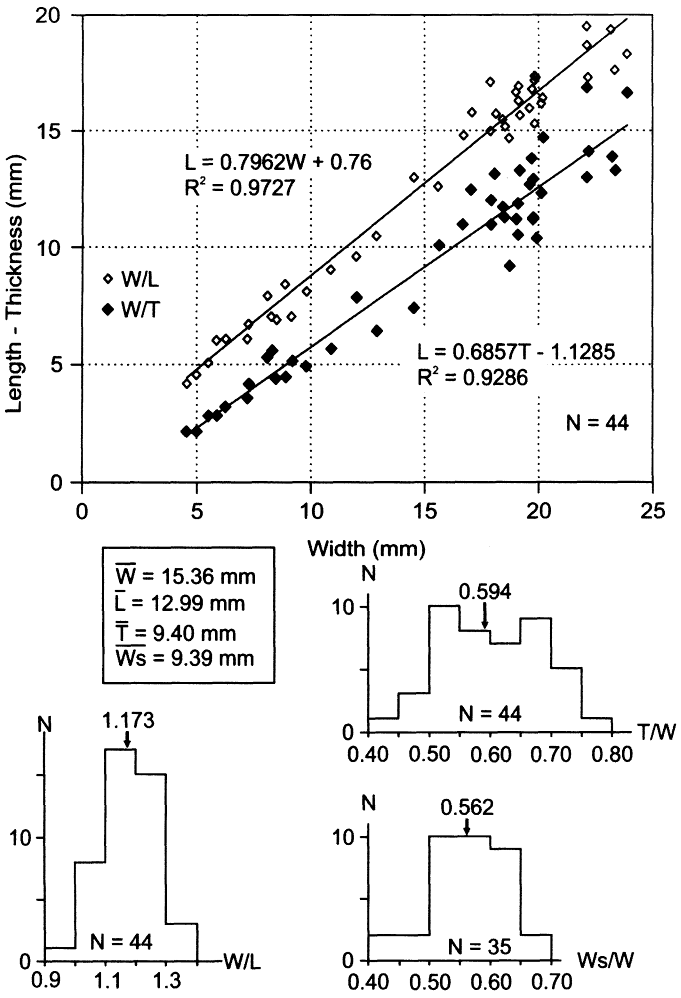

FIGURE 22—*Crinisarina stainbrooki*. Scatter diagrams of shell width to shell length, shell width to sulcus width, and shell width to shell thickness; frequency diagrams of W/L, T/W, and Ws/W. Arrows = means. For abbreviations, see text.

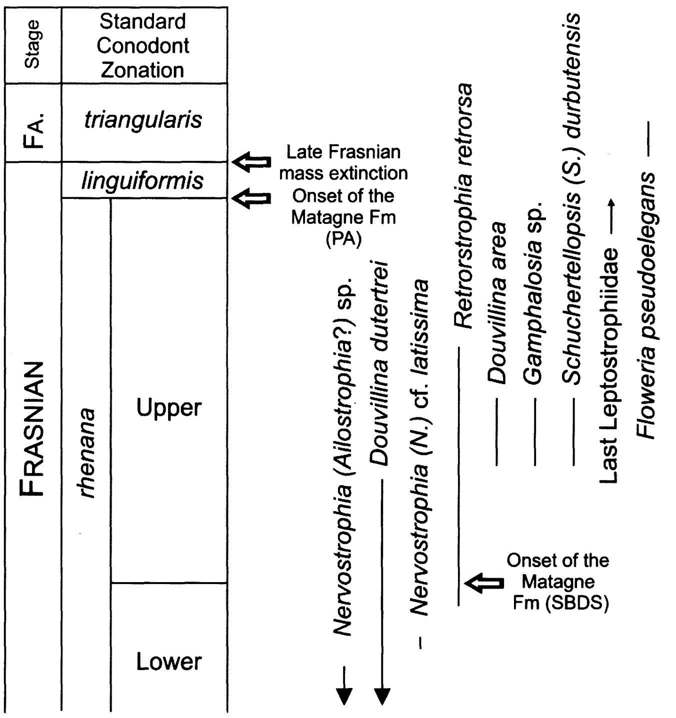

FIGURE 23—Distribution of strophomenids and orthotetids in the Late Frasnian and in the Early Famennian of the Namur-Dinant Basin. Abbreviations: FA, Famennian; Fm, Formation; PA, Philippeville Anticlinorium; SBDS, southern border of the Dinant Synclinorium.

