

# New observations on Upper Devonian brachiopods from the Namur-Dinant Basin (Belgium)

**Bernard MOTTEQUIN**

Université de Liège, Paléontologie animale,  
bât. B18, B-4000 Liège 1 (Belgium)  
and University of Dublin (Trinity College),  
Department of Geology,  
Dublin 2 (Ireland)  
mottequb@tcd.ie

Mottequin B. 2008. — New observations on Upper Devonian brachiopods from the Namur-Dinant Basin (Belgium). *Geodiversitas* 30 (3): 455-537.

## ABSTRACT

Brachiopods (Productida [except Chonetidina], Orthida, Athyridida, Spiriferida [Adolfiidae, Reticulariidae, Ambocoeliidae, Thomasariidae], and Spiriferinida) recovered in the interval, in terms of the standard conodont zonation, between the *Palmatolepis hassi* and *P. triangularis* zones (Late Middle Frasnian to Early Famennian) in the Namur-Dinant Basin (Belgium) are described. The orders and suborders investigated include 32 species: 21 are described in open nomenclature, seven are previously known, four are new of which three are assigned to previously known genera: *Aulacella aggeris* n. sp., *Dicamara plutonis* n. sp., and *Warrenella* (*Warrenella*) *aquaealbae* n. sp. The fourth species belonging to a newly defined genus: *Neptunathyris buxi* n. gen., n. sp. A major brachiopod faunal change occurs at the top of the *P. rhenana* Zone in southern Belgium, with the disappearance of most existing species in parallel with the deterioration of the oxygenation conditions preceding the Upper Kelwasser Event. Only an impoverished fauna (Lingulida, Chonetidina, Rhynchonellida) has been collected in the *P. linguiformis* Zone. The recovery of the Famennian brachiopods after the end-Frasnian biotic crisis was rapid in the basal Famennian but, despite their great abundance, their diversity was relatively low. New cosmopolitan genera appeared at this time especially among the rhynchonellids, athyridids and spiriferids with new species of pre-existing orthid and orthotetid genera.

## KEY WORDS

Brachiopoda,  
Productida,  
Orthida,  
Athyridida,  
Spiriferida,  
Spiriferinida,  
Mid- to Late Frasnian,  
Early Famennian,  
Namur-Dinant Basin,  
Belgium.

## RÉSUMÉ

*Nouvelles observations sur les brachiopodes du Dévonien supérieur du Bassin de Namur-Dinant (Belgique).*

Les brachiopodes (Productida [Chonetidina exceptés], Orthida, Athyridida, Spiriferida [Adolfiidae, Reticulariidae, Ambocoeliidae, Thomasariidae] et Spiriferinida) collectés dans l'intervalle compris, en termes de zonation standard à conodontes, entre les zones à *Palmatolepis bassi* et *P. triangularis* (Frasnien moyen tardif à Famennien inférieur) dans le Bassin de Namur-Dinant (Belgique) sont décrits. Parmi les 32 espèces reconnues, 21 sont laissées en nomenclature ouverte, sept sont déjà connues, quatre sont nouvelles dont trois attribuées à des genres décrits précédemment: *Aulacella aggeris* n. sp., *Dicamara plutonis* n. sp., et *Warrenella (Warrenella) aquaealbae* n. sp. La quatrième appartient à un genre nouvellement défini: *Neptunathyris buxi* n. gen., n. sp. Dans le Bassin de Namur-Dinant, un changement majeur se produit parmi les faunes de brachiopodes au sommet de la zone à *P. rhenana* où la plupart des espèces existantes disparaissent, parallèlement à la détérioration des conditions d'oxygénation précédant l'événement Kellwasser supérieur. Seule une faune appauvrie (Lingulida, Chonetidina, Rhynchonellida) a été recueillie au sein de la zone à *P. linguiformis*. Si, après la crise biologique de la fin du Frasnien, la renaissance des brachiopodes fut rapide au Famennien, leur diversité était relativement faible malgré leur grande abondance. De nouveaux genres cosmopolites apparurent à cette période, principalement parmi les rhynchonellides, athyridides et spiriférides ainsi que de nouvelles espèces appartenant à des genres préexistants d'orthides et d'orthotétides.

## MOTS CLÉS

Brachiopoda,  
Productida,  
Orthida,  
Athyridida,  
Spiriferida,  
Spiriferinida,  
Frasnien moyen à  
supérieur,  
Famennien inférieur,  
Bassin de Namur-Dinant,  
Belgique.

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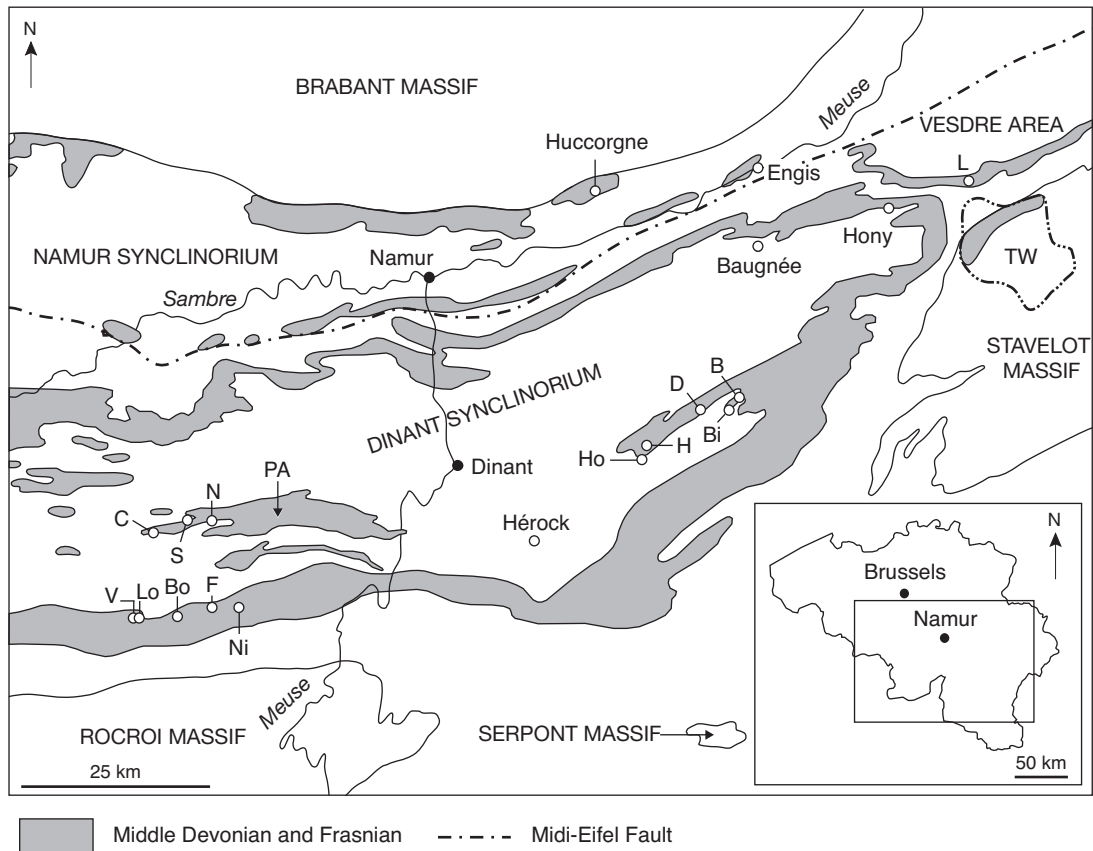


FIG. 1. — Schematic geological map of southern Belgium. Abbreviations: **B**, Barvaux; **Bi**, Biron; **Bo**, Boussu-en-Fagne; **C**, Cerfontaine; **D**, Deulin; **F**, Frasnes; **H**, Heure; **Ho**, Hogné; **L**, Lambermont; **Lo**, Lomporet; **N**, Neuville; **Ni**, Nismes; **PA**, Philippeville Anticlinorium;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

## INTRODUCTION

Late Devonian rocks crop out extensively across southern Belgium (Fig. 1), the region which corresponds to the historical type area of the Frasnian and Famennian stages (see reviews in Coen-Aubert & Boulvain 2006 and Thorez *et al.* 2006). They usually contain diversified marine macrofaunas whose brachiopods constitute generally a large part of the assemblages. However, representatives of several brachiopod orders have never been illustrated and/or studied in detail although they are generally abundant. This is notably the case for representatives of the orders Orthida, Productida and Athyridida. The latest comprehensive lists of Devonian

brachiopod species from southern Belgium date back to Maillieux (1941a, b)!

The purpose of this paper is to describe the Productida (except the Chonetidina which have not yet been studied), Orthida, Athyridida (except the species of *Crinisarina*, see Mottequin [2008]), Spiriferida (Adolfiidae, Reticulariidae, Ambocoeiliidae, Thomasariidae) and Spiriferinida from the late Middle Frasnian to Early Famennian of the Namur-Dinant Basin (see below), i.e. in terms of standard conodont zonation, the interval spanning the *Palmatolepis hassi* Zone to the *P. triangularis* Zone. Only a small part of the brachiopod faunas occurring in this interval, which have been described by Mottequin (2005b), is presented in this paper.

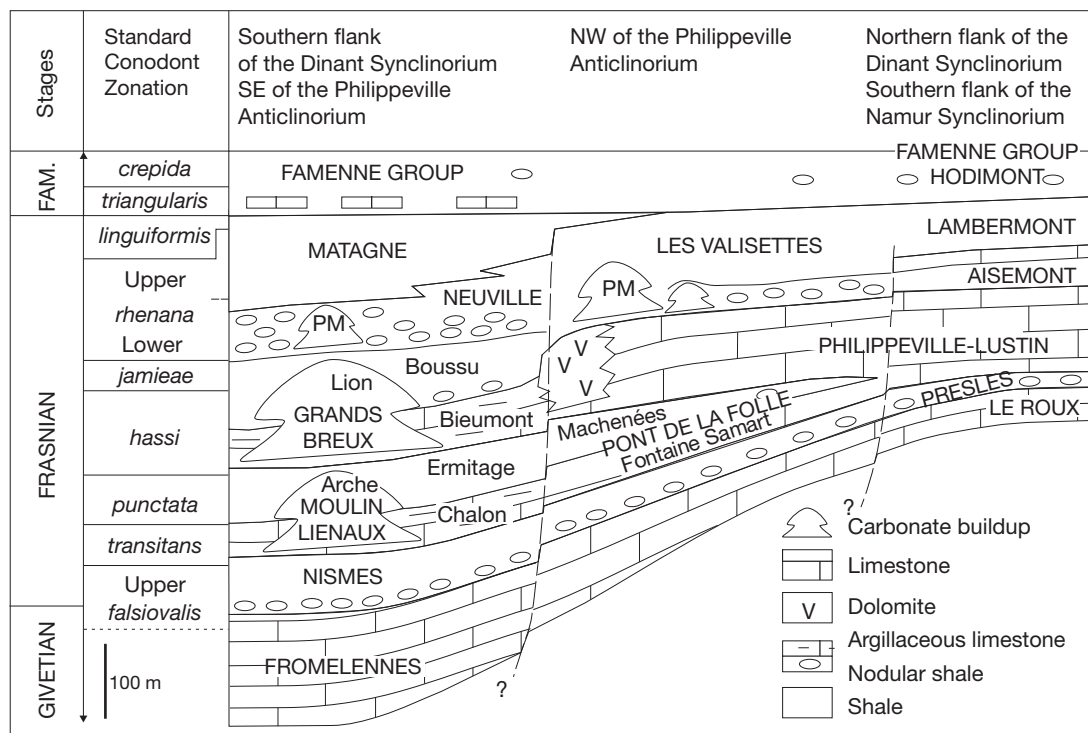


FIG. 2. — Schematic N-S cross section and main lithostratigraphic units of the Namur-Dinant Basin before the Variscan Orogeny (after Boulvain *et al.* 2004). Formations are in capitals, members in lower case. Abbreviations: **FAM.**, Famennian; **PM**, Petit-Mont Member.

The systematic descriptions are followed by a discussion of the consequences of the Late Frasnian mass extinction on some of the orders studied herein; the causes of this major biological crisis are still disputed (Racki 2005).

Tables 1 to 4 as well as the geological and geographical data of the sampled localities are placed in the Appendices 1 and 2, respectively, at the end of the paper.

### STRATIGRAPHY AND BIOSTRATIGRAPHY

The material studied originates from 26 late Middle Frasnian to Early Famennian sections (*Palmatolepis hassi* to *P. triangularis* zones) of different localities from the Namur and Dinant synclinoria, the Philippeville Anticlinorium and the Vesdre area (Fig. 1). These Variscan structural units constituted

the Namur-Dinant Basin during the Devonian that developed along the southeastern margin of Laurussia (Golonka 2000). The succession of facies reflects a ramp setting with several breaks of slope (Fig. 2). The distal part of the Namur-Dinant Basin (southern flank of the Dinant Synclinorium) recorded the development of three carbonate mud mound levels (Arche, Lion and Petit-Mont members) separated by argillaceous episodes. The material belongs to nine formations that are described below. Maillieux & Demanet (1929: table 2) introduced the first detailed stratigraphic subdivisions of the Frasnian of the Namur-Dinant Basin; they were based on palaeontological and lithological criteria. These former subdivisions (e.g., “F2i”, “F2j”) are mentioned in several places in this paper (Fig. 3). For more details concerning the Frasnian and Famennian lithostratigraphic units from Belgium, see Boulvain *et al.* (1999), Bultynck & Dejonghe (2002) and Thorez *et al.* (2006).