Zone (Les Valisettes and Lambermont formations), but no orthotetid occurs in the *linguiformis* Zone in southern Belgium. According to Stigall Rode (2005), the genus *Floweria* did not cross the Frasnian/Famennian boundary, but that is challenged by the presence of *F. pseudoelegans* within the lowermost part of the Famenne Group of basal Famennian age (Lower (?)/Middle *triangularis* zones) (Fig. 23).

Grunt and Racki (1998) have already discussed the consequences of the late Frasnian biological crisis for the athyridids. It was responsible for the disappearance of the Plicathyridininae (Alvarez, 2003) and Helenathyridinae (Baliński, 1995b). Rzhonsnitskaya and Modzalevskaya (1996) indicated that representatives of the Plicathyridininae (e.g., *Anathyris*) were present only on the Russian Platform and in the Altai-Sayan Province during the Frasnian; however, the genus *Anathyris* is still reported in the Moulin Liénaux Formation (Ermitage Member; *punctata* to *hassi* zones) in southern Belgium (Maillieux, 1940). According to Alvarez and Modzalevskaya (2001), the turnover rate among the Athyridida reached a peak during the Famennian, notably with the appearance of the Cleiothyridininae, whereas the Eifelian-Frasnian interval recorded a sharp decline of their origination rate. Nevertheless, the first appearance of the Cleiothyridininae occurs earlier, as Alvarez (1990) reported *Cleiothyridina* sp. in the late Givetian to early Frasnian Portilla Formation in the Cantabrian Zone (northwestern Spain), and the genus is reported here in the late Frasnian of Belgium. At present, *Cleiothyridina davidsoni* is the only known brachiopod species to cross the Frasnian/Famennian boundary in the Namur-Dinant Basin and can be categorized as a Lazarus taxon. Indeed, this species occurs in the Neuville Formation (Lower *rhenana* Zone) but is absent in the Matagne-Les Valisettes interval (Upper *rhenana* and *linguiformis* zones), before reappearing within the lower part of the Famenne Group (Lower (?)/Middle *triangularis* zones). Other Lazarus taxa will probably be added when the early Famennian Productida as well as the inarticulate brachiopods will have been studied in detail.

CONCLUSIONS

This study, mainly based on new collections of material, substantially improves our knowledge of the diversity and stratigraphic distribution of strophomenid and orthotetid brachiopods occurring in the late middle Frasnian to the early Famennian (*hassi* to *triangularis* conodont zones) of the Namur-Dinant Basin (southern Belgium). In this area, the last Frasnian strophomenids disappeared in the Upper *rhenana* Zone, well below the Frasnian/Famennian boundary. Moreover, the revision of the early Famennian representatives of the subfamily Cleiothyridininae (*Cleiothyridina* and *Crinisarina*) from the Namur-Dinant Basin gave prominence to the significant role played by these athyridids in the post-extinction recovery together with spiriferids and rhynchonellids during the *triangularis* Zone.

ACKNOWLEDGMENTS

This paper forms part of my Ph.D. thesis supervised by J. Godefroid, Institut royal des Sciences naturelles de Belgique, and E. Poty, Université de Liège, which was supported by the Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture (FRIA) and by the Belgian Science Policy. J. W. M. Thompson, United States National Museum, D. Brice, Faculté Libre des Sciences et Technologies de Lille, T. Oudoire, Musée d'Histoire naturelle de Lille, and J.-C. Horrenberger, Université Louis Pasteur, kindly gave access to collections under their care. P. Sartenaer and W. Miseur, both at the Institut royal des Sciences naturelles de Belgique, made available the material collected by him in the Senzeille railway section and did the photographic work, respectively. J. García-Alcalde, Universidad de Oviedo, provided constructive comments on strophomenid and orthotetid systematics. G.

Sevastopulo, Trinity College, advised on linguistic aspects of some parts of the paper before submission. The manuscript benefited from the reviews of F. Alvarez, Universidad de Oviedo and M. V. Pardo Alonso, Universitat de València, as well as the editorial help of Keith Dewing, Geological Survey of Canada. I am deeply grateful to all of them.

REFERENCES

Alekseeva, R. E. 2003. Devonian Nervostrophiinae (Strophomenida, Brachiopoda) of the Russian Platform. Paleontologicheskii Zhurnal, 2003(2): 21–32. (In Russian)

Alekseeva, R. E. and N. V. Olenova. 2000. Katalog kollkstii devonskikh brachiopod Vostochno-Evropeyskoy platformy (materaly A. H. Lyashenko). Byulleten' KF VNIGNI, 2:1–58. (In Russian)

Alvarez, F. 1990. Devonian athyrid brachiopods from the Cantabrian Zone (NW Spain). Biostratigraphie du Paléozoïque, 11:1–311.

Alvarez, F. 2003. Convergence in the evolution of Palaeozoic and Mesozoic brachiopods. Journal of the Royal Society of New Zealand, 33:189–211.

Alvarez, F. and T. L. Modzalevskaya. 2001. Trends in athyridide diversity dynamics, p. 212–223. *In* C. H. C. Brunton, L. R. Cocks, and S. Long (eds.), Brachiopods Past and Present. The Systematics Association Special Volume Series, 63.

Alvarez, F. and J. Y. Rong. 2002. Athyridida, p. 1475–1601. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda (revised) 4. Geological Society of America and University of Kansas Press, Lawrence.

Alvarez, F., J. Y. Rong, and A. J. Boucot. 1998. The classification of athyridid brachiopods. Journal of Paleontology, 72:827–855.

Asselberghs, E. 1912. Description d'une faune frasnienne inférieure du bord nord du bassin de Namur. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie, Mémoires, 26:1–47.

Baliński, A. 1995a. Brachiopods and conodont biostratigraphy of the Famennian from the Dębnik Anticline, southern Poland. Palaeontologica Polonica, 54:1–85.

Baliński, A. 1995b. Devonian Athyridoid brachiopods with double spiralia. Acta Palaeontologica Polonica, 40:129–148.

Baliński, A. 2002. Frasnian-Famennian brachiopod extinction and recovery in southern Poland. Acta Palaeontologica Polonica, 47:289–305.

Bassett, M. G. 1984. Life strategies of Silurian brachiopods, p. 237–263. *In* M. G. Basset and J. D. Lawson (eds.), Autoecology of Silurian organisms. Special Papers in Palaeontology, 32.

Boucot, A. J. 1959. A new family and genus of Silurian orthotetacid brachiopods. Journal of Paleontology, 33:25–28.

Boucot, A. J., J. G. Johnson, and R. D. Staton. 1964. On some atrypoid, retzioid, and athyridoid Brachiopoda. Journal of Paleontology, 38:805–822.

Boulvain, F. 1993. Sédimentologie et diagenèse des monticules micritiques "F2J" du Frasnien de l'Ardenne. Service géologique de Belgique, Professional Paper, 260:1–427.

Boulvain, F., P. Bultynck, M. Coen, M. Coen-Aubert, D. Lacroix, M. Laloux, J. G. Casier, L. Dejonghe, V. Dumoulin, P. Ghysel, J. Godefroid, S. Helsen, N. A. Mouravieff, P. Sartenaer, F. Tourneur, and M. Vanguestaine. 1999. Les formations du Frasnien de la Belgique. Memoirs of the Geological Survey of Belgium, 44:1–126.