Conodont Zones	Formations	Southern border of the Dinant Synclinorium	Philippeville Anticlinorium	Northern border of the Dinant Synclinorium, southern border of the Namur Synclinorium, Vesdre area
<i>linguiformis</i>	Grand Breux	BARVAUX (F3N)	MATAGNE (F3B)	LAMBERMONT (F3 II)
Upper <i>rhenana</i>		MATAGNE (F3B)	LES VALISETTES (F2i)	
Lower		PM (F2j) NEUVILLE (F2i)	PM (F2j) NEUVILLE (F2i)	AISEMONT (F3 II)
<i>jamieae</i>	Grand Breux	Boussu-en-Fagne (F2i)	PHILIPPEVILLE (F2g, F2h)	LUSTIN (F2 II b, F2 II c)
Upper <i>hassi</i>		Lion (F2h)		
Lower		Bieumont (F2g)		
<i>punctata</i>	Moulin Liénaux	Ermitage (F2e, F2f)	PONT DE LA FOLLE	Machenées (F2e)
<i>transitans</i>		Arche (F2d)		Fontaine Samart (?)
Upper <i>falsiovalis</i>		Chalon (F2c)		
		NISMES (F2a, F2b)	NISMES	PRESLES/NISMES (F2 II a)

FIG. 3. — Frasnian lithostratigraphic units of the Namur-Dinant Basin; the former stratigraphic subdivisions introduced by Maillieux & Demanet (1929) are indicated between brackets. The conodont zonation (Bultynck *et al.* 2000) is related only to the southern border of the Dinant Synclinorium. Formations are in capitals, members in lower case. Abbreviation: **PM**, Petit-Mont Member.

#### SOUTHERN BORDER OF THE DINANT SYNCLINORIUM AND PHILIPPEVILLE ANTICLINORIUM

The Grand Breux Formation (*P. hassi* to Lower *P. rhenana* zones) is composed of the Bieumont, Lion and Boussu-en-Fagne members. In the Frasnes area where the reference sections are located, the Bieumont Member begins with 16 m of micritic to bioclastic, argillaceous to nodular limestone and ends with 21 m of micritic to argillaceous limestone (Coen-Aubert 1994). The Lion Member includes greyish massive carbonate buildups, up to 250 m thick (Monty *et al.* 1988). The Boussu-en-Fagne Member attains up to 81 m in thickness (Coen-Aubert & Boulvain *in* Boulvain *et al.* 1999) and is mainly composed of shales with some nodular levels and limestone beds.

The Neuville Formation (Lower *P. rhenana* Zone) consists of nodular limestone with intercalations

of shales in the Philippeville Anticlinorium where its thickness is always small (about 10 m). On the southern flank of the Dinant Synclinorium, shales with limestone nodules predominate and the formation attains up to 110 m in thickness (Coen 1977) but it thins eastward. The reddish carbonate buildups (30 to 80 m thick), developed within the formation, are assigned to the Petit-Mont Member (Boulvain *et al. in* Boulvain *et al.* 1999).

The Matagne Formation starts with one or several beds of limestone with goniatites and bivalves followed by fine greenish-brown to black shales. Its thickness attains more than 50 m on the southern flank of the Dinant Synclinorium but is reduced to about 10 m in the Philippeville Anticlinorium (Coen *et al. in* Boulvain *et al.* 1999). It is highly diachronous because it begins in the basal part of the Upper *P. rhenana* Zone on the southern flank of the Dinant Synclinorium whereas it is only developed

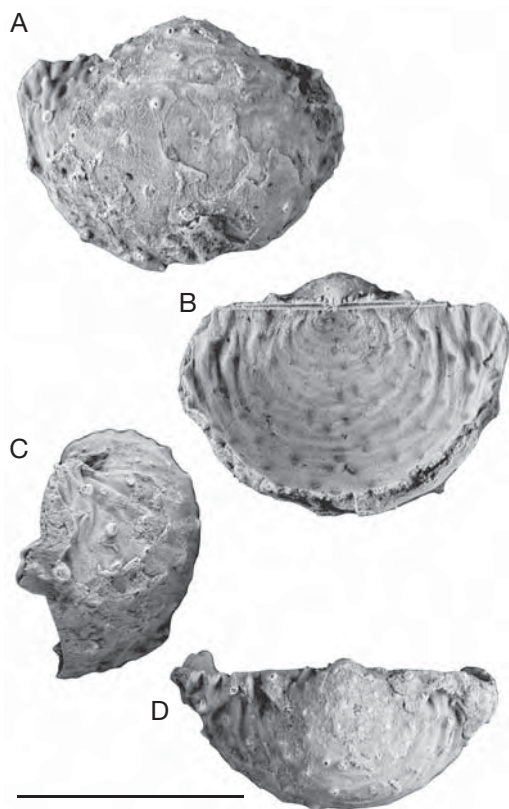


FIG. 4. — *Productella subaculeata* (Murchison, 1840), almost complete shell (IRScNB a12369), loc. BM-2003-6, Grands Breux Formation (Boussu-en-Fagne Member): A, ventral view; B, dorsal view; C, lateral view; D, posterior view. Scale bar: 10 mm.

in the *P. linguiformis* Zone in the Philippeville Anticlinorium (Bultynck *et al.* 1998).

On the southeastern border of the Dinant Synclinorium, the Matagne Formation is replaced by the Barvaux Formation (about 90 m thick; Upper *P. rhenana* to Lower *P. triangularis* zones), characterized by purplish to green shales with some sandy layers and nodules (Coen *in* Boulvain *et al.* 1999).

The Famenne Group includes the Senzeille and Mariembourg formations. Bultynck & Dejonghe (2002) proposed to make no distinction between these two lithostratigraphic units and only to designate them by the term Famenne Group because the boundary between these two formations is mainly based on a discrete oolitic ironstone bed or on palaeontological

markers (rhynchonellid index species). The “Senzeille Formation” (Lower to Upper *P. triangularis* zones) consists of olive-green to greyish-green shales with thin limestone and sandstone layers; its thickness reaches 150 m on the southern margin of the Dinant Synclinorium according to Bultynck & Dejonghe (2002). The essentially shaly Mariembourg Formation (*P. crepida* Zone) has not been sampled.

#### NORTHERN BORDER OF THE DINANT SYNCLINORIUM, NAMUR SYNCLINORIUM AND VESDRE AREA

The Aisemont Formation (about 20 m; Lower to basal part of the Upper *P. rhenana* Zone) comprises limestones and argillaceous limestones in its lower and upper parts; the middle part consists of shales and nodular shales (Lacroix *in* Boulvain *et al.* 1999). Both limestone horizons are known in the Belgian literature as the first and second “biostromes with *Phillipsastrea*” of Coen-Aubert & Lacroix (1979) but the “second biostrome” is devoid of biostromal units (Poty & Chevalier 2007).

The Lambermont Formation (50 to 100 m thick; Upper *P. rhenana* to *P. triangularis* zones) mainly consists of shales and nodular shales with intercalations of limestone beds (Laloux & Ghysel *in* Boulvain *et al.* 1999). Its middle part is characterized by the “third biostrome with *Phillipsastrea*” (Coen-Aubert & Lacroix 1979), especially developed in the Vesdre area and consisting of argillaceous, nodular limestones and calcareous shales with a biostromal bed rich in massive rugose corals.

The Hodimont Formation (Upper *P. triangularis* to Lower *P. marginifera* zones) consists of grey-green or purple micaceous shales (siltstones) including limestone nodules and decimetre-thick red layers of oolitic hematite (Laloux *et al.* 1996); its thickness varies between 50 to 110 m.

#### MATERIAL AND METHODS

All the material is deposited at the Palaeontological Department of the Institut royal des Sciences naturelles de Belgique in Brussels and is catalogued with the prefix IRScNB. The specimens with the prefix MB are curated in the Museum für Naturkunde,

Humboldt-Universität, Berlin (Germany). The prefix MGL is for the Musée d'Histoire naturelle de Lille (formerly Musée Gosselet), Lille (France). The prefix SUI indicates the Paleontology Repository, University of Iowa, Iowa City (USA). The prefix ULP is for the Université Louis Pasteur, Institut de Géologie, Strasbourg (France).

The classification follows the *Treatise on Invertebrate Paleontology* (Kaesler 2000a, b, 2002, 2006).

The prefixes BM and JG indicate respectively B. Mottequin and J. Godefroid's localities. The name of a locality followed by a number (e.g., Senzeille 6840) corresponds to the name of an outcrop as it is recorded in the files of the IRScNB.

## SYSTEMATICS

### Order PRODUCTIDA

Sarytcheva & Sokolskaya, 1959

Suborder PRODUCTIDINA Waagen, 1883

Superfamily PRODUCTOIDEA Gray, 1840

Family PRODUCTELLIDAE Schuchert, 1929

Subfamily PRODUCTELLINAE Schuchert, 1929

Genus *Productella* Hall, 1867

TYPE SPECIES. — *Productus subaculeatus* Murchison, 1840 by subsequent designation (Oehlert 1887a: 1279).

*Productella subaculeata* (Murchison, 1840)

(Fig. 4)

*Productus subaculeatus* Murchison, 1840: 255, pl. 2, figs 9a-c. — Maillieux 1909b: 143.

*Productella subaculeata* — Maillieux 1922b: 18; 1933: 81; 1940: 26; 1941b: 7. — Maillieux in Kaisin *et al.* 1922 (?): 23. — Maillieux in Asselberghs & Maillieux 1925: 166. — Dumon 1929: 164.

MATERIAL EXAMINED. — BM-2003-6 (12 articulated specimens, 23 ventral valves); BM-2003-7 (nine articulated specimens, 14 ventral valves).

#### REMARKS

These small-sized and strongly concavoconvex shells are characterized by a narrow ginglymus in both valves, few spine bases, more or less aligned, and rugae on both

valves (especially prominent posterolaterally); they are assigned to Murchison's species. Veevers (1959a: 902, 903, text-figs 1, 2) and Brousmiche (1973: 120-130, pl. 15, figs 1-35, pl. 16, figs 1-5, pl. 17, figs 1-8, 24-29) revised the species on the basis of specimens from Ferques (Boulonnais, France). *Productella larminati* Rigaux, 1908 and *P. dutertrei* Rigaux, 1908 have been included in *P. subaculeata* by Brousmiche (1973) after the results of statistical study applied to her material. According to Brice (1988: table 2), *P. subaculeata* is recognized from the Blacourt Formation (term b of the Griset Member) up to the Hydrequent Formation in the Boulonnais. In the Namur-Dinant Basin, *P. subaculeata* occurs within the Grands Breux Formation (Boussu-en-Fagne Member) and probably in the lower part of the Neuville Formation at the southern border of the Dinant Synclinorium on the basis of the current data; it is also reported within the Neuville Formation in the Philippeville Anticlinorium.

*Productella* sp.

(Fig. 5; Table 1)

MATERIAL EXAMINED. — BM-2001-2 (16 articulated specimens, 16 ventral valves); BM-2002-1 (22 articulated specimens, 59 ventral valves); BM-2002-8 (two articulated specimens, one ventral valve); BM-2003-3 (three articulated specimens, four ventral valves); BM-2003-4 (two articulated specimens, one ventral valve); BM-2003-5 (three articulated specimens, six ventral valves).