Boulvain, F., P. Cornet, A. C. da Silva, G. Delaite, B. Demany, M. Humblet, M. Renard, and M. Coen-Aubert. 2004. Reconstructing atoll-like mounds from the Frasnian of Belgium. Facies, 50:313–326.

Brice, D. 1988. Brachiopodes du Dévonien de Ferques, p. 323–395. In D. Brice (ed.), Le Dévonien de Ferques. Bas-Boulonnais (N. France). Paléontologie – Sédimentologie – Stratigraphie – Tectonique. Biostratigraphie du Paléozoïque, 7.

Brice, D. 2003. Brachiopod assemblages in the Devonian of Ferques (Boulonnais, France). Relations to palaeoenvironments and global eustatic curves. Bulletin of Geosciences, 78:405–417.

Brice, D., P. Carls, L. R. M. Cocks, P. Copper, J. L. García-Alcalde, J. Godefroid, and P. R. Racheboeuf. 2000. Brachiopoda, p. 65–86. *In* P. Bultynck (ed.), Subcommission on Devonian Stratigraphy. Fossil groups important for boundary definition. Courier Forschungsinstitut Senckenberg, 220.

Brunton, C. H. C. 1984. Silicified brachiopods from the Viséan of County Fermanagh (III). Rhynchonellids, Spiriferids and Terebratulids. Bulletin of the British Museum (Natural History), Geology, 16:1–70.

Brunton, C. H. C. 2007. Orthotetida, p. 2674–2677. *In* P. A. Selden (ed.), Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda (revised) 6 (supplement). Geological Society of America and University of Kansas Press, Lawrence.

Buckman, S. S. 1906. Brachiopod nomenclature: *Epithyris*, *Hypothyris*, *Cleiothyris* Phillips, 1841. Annals and Magazine of Natural History (series 7), 18(107):321–327.

Bultynck, P. and L. Dejonghe. 2002. Devonian lithostratigraphic units (Belgium), p. 39–69. *In* P. Bultynck and L. Dejonghe (eds.), Lithostratigraphic scale of Belgium. Geologica Belgica, 4.

Bultynck, P. and F. Martin. 1995. Assessment of an old stratotype: the Frasnian/Famennian boundary at Senzeilles, southern Belgium. Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 65:5–34.

Caster, K. E. 1939. A Devonian fauna from Colombia. Bulletin of American Paleontology, 24:1–218.

Chen, X. Q. and H. K. Xu. 2000. Brachiopod fauna of the Shashishan Formation (mid Famennian) in Kruktag, South Tianshan. Records of the Western Australian Museum, Supplement, 58:37–57.

Cocks, L. R. M. and J. Y. Rong. 2000. Strophomenida, p. 216–348. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda (revised) 2. Geological Society of America and University of Kansas Press, Lawrence.

Cocks, L. R. M. and J. Y. Rong. 2007. Strophomenida, p. 2598–2627. *In* P. A. Selden (ed.), Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda (revised) 6. Geological Society of America and University of Kansas Press, Lawrence.

Coen, M. 1974. Le Frasnien de la bordure orientale du Bassin de Dinant. Annales de la Société géologique de Belgique, 97:67–103.

Coen-Aubert, M. 1994. Stratigraphie et systématique des Rugueux de la partie moyenne du Frasnien de Frasnes-lez-Couvin (Belgique). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 64:21–56.

Coen-Aubert, M. and F. Boulvain. 2006. Frasnian, p. 19–25. *In* L. Dejonghe (ed.), Current status of chronostratigraphic units named from Belgium and adjacent areas. Geologica Belgica, 9.

Cooper, G. A. and J. T. Dutro. 1982. Devonian brachiopods of New Mexico. Bulletins of American Paleontology, 82–83:1–215.

Copper, P. 1986. Frasnian/Famennian mass extinction and cold-water oceans. Geology, 14:835–839.