#### REMARKS

Productellids of medium size collected at the base of the Lambermont Formation and within the Les Valisettes Formations are assigned to the genus *Productella*. They are characterized by strongly concavoconvex and wider than long shell with linear ginglymus on both valves. On the ventral valve, the density of large spine bases is quite variable. Some shells display elongate spine bases resembling costae. Rugae are well developed in the posterior part of the ventral valve (less developed on dorsal valve) and up to three cardinal spines on each side of the umbo have been observed. Although the species occurs in abundance in some localities, the specimens are generally incomplete and/or distorted. Medium-sized forms have been described in the Frasnian of the Boulonnais by Rigaux (1908: 32, 33)

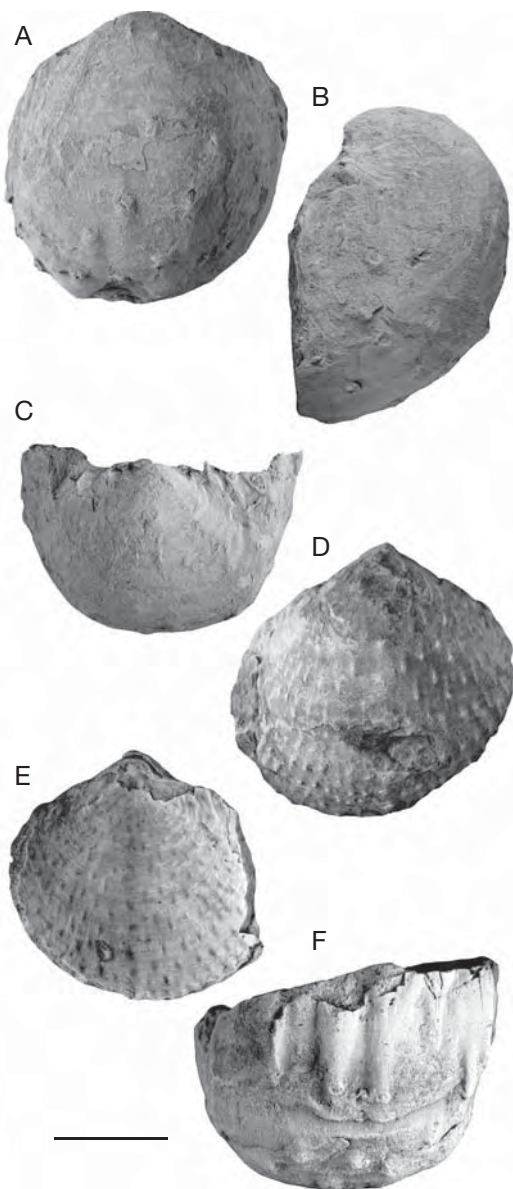


FIG. 5. — *Productella* sp.: **A-C**, complete ventral valve (IRScNB a12372), loc. BM-2001-2, Lambermont Formation; **D, E**, almost complete shell (IRScNB a12374), loc. BM-2002-1, Lambermont Formation; **F**, almost complete ventral valve (IRScNB a12375), loc. BM-2001-2, Lambermont Formation; **A, D**, ventral views; **B**, lateral view; **C**, posterior view; **E**, dorsal view; **F**, anterior view. Scale bar: 10 mm.

as *Productella dutertrei* for which he gave the following measurements: width: 38 mm; length: 32 mm; thickness: 22 mm. In her revision of the Productidina

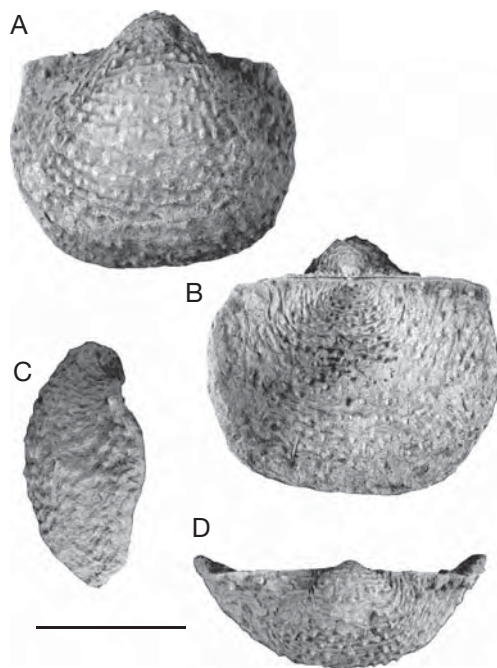


FIG. 6. — ?*Caucasiproductus* sp., complete shell (IRScNB a12376), loc. BM-2003-12, Neuville Formation: **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view. Scale bar: 10 mm.

of the Devonian from Ferques, Brousmiche (1973: 120) indicated: “Les espèces *Productella larminati* et probablement *Productella dutertrei* ne sont en fait que des variantes de *Productella subaculeata*.” The doubt concerning *P. dutertrei* is due to the small number of available specimens which did not permit a statistical study. According to Brousmiche (1973: 134), their “gigantic” size may be explained by particular ecologic conditions. In the Belgian material, numerous specimens display elongate spine bases looking like discontinuous costae as in the genus *Spinulicosta* Nalivkin, 1937. This feature seems to be more pronounced than in the specimens figured by Rigaux (1908: pl. 2, fig. 20) and Brousmiche (1973: pl. 15, fig. 30). Some of them are indeed 2.5 times wider than the neotype of *P. subaculeata* selected by Brousmiche (1973: 120). *Productella* sp. has been collected within the Frasnian part of the Lambermont Formation (northern part of the Dinant Synclinorium, Vesdre area) as well as in the Les Valisettes Formation (Philippeville Anticlinorium).



Superfamily ECHINOCONCHOIDEA Stehli, 1954  
 Family SENTOSIIDAE McKellar, 1970  
 Subfamily CAUCASIPRODUCTINAE Lazarev, 1987

Genus *Caucasiproductus* Lazarev, 1987

TYPE SPECIES. — *Caucasiproductus gretchishnikovae* Lazarev, 1987, by monotypy.

?*Caucasiproductus* sp.  
 (Figs 6; 7; Table 1)

*Strophalosia productoides* – Maillieux 1909b: 122, 142, 143.

*Strophalosia productoides* – Maillieux 1922b: 18; 1933: 81; 1939: 3; 1940: 26; 1941b: 7. — Maillieux in Asselberghs & Maillieux 1925: 166. — Dumon 1929: 164.

MATERIAL EXAMINED. — BM-2003-6 (two articulated specimens); BM-2003-7 (five articulated specimens), BM-2003-9 (one articulated specimen); BM-2003-11 (41 articulated specimens, 15 ventral valves).

#### DESCRIPTION

Shell medium-sized, wider than long (width/length ratio: 1.11-1.45), semi-oval to semicircular in outline; lateral margins more or less rounded, anterior margin straight; ginglymus in both valves.

Ventral valve regularly curved in lateral profile with an accentuation in the umbonal area (ventral valve unrolled length/length ratio: 1.32-1.60), dome-shaped in posterior view; flanks sloping moderately towards lateral commissure; shoulder lines broken by a prominent umbo; shoulder and apical angles between 129-152° and 96-134°, respectively; delthyrium closed by a convex pseudodeltidium (?).

Dorsal valve concave with flanks sloping gently towards the centre of the valve; posterolateral extremities; notothyrium closed by the base of the cardinal process.

On ventral valve, numerous spine bases, thickest on posterolateral extremities; some specimens with an alignment of large spine bases in the plane of symmetry. On dorsal valve, spines numerous, thin, disposed parallel to the surface; rugae developed on both valves.

Ventral interior with short teeth; apical cavity large; median septum short.

Dorsal interior with bilobed cardinal process; dental sockets small; median septum low and long (about the half of the unrolled length of the valve).

#### DISCUSSION

These specimens are tentatively assigned to *Caucasiproductus* because they have spines on both valves and a short ventral septum, but the absence of dissociated dorsal valves prevents detailed study of their internal morphology (angle of divergence of the inner socket ridges, etc.); the transverse sections gave some but still insufficient information. This species has been long misidentified with *Orthis productoides* Murchison, 1840 from the Boulonnais. The examination of the types designated by Brousmiche (1973: 130) housed at the MGL indicates that the Belgian specimens differ clearly from Murchison's species by their ventral area which is markedly less developed and by the absence of a cicatrix at the ventral umbo. Brousmiche (1973: 130, 131, pl. 16, figs 14-17, pl. 17, figs 18-23) revised Murchison's species and assigned it to the genus *Whidbornella* Reed, 1943 following Muir-Wood & Cooper (1960: 163) but Lazarev (1989: 39) included it in his new genus *Rhytialosia*.

#### DISTRIBUTION

?*Caucasiproductus* sp. occurs in the Grands Breux (Boussu-en-Fagne Member) and Neuville formations (southern and southeastern flanks of the Dinant Synclinorium). It is likely that the specimens from the "schistes de Barvaux" listed by Maillieux (1939: 3; 1941b: 7) originate from the Barvaux Formation as defined by Coen (in Boulvain *et al.* 1999) but, up to now, recent surveys of the formation failed to find new specimens.

Superfamily LINOPRODUCTOIDEA Stehli, 1954

Family MONTICULIFERIDAE

Muir-Wood & Cooper, 1960

Subfamily DEVONOPRODUCTINAE

Muir-Wood & Cooper, 1960

Genus *Devonoproductus* Stainbrook, 1943

TYPE SPECIES. — *Productella walcotti* Fenton & Fenton, 1924, by original designation.

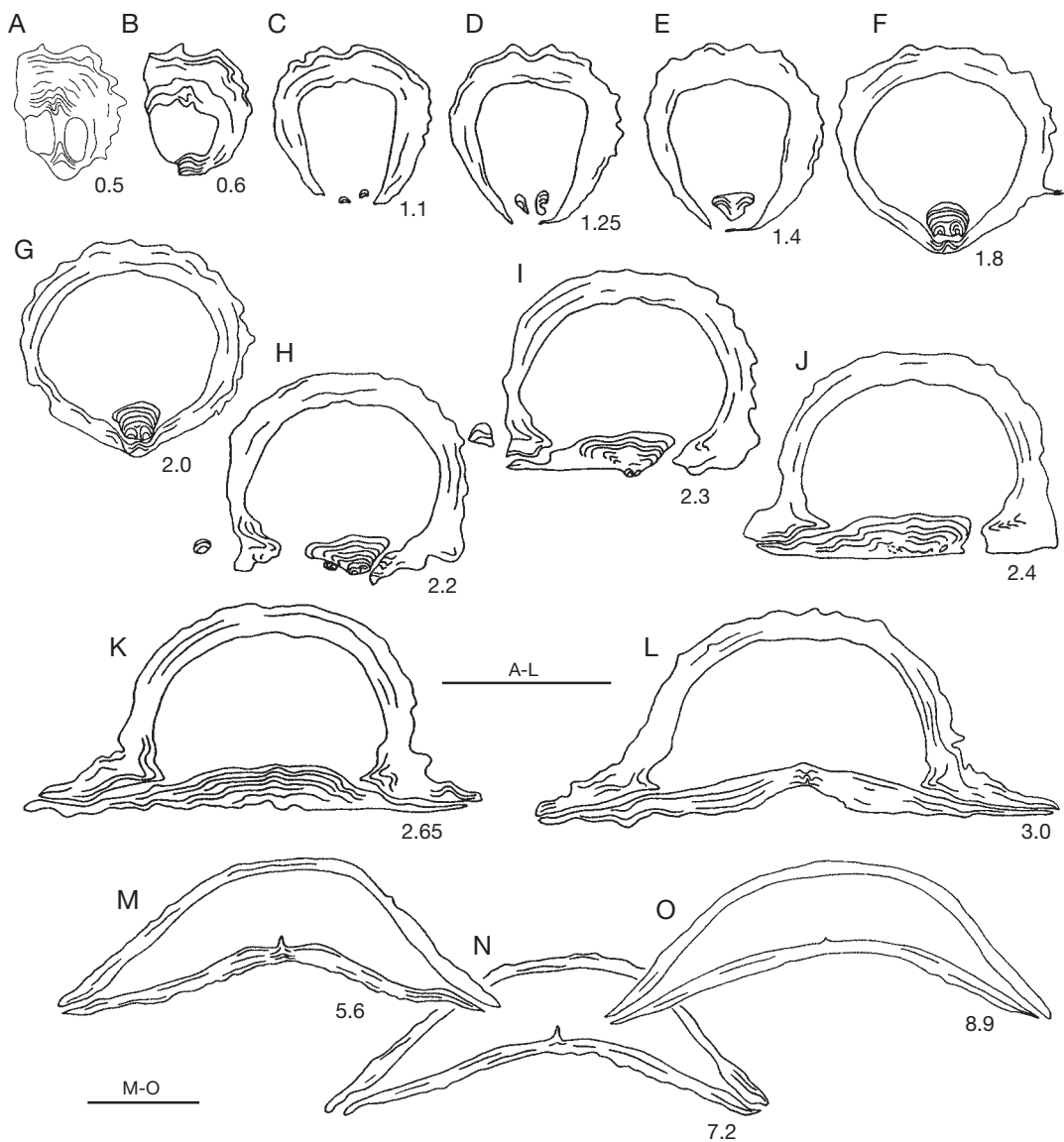


FIG. 7. — Transverse serial sections of ?*Causiproductus* sp. (IRScNB a12385), loc. BM-2003-11, Grands Breux Formation (Boussu-en-Fagne Member). Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

*Devonoproductus* sp. A  
(Figs 8A-H; 9; Table 1)

MATERIAL EXAMINED. — BM-2002-8 (four articulated specimens, one ventral valve); BM-2003-3 (30 articulated specimens, five ventral valves); BM-2003-4b (two articulated specimens, one dorsal valve).

DESCRIPTION

Shell large for the genus, wider than long (width/length ratio: 1.08-1.25), concavoconvex, rounded subquadrangular to subcircular in outline; posterolateral margins straight; anterior margin rounded; posterolateral commissure slightly deflected ventrally,

anterior margin rectimarginate; widest at mid-length or posteriorly.

Ventral valve dome-shaped in posterior view; flanks sloping moderately towards lateral commissure; in lateral profile, upper surface regularly curved except in the umbonal area where it is more pronounced (ventral valve unrolled length/length ratio: 1.25-1.52); shoulders line broken by a prominent umbo; shoulders and apical angle between 126-146° and 98-114°, respectively; ginglymus narrow, strongly curved.

Dorsal valve of variable concavity, but generally strong; flanks sloping moderately towards the centre of the valve; posterolateral extremities flattened.

On ventral valve, costellae with spine bases (diameter close to 0.5 mm) (the poor state of preservation did not permit an analysis of the mode of increase of the costellae); growth lamellae rare. On dorsal valve, numerous growth lamellae with indistinct capillae developed in the visceral disc (9-11/5 mm), more widely spaced close to the anterior margin.