Dastanpour, M. and A. Aftabi. 2002. The cause of biomass extinction at the Frasnian-Famennian boundary, the Kerman province southeastern, central Iran. Journal of Sciences, Islamic Republic of Iran, 13:45–49.

Davidson, T. 1881. On genera and species of spiral-bearing Brachiopoda from specimens developed by Rev. Norman Glass: with notes on the results obtained by Mr. George Maw from extensive washing of the Wenlock and Ludlow shales of Shropshire. Geological Magazine, 8:1–13.

Day, J. 1998. Distribution of latest Givetian-Frasnian Atrypida (Brachiopoda) in central and western North America. Acta Palaeontologica Polonica, 43: 205–240.

Dutro, J. T., R. B. Blodgett, and C. G. Mull. 1994. *Cyrtospirifer* from Upper Devonian rocks of the Endicott Group, west-central Brooks Range, Alaska, p. 133–141. *In* A. B. Till and T. E Moore (eds.), Geologic studies in Alaska by the U.S. Geological Survey, 1993. U.S. Geological Survey Bulletin 2107.

García-Alcalde, J. L. 1973. Braquiopódos devónicos de la cordillera cantábrica. 7) Familia Leptostrophiidae Caster, 1939 (Strophomenida). Parte 2 (y última). Breviora Geológica Astúrica, 17(3):43–48.

Gischler, E., A. Baliński, A. Fuchs, and D. Heidelberger. 2004. Famennian brachiopod and gastropod occurrences on top of Devonian seamounts, Elbingerode and Iberg Reefs, Harz Mts, Germany. Senckenbergiana lethaea, 84:125–139.

Godefroid, J. and S. Helsen. 1998. The last Frasnian Atrypida (Brachiopoda) in southern Belgium. Acta Palaeontologica Polonica, 43:241–272.

Golonka, J. 2000. Cambrian-Neogene plate tectonic maps. Jagiellonian University Publishing House, Cracow, 125 p.

Gosselet, J. 1877. Quelques documents pour l'étude des Schistes de Famenne. Annales de la Société géologique du Nord, 4:303–320.

Gosselet, J. 1880. Esquisse géologique du Nord de la France et des contrées voisines. 1^{er} fascicule. Terrains primaires. Société géologique du Nord, Lille, 167 p.

Gosselet, J. 1888. L'Ardenne. Ministère des travaux publics, Mémoires pour servir à l'explication de la carte géologique détaillée de la France. Baudry & Cie, Paris, 889 p.

Grant, R. E. 1980. Koskinoid perforations in brachiopod shells: function and mode of formation. Lethaia, 13:313–319.

Gratsianova, R. T. 1974. "Schuchertellas" of the early and middle Devonian in the South of West Siberia. *In* O. A. Betekhitina (ed.), Sreda i Zhizn v Geologicheskom Prosholm (Paleoekologicheskie Problemy). Akademiia Nauk SSSR Sibirskoe otdelenie Institut Geologii i Geofiziki, Trudy, 84:77–87. (In Russian)

Grunt, T. A. and G. Racki. 1998. Late Frasnian Athyridida (Brachiopoda) from Poland and the Late Devonian biotic turnover. Acta Palaeontologica Polonica, 43:361–378.

Hall, J. 1843. Survey of the Fourth Geological District. Natural History of New York, Geology, Vol. 4. Carroll & Cook, Albany, 525 p.

Hall, J. 1858. Report of the Geological Survey of the State of Iowa; embracing the results of investigations made during portions of the years

1855–1857. Vol. 1, Pt. 2, p. 473–724. *In* Palaeontology of Iowa. Published by the authority of the legislature of Iowa, Des Moines.

Henry, T. W. and M. Gordon Jr. 1985. Chesterian davidsoniacean and orthotetacean brachiopods, Ozark region of Arkansas and Oklahoma. Journal of Paleontology, 59:32–59.

International Commission on Zoological Nomenclature. 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature, London, 306 p.

Johnson, J. G., G. Klapper, and C. A. Sandberg. 1985. Devonian eustatic fluctuations in Euramerica. Bulletin of the Geological Society of America, 96:567–587.

Johnson, J. G., A. Reso, and M. Stephens. 1969. Late Upper Devonian brachiopods from the West Range Limestone of Nevada. Journal of Paleontology, 43:1351–1368.

Jux, U. and F. Strauch. 1966. Die Mitteldevonische brachiopoden-gattung *Uncites* Defrance 1825. Palaeontographica, Abteilung A, 125(4–6):176–222.

Kayser, E. 1881. Ueber einige neue devonische Brachiopoden. Zeitschrift der Deutschen Geologischen Gesellschaft, 33:331–337.

King, W. 1846. Remarks on certain genera belonging to the class Palliobranchiata. Annals and Magazine of Natural History (series 1), 18:26–42,83–94.

Klähn, H. 1912. Die Brachiopoden der Frasne-Stufe bei Aachen. Jahrbuch der Köninglich Preussischen Geologischen Landenstalt, 33:1–39.

Koninck, L. G. de. 1882. Description de trois nouvelles espèces famenniennes. Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique (3ème série), 4:521–525.

Lyashenko, A. I. 1959. Atlas of Brachiopods and Stratigraphy of the Devonian Russian Platform. Gostoptechnizat, Moskova, 451 p. (In Russian)

Long, S. L. and C. H. C. Brunton. 2005. The problematic cemented Devonian brachiopod *Schuchertellopsis durbutensis* Maillieux, 1939. Geobios, 38:107–112.

Maillieux, E. 1939. La faune des schistes de Barvaux-sur-Ourthe (Frasnien supérieur). Bulletin du Musée royal d'Histoire naturelle de Belgique, 15(53):1–8.

Maillieux, E. 1940. Contribution à la connaissance du Frasnien moyen (Assise de Frasnes) de la Belgique. Bulletin du Musée royal d'Histoire naturelle de Belgique, 16(14):1–44.

Maillieux, E. 1941. Répartition des Brachiopodes dans le Dévonien de l'Ardenne. Bulletin du Musée royal d'Histoire naturelle de Belgique, 17(30):1–14.

Manankov, I. N. 1979. Strophomenids of the Late Palaeozoic of Siberia and the Arctic. Akademiia Nauk SSSR, Paleontologicheskii Institut, Trudy 171: 1–101. (In Russian)

Martínez-Chacón, M. L. and J. L. García-Alcalde. 1978. La génesis del koskinoide en Braquiopódos Articulados. Revista de la Facultad de Ciencias de la Universidad de Oviedo, 17–19:261–279.

McGhee, G. R. Jr. 1996. The Late Devonian mass extinction. Columbia University Press, New York, 303 p.

M'Coy, F. 1844. A Synopsis of the Characters of the Carboniferous Limestone Fossils of Ireland. Printed at the University Press by M. H. Gill, Dublin, 207 p.

Merriam, C. W. 1940. Devonian stratigraphy and paleontology of the Roberts Mountains Region, Nevada. Geological Society of America, Special Papers, 25:1–114.

Mottequin, B. 2004. The genus *Iowatrypa* Copper, 1973 (Brachiopoda) in the Les Valisettes Formation (late Frasnian of the Philippeville Anticlinorium, southern Belgium). Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre, 74:35–44.

Mottequin, B. 2005. Les Brachiopodes de la transition Frasnien/Famennien dans le Bassin de Namur-Dinant (Belgique). Systématique-Paléoécologie-Biostratigraphie-Extinctions. Unpublished Ph.D. dissertation, University of Liège at Liège, 427 p.

Muir-Wood, H. M. and G. A. Cooper. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). Geological Society of America Memoir, 81:1–447.