Ventral interior with small and short teeth; apical cavity large, not subdivided by a median septum.

Dorsal interior with large and bilobed cardinal process; median septum extending to the half of the unrolled length of the valve, originating anteriorly to the base of the cardinal process.

## DISCUSSION

These specimens have been previously identified as *Productella sericea* (= *Devonoproductus sericeus* (von Buch, 1838)) by Maillieux (1940: 26). Von Buch's species is poorly known and would have to be re-investigated because, to the knowledge of the author, only Dames (1868: pl. 11, fig. 4) illustrated specimens from its *stratum typicum* (Oberkunzendorf limestone in Silesia). Racki (1992: 301, 302, figs 2F, G, 3L-N, R) described specimens identified as *D. sericeus* originating from the Late Givetian and the Early Frasnian of the Holy Cross Mountains (Poland). Those from the Frasnian of the Russian Platform identified as *D. sericeus* by Liashenko (1959: 131, pl. 22, figs 1, 2) have been included later in *D. gracilis* (Liashenko, 1973). Until von Buch's species becomes better known, I prefer to keep the Belgian form in open nomenclature. *Devonoproductus* sp. A is separated from the Russian

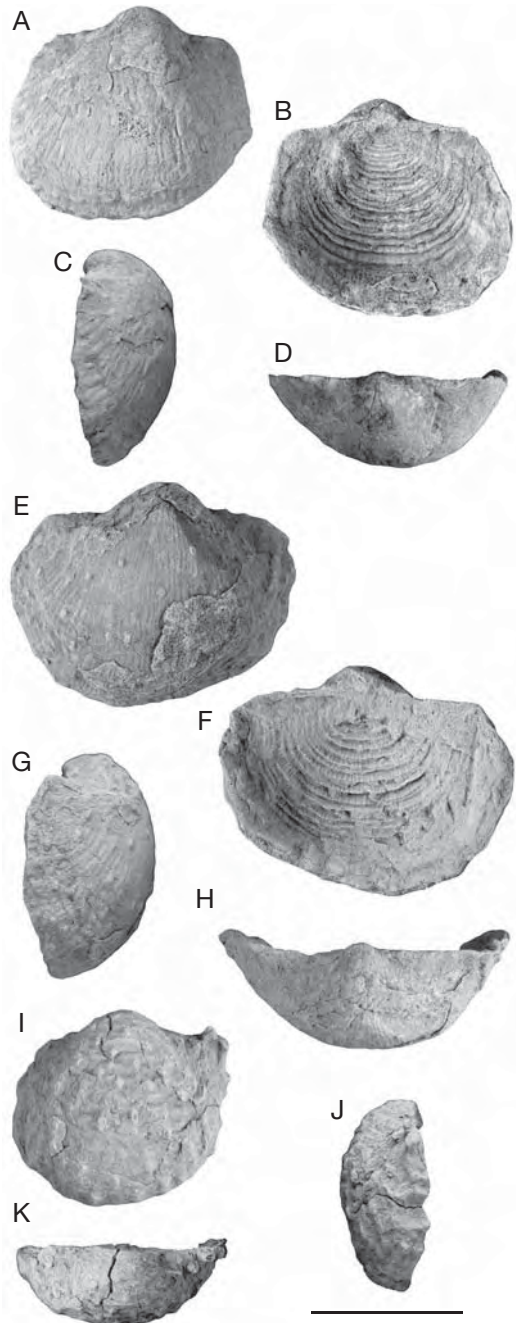


FIG. 8. — A-H, *Devonoproductus* sp. A, loc. BM-2003-3, Les Valisettes Formation; A-D, slightly deformed shell (IRScNB a12386); E-H, complete shell (IRScNB a12387); I-K, *?Rhytialosia* sp., almost complete shell (IRScNB a12394), loc. BM-2003-3, Les Valisettes Formation; A, E, I, ventral views; B, G, dorsal views; C, F, J, lateral views; D, H, K, posterior views. Scale bar: 10 mm.

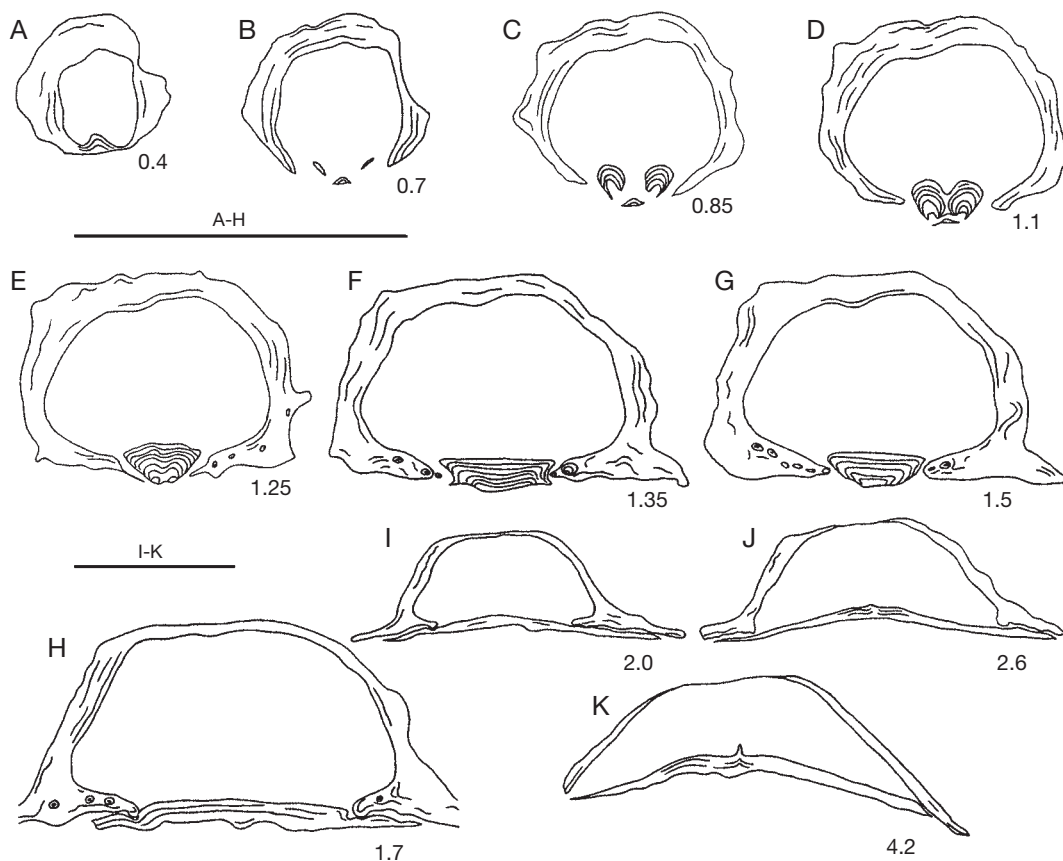


FIG. 9. — Transverse serial sections of *Devonoproductus* sp. A (IRScNB a12393), loc. BM-2003-3, Les Valisettes Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

species *D. karasikae* (Liashenko, 1958), *D. gracilis* and *D. jaregae* Alekseeva & Oleneva, 2000 by its greater size, its more inflated ventral valve and its lower density of spines. *Devonoproductus* sp. A is distinguished from *D. walcotti* (Fenton & Fenton, 1924) by its wider than long shell, a less prominent umbo, and a lower density of spines. The shell of *Devonoproductus* sp. A is larger and more developed in width than that of *D. intermedius* Cooper & Dutro, 1982. *Devonoproductus* sp. A differs from *D. secundus* Crickmay, 1963 by its wider than long shell and a more curved beak. *Devonoproductus* sp. A reaches a size nearly twice that of *D. aff. leonensis* Garcia-Alcalde, 1973 (*nomen nudum*) described by Racheboeuf (1984: 156, 157) and does not display a cicatrix.

#### DISTRIBUTION

*Devonoproductus* sp. A occurs within the Les Valisettes Formation (Philippeville Anticlinorium). Some specimens belonging to the genus *Devonoproductus* have been collected in the Grands Breux Formation (Boussu-en-Fagne Member) on the southern flank of the Dinant Synclinorium (BM-2003-10) but their poor state of preservation precludes a specific identification.

#### Subfamily RHYTIALOSIINAE Lazarev, 1989

#### Genus *Rhytialosia* Lazarev, 1989

TYPE SPECIES. — *Productus petini* Nalivkin, 1930, by original designation.

*?Rhytialosia* sp.  
(Fig. 8I-K; Table 1)

MATERIAL EXAMINED. — BM-2003-3 (seven articulated valves).

REMARKS

The main external characters of these concavoconvex shells are: cicatrix present at the ventral umbo, ventral area well-developed, rugae more prominent ventrally, recumbent spines only on ventral valve and thickened near the hinge. The rarity of the material and the lack of knowledge about the internal characters combined with their poor state of preservation did not permit a more accurate identification. Up to now, *?Rhytialosia* sp. has been collected only within the Les Valisettes Formation (Philippeville Anticlinorium).

Order ORTHIDA Schuchert & Cooper, 1932  
Suborder DALMANELLIDINA Moore, 1952  
Superfamily DALMANELLOIDEA Schuchert, 1913  
Family DALMANELLIDAE Schuchert, 1913  
Subfamily CORTEZORTHINAE  
Johnson & Talent, 1967

Genus *Cariniferella* Schuchert & Cooper, 1931

TYPE SPECIES. — *Orthis carinata* Hall, 1843, by original designation.

*Cariniferella* sp. A  
(Figs 10-12)

MATERIAL EXAMINED. — BM-2002-8 (one articulated specimen, one ventral valve); BM-2003-10 (five articulated specimens); JG-1995-4 (three articulated specimens); Couvin 6158p. (39 articulated specimens, one ventral valve, one dorsal valve).

DESCRIPTION

Shell small-sized, wider than long (width/length ratio: 1.13-1.37), dorsibiconvex to ventribiconvex, generally rounded subrectangular in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.36-0.64); widest about mid-length or more anteriorly in more rounded specimens; anterior margin straight or slightly excavated by sulcus; anterior commissure unisulcate.

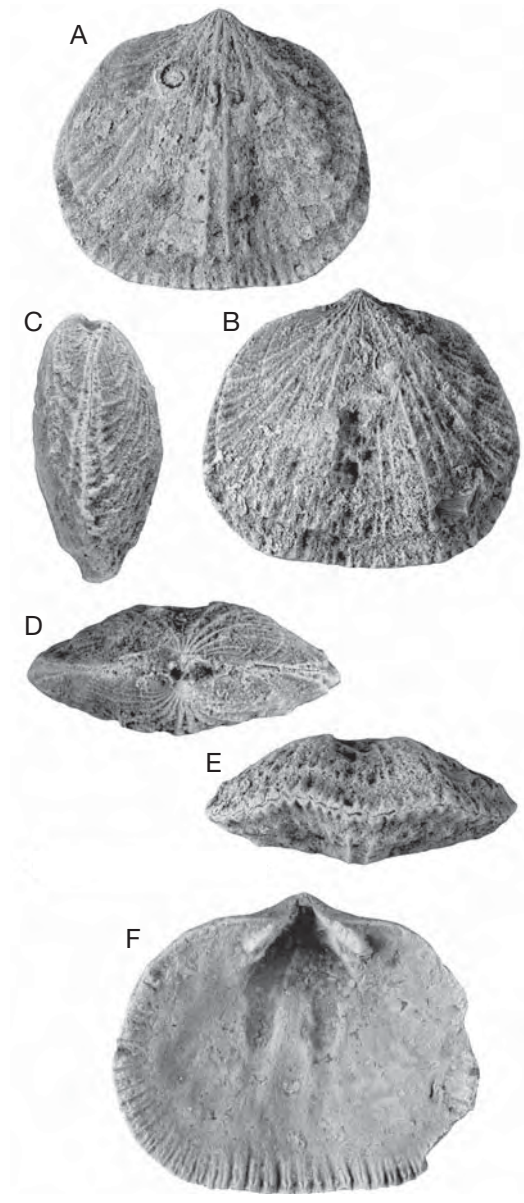


FIG. 10. — *Cariniferella* sp. A, Grands Breux Formation (Boussu-en-Fagne Member): **A-E**, complete shell (IRScNB a12345), loc. BM-2003-10; **F**, ventral valve (IRScNB a12347), loc. Couvin 6158p.; **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view; **F**, internal view. Scale bar: 10 mm.