Murchison, R. I. 1840. Description de quelques-unes des coquilles fossiles les plus abondantes dans les couches dévoniennes du Bas-Boulonnais. Bulletin de la Société géologique de France, 11:250–256.

Oehlert, D. P. 1887. Appendice: Brachiopodes; notions sur l'anatomie et la physiologie des brachiopodes, p. 1189–1334. *In* P. H. Fischler (ed.), Manuel de Conchyliologie et de Paléontologie conchyliologique ou histoire naturelle des Mollusques vivants et fossiles, Pt. 11, F. Savy, Paris.

Öpik, A. A. 1934. Über Klitamboniten. Universitatis Tartuensis (Dorpatensis). Acta et Commentationes, series A, 26(5):1–239.

Pardo Alonso, M. V. 2002. Revisión de Douvillininae (Brachiopoda) de la Zona Centroibérica meridional (Devónico Superior, España). Revista Española de Paleontologia, 17:157–164.

Poty, E. and E. Chevalier. 2007. Late Frasnian phillipsastreid biostromes in Belgium, p. 143–161. *In* J. J. Alvaro, M. Aretz, F. Boulvain, A. Munnecke, D. Vachard, and E. Venin (eds.), Palaeozoic reefs and bioaccumulations: climatic and evolutionary controls. Geological Society Special Publication 275.

Quenstedt, F. A. 1868–1871. Petrefactenkunde Deutschlands. Die Brachiopoden. Pt. 1. Vol. 2. L. F. Fues, Leipzig & Tübingen, 748 p.

Racki, G. 2005. Toward understanding Late Devonian global events: few answers, many questions, p. 5–36. *In* D. J. Over, J. R. Morrow, and P. B. Wignall (eds.), Understanding Late Devonian and Permian–Triassic Biotic and Climatic Events: Towards an Integrated Approach. Developments in Palaeontology and Stratigraphy, 20.

Raymond, P. E. 1909. The fauna of the Upper Devonian in Montana. Pt. 1. The fossils of the red shales. Annals of the Carnegie Museum, 5:141–158.

Reed, F. R. C. 1929. New Devonian fossils from Burma. Records of the Geological Survey of India, 62:229–257.

Rigaux, E. 1873. Notes pour servir à la géologie du Boulonnais. Description de quelques Brachiopodes du terrain Dévonien de Ferques. Mémoires de la Société Académique de l'Arrondissement de Boulogne-sur-Mer, 5:1–16.

Rigaux, E. 1908. Le Dévonien de Ferques et ses brachiopodes. Deligny Editeur, Boulogne-sur-Mer, 33 p.

Rong, J. Y. and L. R. M. Cocks. 1994. True *Strophomena* and a revision of the classification and evolution of strophomenoid and "strophodontoid" brachiopods. Palaeontology, 37:651–694.

Rudwick, M. J. S. 1970. Living and fossil Brachiopods. Hutchinson University Library, London, 199 p.

Rzhonsnitskaya, M. A. and T. L. Modzalevskaya. 1996. Evolution of Devonian plicathyridine brachiopods, Northern Eurasia, p. 233–238. *In* P. Copper and J. Jin (eds.), Brachiopods. Proceedings of the Third International Brachiopod Congress Sudbury, Ontario, Canada, 2–5 September 1995. A. A. Balkema, Rotterdam.

Sartenaer, P. 1960. Visage 1960 de la "tranchée de Senzeilles" (partie famennienne). Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie, 68:430–442.

Sartenaer, P. 1970. Le contact Frasnien/Famennien dans la région de Houyet - Han-sur-Lesse. Annales de la Société géologique de Belgique, 92:345–357.

Savage, N. M., G. D. Eberlein, and M. Churkin. 1978. Upper Devonian brachiopods from the Port Refugio Formation, Suemez Island, southeastern Alaska. Journal of Paleontology, 52:370–393.

Schumann, D. 1969. "Byssus" – artige Stielmuskel – Konvergenzen bei artikulaten Brachiopoden. Neues Jahrbuch für Geologie und Palaeontologie, Abhandlungen, 133:199–210.