Ventral valve regularly and moderately curved in lateral profile; flanks sloping gently towards lateral commissure; posterolateral areas in some specimens

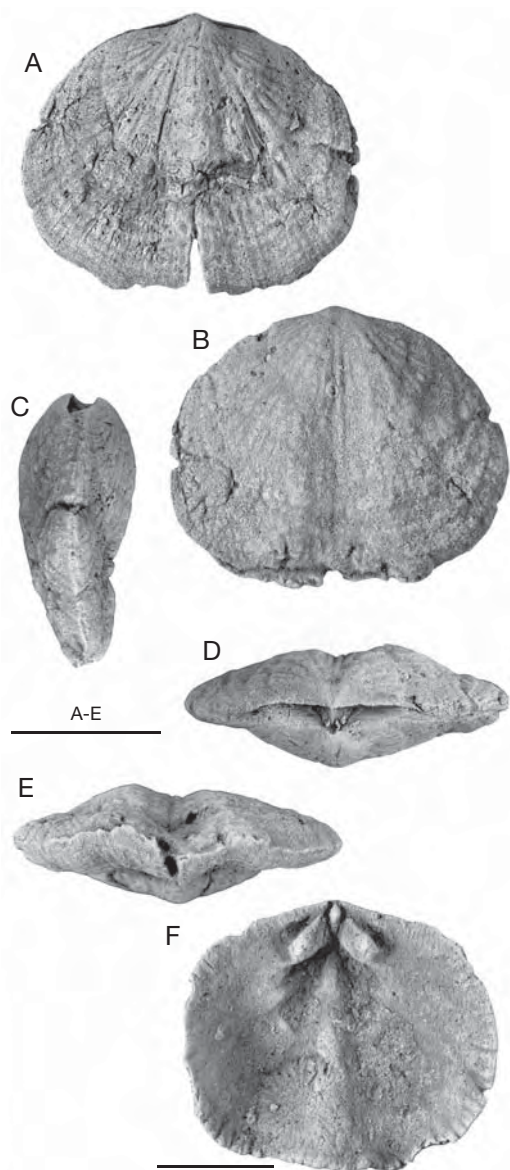


FIG. 11. — *Cariniferella* sp. A, Grands Breux Formation (Boussu-en-Fagne Member): **A-E**, complete shell (IRScNB a12348), loc. Couvin 6158p.; **F**, dorsal valve (IRScNB a12346), loc. Couvin 6158p.; **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view; **F**, internal view. Scale bars: A-E, 10 mm; F, 5 mm.

flattened; fold originating near the beak, variable in height, with rounded top; beak hardly curved; shoulder lines broken; shoulder and apical angles

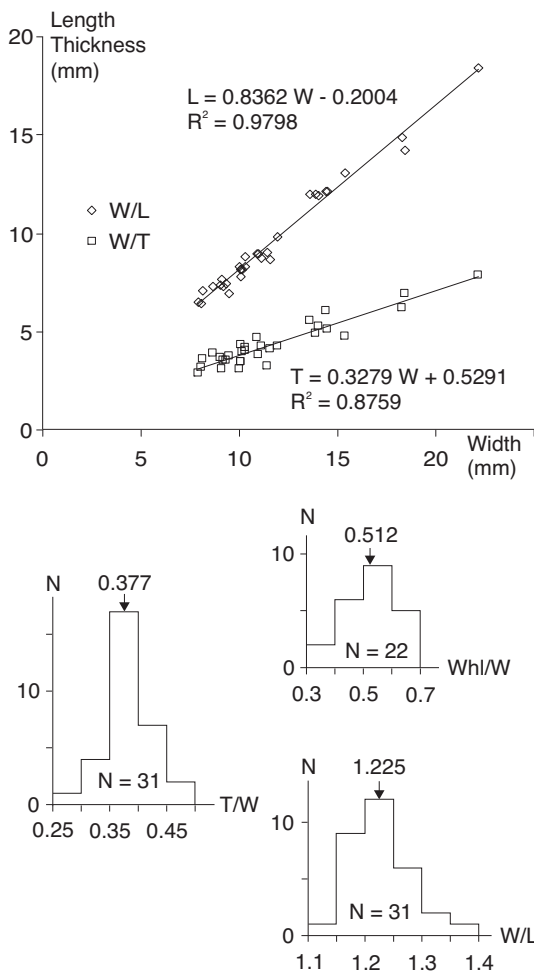


FIG. 12. — *Cariniferella* sp. A (loc. BM-2003-10, JG-1995-4, and Couvin 6158p., Grands Breux Formation [Boussu-en-Fagne Member]). Scatter diagrams of shell width (**W**) to shell length (**L**), shell width to shell thickness (**T**); frequency diagrams of **W/L**, **T/W**, and **Whl** (hinge line width)/**W**. Arrows indicate the means.

between 125-135° and 105-119°, respectively; interarea cata-apsacline (up to 1.7 mm in height), concave; delthyrium open.

Dorsal valve regularly and moderately curved in lateral profile; sulcus wide (sulcus width/width ratio: 0.40-0.51), originating close to beak; tongue 3.59-6.64 times wider than high, subrounded to subtriangular in outline; interarea orthocline, flat, less developed than the ventral one; notothyrium closed by cardinal process.

Ornamentation fascicostellate; costellae appearing by bifurcation of costae; 11-12 costae and costellae per 5 mm at the anterior margin; growth lamellae rare, irregularly spaced.

Ventral interior with short and simple teeth; muscle field cordiform, not delimited by crests, excavated, extending to the half of the valve length.

Dorsal interior with long and trilobed cardinal process; dental sockets anteriorly delimited by brachio-phores, open laterally; brachio-phores robust, bounding posteriorly the muscle field; muscle field deeply excavated, divided by a prominent median ridge; boundary between the posterior and anterior adductor muscles not clear due to poor preservation.

#### DISCUSSION

These specimens could belong to a new species but the material is considered as insufficient at this stage. *Cariniferella* sp. A has been previously misidentified as *C. dumontiana* (de Verneuil, 1850) from which it differs clearly in its smaller size, its more rounded and less transverse outline. *Cariniferella* sp. A displays a coarser ornamentation than *C. elmira* (Williams, 1908) and, moreover, its cardinal angles are more rounded. *Cariniferella* sp. A differs from *C. virginia* (Williams, 1908) by its less transverse outline, as well as by its maximum width located about mid-length or more anteriorly and not close to the posterior margin as it is the case for the North American species. *Cariniferella* sp. A is differentiated from *C. iowaensis* Stainbrook, 1945 by its less inflated shell and by its less curved ventral beak. *Cariniferella* sp. A differs from *C. mistiaeni* Brice, 1981 by its slightly coarser ornamentation, its less developed sulcus and fold, as well as by its less transverse outline. *Cariniferella* sp. A is less inflated than *C. alleni* Cooper & Dutro, 1982 and its anterior margin is less excavated. *Cariniferella* sp. A displays a flattened profile similar to that of *C. costellata* Cooper & Dutro, 1982 but it attains a greater size and its outline is less transverse.

#### DISTRIBUTION

At the southern border of the Dinant Synclinorium, *Cariniferella* sp. A is known in the Grands Breux (Boussu-en-Fagne Member) and Neuville formations; the species occurs also within the latter formation in the Philippeville Anticlinorium.

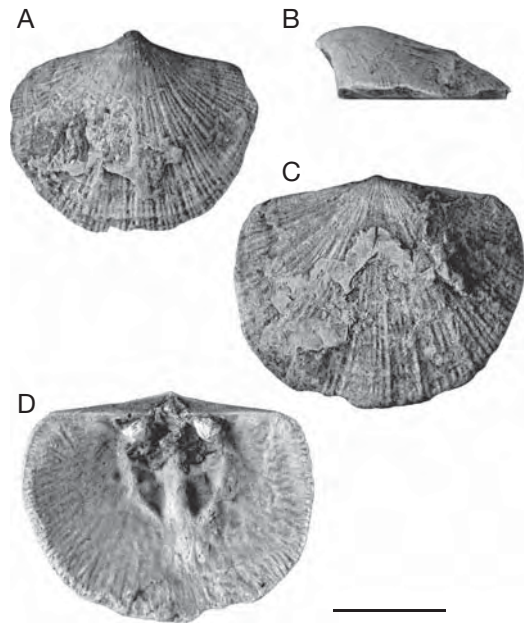


FIG. 13. — ?*Isorthinae* gen. et sp. indet., loc. BM-2004-1, Les Valisettes Formation: **A, B**, ventral valve (IRScNB a12350); **C, D**, dorsal valve (IRScNB a12349); **A**, external view; **B**, lateral view; **C**, external view; **D**, internal view. Scale bar: 5 mm.

#### Subfamily ?ISORTHINAE Schuchert & Cooper, 1931

#### ?*Isorthinae* gen. and sp. indet. (Fig. 13; Table 2)

**MATERIAL EXAMINED.** — BM-2004-1 (one ventral valve, two dorsal valves); BM-2004-2 (one dorsal valve); Senzeille 6840 (one ventral valve).

#### DESCRIPTION

Shell small-sized, probably ventribiconvex (only dissociated valves available); wider than long, semi-elliptical in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.76-0.85); widest in the posterior part of the shell; lateral and anterior margin rounded; anterior commissure recrimarginate or very slightly unisulcate.

Ventral valve weakly convex; flanks sloping moderately towards lateral commissure; no sulcus; shoulder lines broken by prominent umbo; shoulder and apical angles between 134-135° and 105-114°, respectively; interarea triangular, 3.21-3.23 times

wider than high, cata-apsaline, slightly concave; delthyrium wide, open.

Dorsal valve semi-elliptical in outline; sulcus shallow, poorly defined, originating in the posterior part of the valve; interarea linear, anacline, slightly concave.

Ornamentation multicostellate; costellae increasing by intercalation (bifurcation may occur but the preservation is deficient); about 18 costae and costellae per 5 mm at the anterior margin; some thickened growth lamellae.

Ventral interior not observed.

Dorsal interior with small and laterally open dental sockets; cardinal process bilobed; brachiophores diverging at an angle between 69-92°; brachiophore bases extending anteriorly as ridges bordering the muscle field; muscle field semi-elliptical, its length corresponding to a little bit more than the half of the valve length; anterior adductor muscles small, triangular, separated from the posterior ones by a transverse ridge perpendicular to the prominent median ridge that extends beyond the muscle field; internal surface crenulated along the anterior and lateral margins.

#### DISCUSSION

These specimens are tentatively assigned to the subfamily Isorthinae because the internal characters of the dorsal valve are in accordance with Harper's (2000: 789) definition of the subfamily, the ventral valve interior is still unknown. The ventral valve originating from the locality Senzeille 6840 has been identified as *Streptorhynchus undiferus* (Schnur) by Maillieux (1941b: 6).

#### DISTRIBUTION

These unidentified Isorthinae are recognized within the Les Valisettes Formation close to the carbonate buildups of the Petit-Mont Member (Philippeville Anticlinorium).

Family RHIPIDOMELLIDAE Schuchert, 1913  
Subfamily RHIPIDOMELLINAE Schuchert, 1913

Genus *Aulacella* Schuchert & Cooper, 1931

TYPE SPECIES. — *Orthis eifliensis* Schnur, 1853, by original designation.

*Aulacella* sp.  
(Fig. 14A-E)

#### REMARKS

Among the orthids collected in Boussu-en-Fagne (BM-2003-10), several specimens differ from *Cariniferella* sp. A by the absence of sulcus and fold, an anterior commissure vaguely undulating and a thinner ornamentation. In anticipation of additional material, they are assigned to the genus *Aulacella*.

*Aulacella aggeris* n. sp.  
(Figs 14F-Q; 15; 16)

*Orthis arcuata* – Gosselet 1877: 319; 1879 (e.p.): 319; 1880: pl. 5, fig. 11; 1888: 540, 558. — Bayet 1888: 47.

*Aulacella arcuata* – Maillieux 1933: 85; 1941b (e.p.): 3. — Sartenaer 1970: 356. — Bultynck & Martin 1995: 9.

HOLOTYPE. — IRScNB a12353.

ETYMOLOGY. — Latin, *agger*, embankment in reference to the banking up of the Senzeille railway section, the historical stratotype of the Frasnian/Famennian boundary.

LOCALITY AND AGE. — Reference section of the Senzeille railway section (Bultynck & Martin 1995), base of the Famenne Group ("Senzeille Formation", *Palmatolepis triangularis* Zone).

MATERIAL EXAMINED. — BM-2003-2 (25 articulated specimens, five ventral valves, five dorsal valves); Senzeille 6839b (86 articulated specimens, three ventral valves, one dorsal valve).

DIAGNOSIS. — Shell wider than long (width/length ratio: 1.09-1.36), dorsibiconvex (maximum width: 15.5 mm; maximum length: 16.3 mm; maximum thickness: 9.4 mm); anterior commissure rectimarginate to uniplicate (rarely paraplicate); 10 or 11 costae and costellae per 5 mm at the anterior margin.

#### DESCRIPTION

Shell medium-sized, wider than long (width/length ratio: 1.09-1.36), dorsibiconvex, subquadrangular in outline; hinge line shorter than greatest width (hinge line width/width: 0.34-0.56); maximum width at about mid-length or slightly anteriorly; anterior commissure rectimarginate to uniplicate, rarely paraplicate.



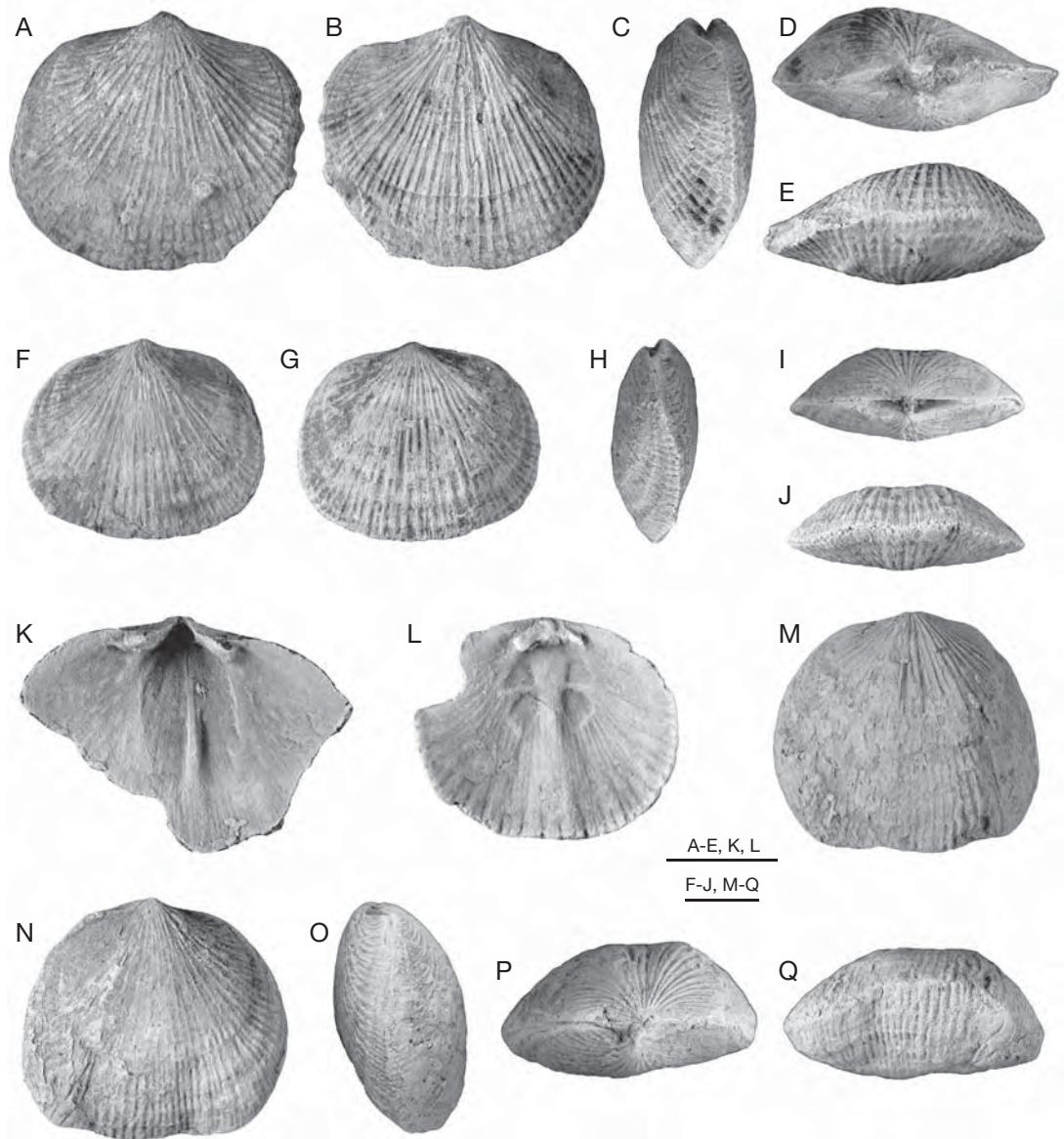


FIG. 14. — **A-E**, *Aulacella* sp., slightly deformed shell (IRScNB a12352), loc. BM-2003-10, Grands Breux Formation (Boussu-en-Fagne Member); **F-Q**, *Aulacella aggeris* n. sp., Famenne Group ("Senzeille Formation"); **F-J**, complete shell (holotype IRScNB a12353), loc. BM-2003-2; **K**, incomplete ventral valve (IRScNB a12354), loc. BM-2003-2; **L**, incomplete dorsal valve (IRScNB a12356), loc. Senzeille 6839b; **M-Q**, slightly deformed complete shell (IRScNB a12355), loc. Senzeille 6839b; **A, F, M**, ventral views; **B, G, N**, dorsal views; **C, H, O**, lateral views; **D, I, P**, posterior views; **E, J, Q**, anterior views; **K, L**, internal views. Scale bars: 5 mm.

Ventral valve regularly convex in lateral profile, semi-elliptical in posterior view; sulcus either absent or shallow, with bottom flattened to rounded

at front (more rarely a slight median fold occurs); tongue little or moderately straightened, semi-oval to trapezoidal in outline (up to 3.75 times wider than

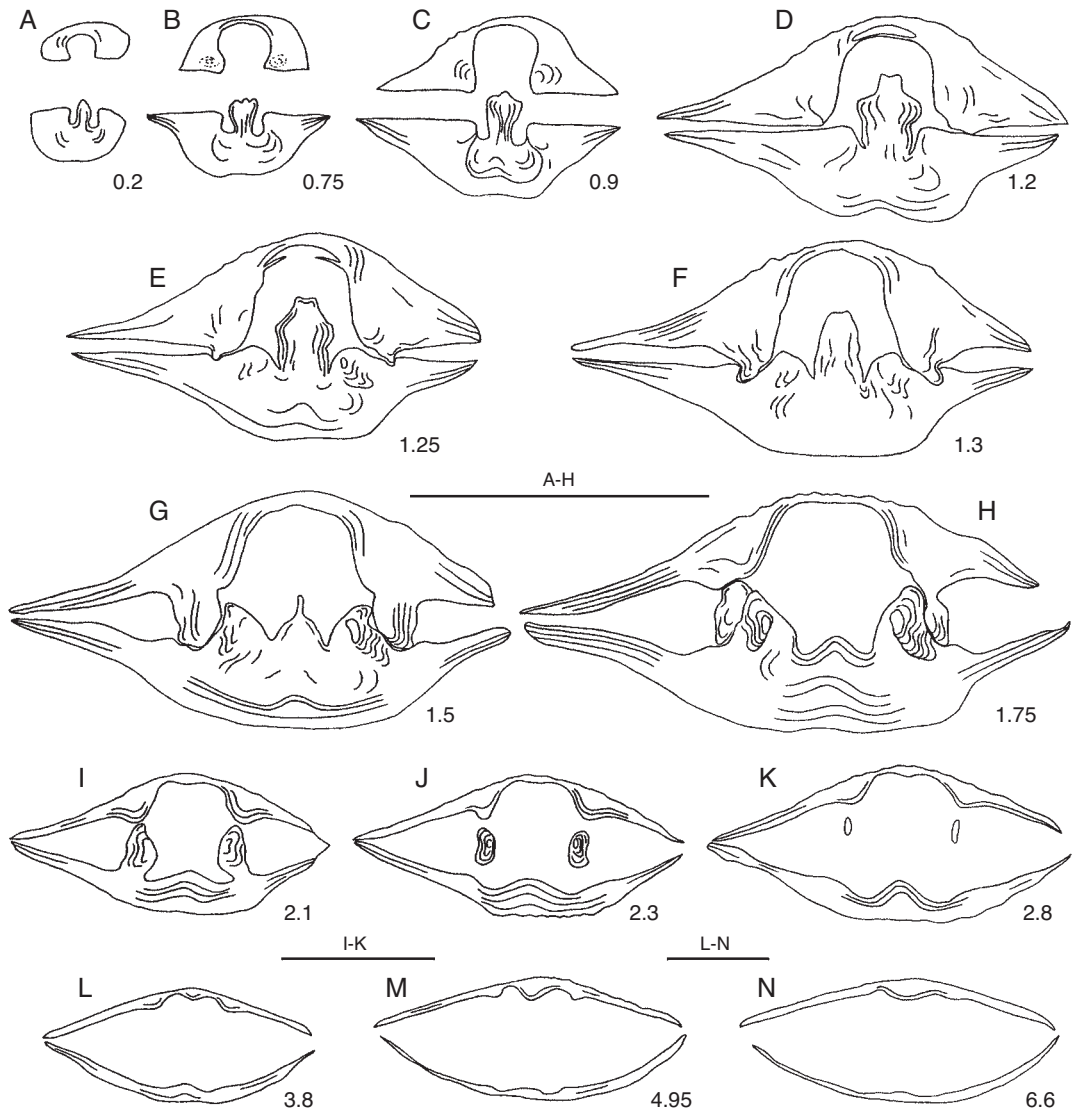


FIG. 15. — Transverse serial sections of *Aulacella aggeris* n. sp. (IRScNB a12357), loc. 6839b, Famenne Group (“Senzeille Formation”). Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

high); shoulder lines broken by prominent umbo; shoulder and apical angles between 137-147° and 107-134°, respectively; interarea low, apsacline, slightly concave; delthyrium open.

Dorsal valve regularly and moderately inflated in lateral profile; highest at about midvalve or more anteriorly but not at the front; median depression in

some specimens developed in its posterior part but reaching rarely the front; interarea orthocline, flat, generally less developed than the ventral one.

Ornamentation fascicostellate; costellae increasing by bifurcation and intercalation; 10-15 costae and costellae per 5 mm at anterior margin; in the middle part of the valves, distance between two successive

growth lamellae 2-2.5 mm (but quite variable!); growth lamellae more crowded close to the commissure.

Ventral interior with small cavity, roughly semi-elliptical in transverse section, developed between the valve floor and the apical cavity (this structure has been also observed by Chen (1984: text-fig. 10) in *Aulacella xinanensis* Chen, 1978); muscle field bilobed, divided anteriorly by a wide median ridge (its unrolled length corresponds more or less to the half of the unrolled length of the valve).

Dorsal interior with cardinal process very well-developed and posteriorly trilobed; dental sockets deep and laterally open; muscle field extending over about the half of the unrolled length of the valve; posterior and anterior adductor muscles of similar size.

#### DISCUSSION

*Aulacella aggeris* n. sp. was long misidentified as *A. arcuata* (Phillips, 1841), a poorly known species from the Middle Devonian of Hope's Nose, near Torquay in south Devon (England) but, however, it differs from the latter by a greater size and a narrower outline. *Aulacella aggeris* n. sp. has a less delimited and less elongated ventral muscle field than that of *A. interlineata* (Sowerby, 1840). *Aulacella aggeris* n. sp. is never as inflated as *A. eifliensis* (Schnur, 1853). Moreover, its outline is more developed in width and its ornamentation is coarser (see Biernat [1959: 26-35]). *Aulacella aggeris* n. sp. differs from *Rhipidomella manticula* Stainbrook, 1947 by its greater size and its equibiconvex to dorsibiconvex profile. This species has been assigned to *Aulacella* by Cooper & Dutro (1982: 39) but they transferred one of the specimens illustrated by Stainbrook (1947: pl. 45, fig. 4) to *Thiemella platys* Cooper & Dutro, 1982. *Aulacella aggeris* n. sp. is distinguished from *A. xinanensis* Chen, 1978 by its larger size, a more flattened profile and its wider outline. *Aulacella aggeris* n. sp. is larger than *A. elliptica* Cooper & Dutro, 1982 from which it also differs in its coarser ornamentation. Relationships and differences between *A. aggeris* n. sp. and *Orthis famenniensis* Gürich, 1903 remain to be clarified and specified.

#### DISTRIBUTION

*Aulacella aggeris* n. sp. is especially abundant within the basal part of the Famenne Group on the southern

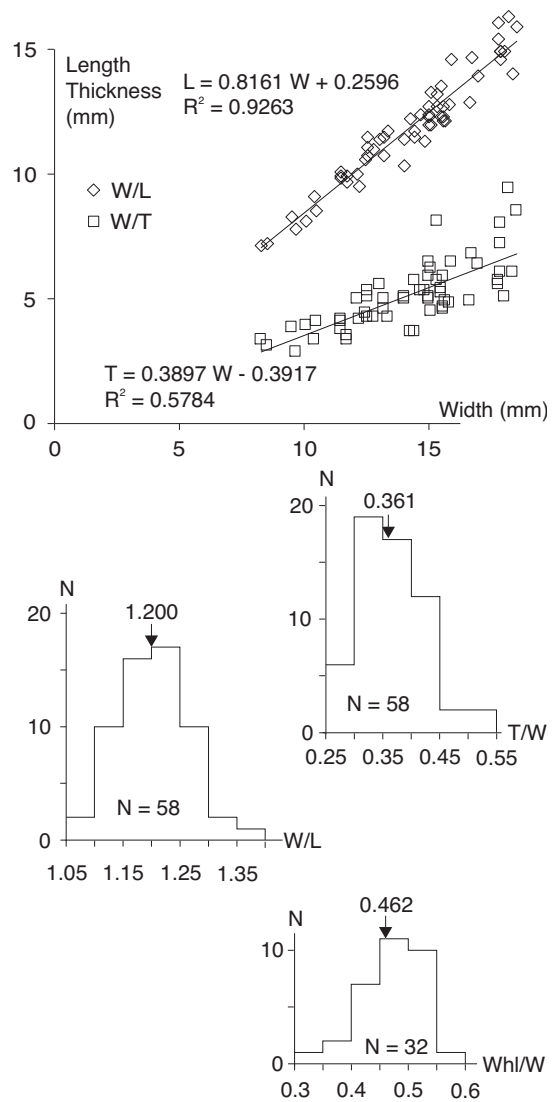


FIG. 16. — *Aulacella aggeris* n. sp. (loc. BM-2003-2, Senzeille 6839p., Famenne Group, "Senzeille Formation"). Scatter diagrams of shell width (W) to shell length (L), shell width to shell thickness (T); frequency diagrams of W/L, T/W, and Whl (hinge line width)/W. Arrows indicate the means.

border of the Dinant Synclinorium, but some badly preserved specimens originating from the base of the Hodimont Formation (northern border of the Dinant Synclinorium) are assigned with doubt to this species. The specimens identified as *Rhipidomella* (*Orthis*) aff. *eifliensis* de Verneuil by Wulff (1923: 44,

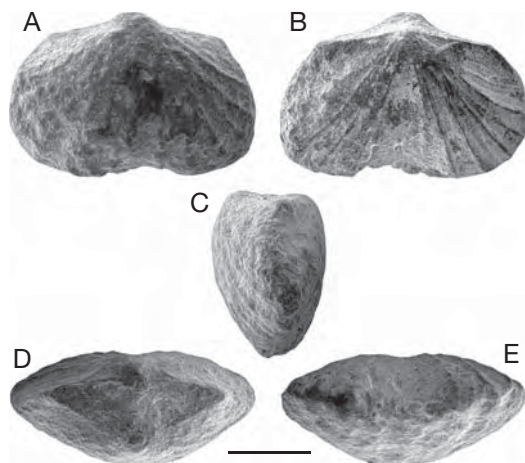


FIG. 17. — *?Hypsomyonia* sp., complete shell (IRScNB a12358), loc. BM-2002-5, Les Valisettes Formation: **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view. Scale bar: 1 mm.