Scotese, C. R. and W. S. McKerrow. 1990. Revised world maps and introduction, p. 1–24. *In* W. S. McKerrow and C. R. Scotese (eds.), Palaeozoic palaeogeography and biogeography. Geological Society of London Memoirs, 12.

Sorauf, J. E. 1984. Devonian stratigraphy of the San Andres Mountains, Dona Ana, Sierra and Socorro counties, New Mexico. New Mexico Bureau of Mines and Mineral Resources Circular, 189:1–32.

Sowerby, J. de C. 1840–1846. The Mineral Conchology of Great Britain, Vol. 7. Published by the author, London, 80 p.

Stainbrook, M. A. 1945. Brachiopoda of the Independence Shale of Iowa. Geological Society of America Memoir, 14:1–74.

Stainbrook, M. A. 1947. Brachiopoda of the Percha Shale of New Mexico and Arizona. Journal of Paleontology, 21:297–328.

Stainbrook, M. A. 1950. Brachiopoda and Stratigraphy of the Aplington Formation of Northern Iowa. Journal of Paleontology, 24:365–385.

Stigall Rode, A. L. 2005. Systematic revision of the middle and late Devonian Brachiopods *Schizophoria (Schizophoria)* and "*Schuchertella*" from North America. Journal of Systematic Palaeontology, 3:133–167.

Struve, W. 1965. *Atrythyris* n. g. und ihre Arten (Athyridae). Senckenbergiana Lethaea, 46(4/6):217–228.

Thayer, C. W. 1974. Marine paleoecology in the Upper Devonian of New York. Lethaia, 7:121–155.

Thorez, J., R. Dreesen, and M. Streel. 2006. Famennian, p. 27–45. In L. Dejonghe (ed.), Current status of chronostratigraphic units named from Belgium and adjacent areas. Geologica Belgica, 9.

Vanguestaine, M., T. Declairfayt, A. Rouhart, and A. Smeesters. 1983. Zonation par acritarches du Frasnien supérieur-Famennien inférieur dans les bassins de Dinant, Namur, Herve et Campine (Dévonien supérieur de Belgique). Annales de la Société géologique de Belgique, 106:121–171.

Verneuil, E. de. 1845. Paléontologie, mollusques, brachiopodes, p. 17–395. *In* R. I. Murchison, E. de Verneuil, and A. de Keyserling (eds.), Géologie de la Russie d'Europe et des Montagnes de l'Oural. Vol. 2. Pt. 3. Paléontologie. John Murray, London and Bertrand, Paris.

Waagen, W. 1884. Salt Range fossils. Vol. 1. Pt. 4. Productus Limestone fossils, Brachiopoda. Memoirs of the Geological Survey of India, Palaeontologia Indica (series 13), 3–4:547–728.

Whalen, M. T., J. Day, G. P. Eberli, and P. W. Homewood. 2002. Microbial carbonates as indicators of environmental change and biotic crises in carbonate systems: examples from the late Devonian, Alberta basin, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology, 181:127–151.

WILLIAMS, A. 1953. The classification of the strophomenoid brachiopods. Washington Academy of Sciences Journal, 43:1–13.

WILLIAMS, A. AND C. H. C. BRUNTON. 1993. Role of the shell structure in the classification of the orthotetidine brachiopods. Palaeontology, 36:931–966.

WILLIAMS, A. AND C. H. C. BRUNTON. 2000. Orthotetidina, p. 644–681. *In* R. L. Kaesler (ed.), Treatise on Invertebrate Paleontology. Pt. H. Brachiopoda (revised) 3. Geological Society of America and University of Kansas Press, Lawrence.

WULFF, R. 1923. Das Famennien der Aachener Gegend. Jahrbuch der Preussischen Geologischen Landesanstalt, 43:1–70.

ACCEPTED 24 APRIL 2008