45, pl. 2, fig. 1) from the Famennian of the Aachen area belong probably to *A. aggeris* n. sp.

Family HYPSONYONIIDAE Wright, 1965

Genus *Hypsomyonia* Cooper, 1955

TYPE SPECIES. — *Hypsomyonia stainbrooki* Cooper, 1955, by monotypy.

*?Hypsomyonia* sp.  
(Fig. 17; Table 2)

MATERIAL EXAMINED. — BM-2002-5 (one articulated specimen).

REMARKS

This identification is made for a very small shell with a roughly elliptical outline displaying the following external characters: unisulcate anterior commissure; short hinge line; widest at about mid-length; ventral valve devoid of fold and sulcus; ventral interarea low, slightly apsacline, weakly concave; dorsal sulcus well-defined, originating close to the apex, ornamentation costellate; costellae increasing by intercalation; 6 or 7 costae and costellae per 1 mm

at the anterior margin. The specimen is externally close to the type species of *Hypsomyonia*. However, its internal characters are unknown; that is why it is tentatively assigned to *Hypsomyonia*, representatives of which have been mentioned in North America by Cooper (1955: 52, 53) and in Australia by Veevers (1959b: 35-37). *?Hypsomyonia* sp. occurs within the Les Valisettes Formation on the southeastern flank of the Dinant Synclinorium.

Superfamily ENTELETOIDEA Waagen, 1884  
Family DRABOVIIDAE Havlíček, 1950  
Subfamily MONELASMINIINAE Harper, 2000

Genus *Monelasma* Cooper, 1955

TYPE SPECIES. — *Orthis deshayesi* Rigaux, 1873, by original designation.

*Monelasma* cf. *deshayesi* (Rigaux, 1873)  
(Figs 18; 19; Table 2)

*Orthis deshayesii* Rigaux, 1873: 50, pl. 1, fig. 4.

*?Skenidium Lemeslii* – Maillieux 1909a: 12.

*Mystrophora deshayesi* – Maillieux 1941b (e.p.): 3.

*Monelasma deshayesi* – Brice 1981: 142.

MATERIAL EXAMINED. — BM-2003-3 (13 articulated specimens, eight ventral valves); BM-2003-4b (nine articulated specimens, six ventral valves, two dorsal valves); BM-2003-6 (11 articulated specimens, one ventral valve).

DESCRIPTION

Shell small-sized, wider than long (width/length ratio: 1.03-1.29), ventribiconvex, semi-elliptic in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.61-0.77); widest at about mid-length; anterior margin straight to rounded; anterior commissure unisulcate.

Ventral valve regularly and moderately curved in lateral profile; flanks sloping moderately towards lateral commissure; beak curved on the interarea; shoulder lines concave to broken; shoulder and apical angles between 125-141° and 107-128°, respectively; interarea well-developed, of variable concavity, cata-apsacline; delthyrium open.

Dorsal valve roughly oval in outline; posterolateral areas inclined to become flat; wide and shallow median depression, originating at about mid-length; tongue rounded, not perpendicular to the commissural plane; interarea anacline, flat, less developed than the ventral one; notothyrium open.

Ornamentation multicostellate; 20-23 costae and costellae per 5 mm at the anterior margin; costellae increasing by intercalation; growth lamellae rare, thickened close to the commissure.

Internal characters not studied.

#### DISCUSSION

The specimens of *Monelasmina* which have been collected in Frasnes and Cerfontaine are compared to *M. deshayesi*. As is the case in *M. deshayesi*, these small shells display a median dorsal depression of variable depth, as well as an unisulcate anterior commissure. However, the specimens from Frasnes are always wider than long, with sometimes a wider hinge line, thus an outline somewhat different from the one of *M. deshayesi*.

#### DISTRIBUTION

*Monelasmina cf. deshayesi* occurs in the Grands Breux Formation (Boussu-en-Fagne Member; southern border of the Dinant Synclinorium) as well as in the Les Valisettes Formation (Philippeville Anticlinorium).

#### *Monelasmina* sp. A (Figs 19-21)

MATERIAL EXAMINED. — BM-2002-5 (26 articulated specimens, 43 ventral valves, 17 dorsal valves).

#### DESCRIPTION

Shell small-sized, more or less equidimensional to wider than long (width/length ratio: 1.02-1.39), ventribiconvex, subcircular in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.66-0.89); widest at about mid-length; anterior commissure rectimarginate to vaguely unisulcate.

Ventral valve regularly convex; beak hardly curved on interarea; umbo prominent; shoulder lines broken; shoulder and apical angles between 129-152°

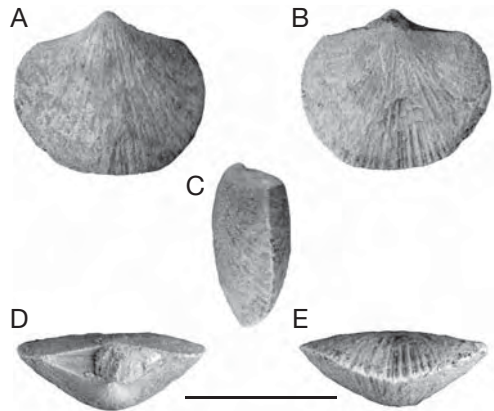


FIG. 18. — *Monelasmina cf. deshayesi* (Rigaux, 1873), complete shell (IRScNB a12361), loc. BM-2003-6, Grands Breux Formation (Boussu-en-Fagne Member): **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view. Scale bar: 5 mm.

and 94-118°, respectively; interarea well-developed, apsacline, concave; delthyrium open.

Dorsal valve regularly convex in lateral profile; median depression occurring exceptionally; tongue absent or hardly developed; interarea anacline, flat to slightly concave, about two times less high than the ventral one; notothyrium open.

Ornamentation multicostellate; costellae appearing by intercalation or more rarely by bifurcation; (19?) 20-25 costae and costellae per 5 mm at the anterior margin; growth lamellae thickened close to the commissure.

Ventral interior with short dental plates supporting teeth rectangular in transverse section; lateral apical cavities small; muscular field not observed.

Dorsal interior with deep notothyrial cavity with bilobed cardinal process; internal crests of dental sockets well-developed; brachiophores thickened, pointed anteriorly; median septum very long, touching the floor of the opposite valve; muscular field limited by low ridges.

#### DISCUSSION

This species has been previously identified as *Monelasmina deshayesi* (Rigaux, 1873) from which it differs by its larger size, its rectimarginate anterior commissure, its more developed ventral interarea and its wider hinge line. *Monelasmina* sp. A differs from *M. cf. deshayesi* by its larger size, a more developed

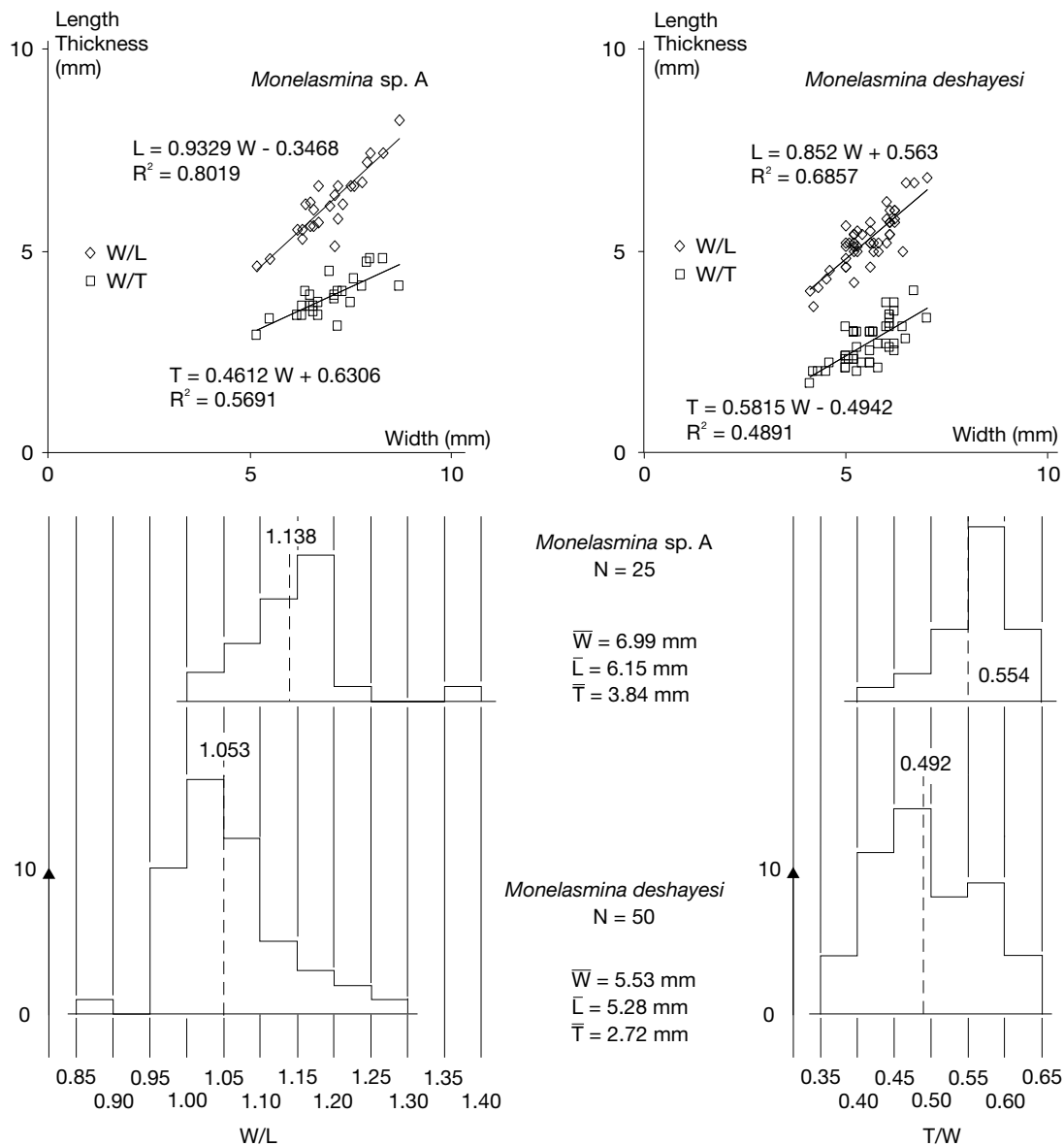


FIG. 19. — Comparison between *Monelasma* sp. A (loc. BM-2002-5, Les Valisettes Formation) and *Monelasma deshayesi* (Rigaux, 1873) (according to Brice's (1981) measurements of specimens from Boulonnais). Scatter diagrams of shell width (W) to shell length (L), shell width to shell thickness (T); frequency diagrams of W/L and T/W. Dotted lines indicate the means.

ventral interarea, a rectimarginate or indistinctly unisulcate anterior commissure. *Monelasma* sp. A is distinguished from *M. besti* Pedder, 1959 by the absence of ventral fold, its wider hinge line and,

thus, a less rounded outline. *Monelasma* sp. A is close to *M. wenjukovi* Liashenko, 1959, but its anterior commissure is generally rectimarginate and its ventral beak is less curved on the interarea.

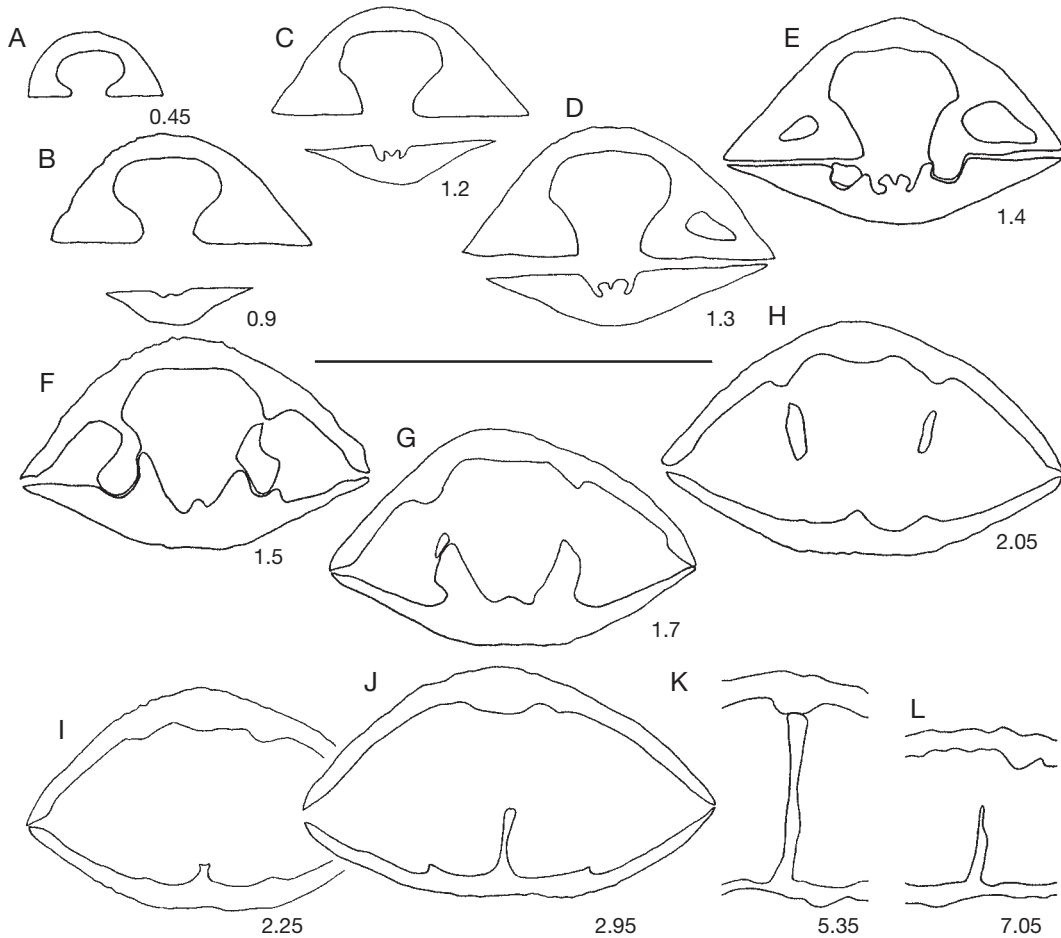


FIG. 20. — Transverse serial sections of *Monelasmina* sp. A (IRScNB a12364), loc. BM-2002-5, Les Valisettes Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bar: 5 mm.

DISTRIBUTION

*Monelasmina* sp. A occurs within the Les Valisettes Formation on the southeastern border of the Dinant Synclinorium, but it could be present also in the Neuville Formation in this area.

Family SCHIZOPHORIIDAE  
Schuchert & LeVene, 1929

Genus *Schizophoria* King, 1850

TYPE SPECIES. — *Conchyoliolithus* (*Anomites*) *resupinatus* Martin, 1809, by original designation.

*Schizophoria* gr. *striatula*  
(von Schlotheim, 1813)  
(Fig. 22)

*Anomites Terebratulites striatulus* von Schlotheim, 1813: pl. 1, fig. 6, non p. 76 (see Biernat [1959], Pocock [1966] and Struve [1964] for a complete synonymy outside Belgium).

REMARKS

The revision of *Schizophoria* species in the Frasnian formations sampled has not been carried out. They are assigned to the group of *S. striatula*, a species

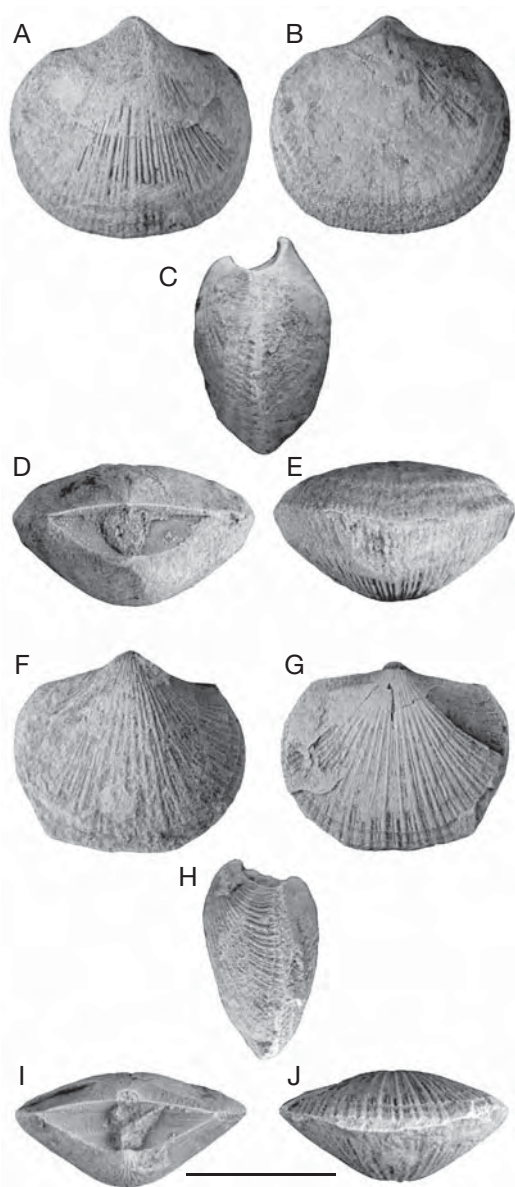


FIG. 21. — *Monelasmina* sp. A, loc. BM-2002-5, Les Valisettes Formation: **A-E**, complete shell (IRScNB a12362); **F-J**, complete shell (IRScNB a12363); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 5 mm.

listed on several occasions, notably by Maillieux (e.g., 1939: 3; 1941b: 4). Struve (1965: 194-197, pl. 1, fig. 1) revised this taxon and indicated that it

would be only Frasnian in age, but he has only figured its lectotype. Pocock (1966: 386, 402) recognized two species in the Frasnian of the Namur-Dinant Basin: *S. (Paraschizophoria) antiqua* Solle, 1936 and *S. striatula* on the basis of the old collections of the IRScNB but a modern study is urgently needed.

*Schizophoria* cf. *simpsoni* Merriam, 1940  
(Fig. 23; Table 2)

*Orthis striatula* – Gosselet 1877: 307; 1879 (e.p.): 397; 1888 (e.p.): 540, 548, 558. — Bayet 1888: 47.

*Schizophoria striatula* – Maillieux 1933: 85; 1941b (e.p.): 4. — Bultynck & Martin 1995: 9.

*Schizophoria simpsoni* Merriam, 1940: 80, pl. 9, figs 2, 3.

MATERIAL EXAMINED. — BM-2003-2 (23 articulated specimens, one ventral valve, three dorsal valves).

DESCRIPTION

Shell wider than long (width/length ratio: 1.17-1.38), dorsibiconvex, subrectangular to elliptical in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.50-0.66); widest at mid-length or more anteriorly; anterior commissure uniplicate or vaguely undulating.

Ventral valve slightly convex in posterior view and resupinate in lateral profile; sulcus originating in the anterior part of the valve, relatively wide, shallow, with flattened bottom; tongue wider than high, suboval in outline, perpendicular to the commissural plane or close this position; umbo moderately prominent; shoulder lines broken; beak straight or slightly curved; interarea apsacline, of variable concavity, clearly higher than the dorsal one; delthyrium open.

Dorsal valve inflated; flanks sloping gently towards lateral commissure; fold rarely developed, only visible close to the anterior margin; interarea ortho-apsacline to ana-apsacline, concave.

Ornamentation multicostellate to fascicostellate; 3 or 4 costae and costellae per 1 mm at the anterior margin; costellae increasing by intercalation; in some specimens, costae and costellae arranged into bundles of 4 or 5; growth lamellae irregularly spaced.

Internal characters not studied.



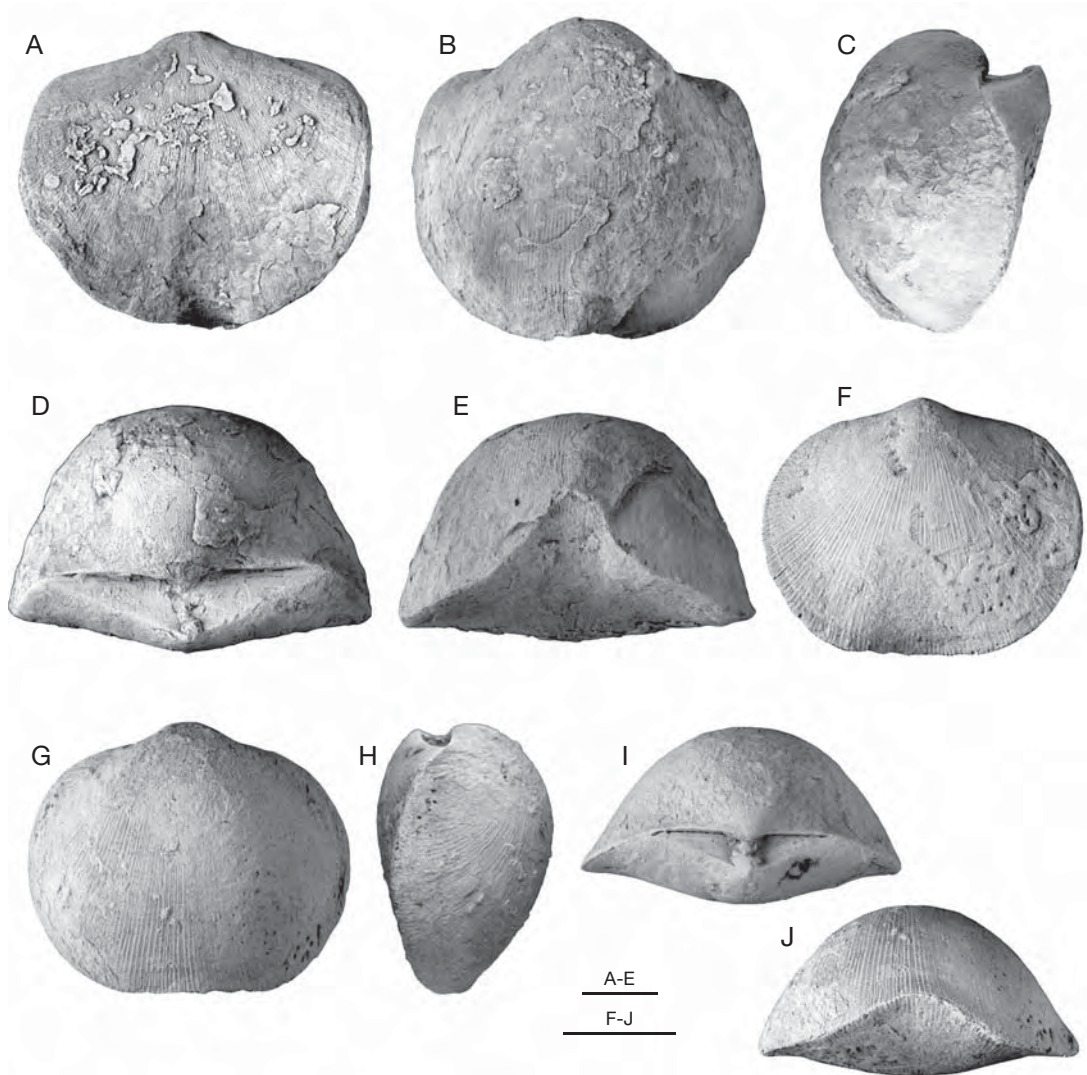


FIG. 22. — *Schizophoria* gr. *striatula* (von Schlotheim, 1813): **A-E**, complete shell (IRScNB a12365), loc. BM-2003-7, Grands Breux Formation (Boussu-en-Fagne Member); **F-J**, complete shell (IRScNB a12366), loc. Durbuy 5337, Barvaux Formation; **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bars: 10 mm.

#### DISCUSSION

The lack of knowledge about their internal morphology prevents assignment of these specimens to one of the subgenera of *Schizophoria*. Nonetheless, they are tentatively assigned to *S. simpsoni* Merriam, 1940 on the basis of their size, outline and the poor development of the sulcus and fold. However, fascicostellate ornamentation has not been

observed in the type material of Merriam's species. Moreover, the internal morphology of both species has not been observed.

#### DISTRIBUTION

*Schizophoria* cf. *simpsoni* occurs in the lower part of the Famenne Group ("Senzeille Formation") on the southern border of the Dinant Synclinorium.

According to Merriam (1940: 80), *S. simpsoni* is known in the Upper Devils Gate Formation (*Cyrtospirifer* Zone) of Nevada where it is associated with *Plicapustula portae* (Merriam, 1940), *Crinisarina angelicoides* (Merriam, 1940) and *Eoparaphorhynchus walcottii* (Merriam, 1940).

#### Order ATHYRIDIDA

Boucot, Johnson & Staton, 1964

Suborder ATHYRIDIDINA

Boucot, Johnson & Staton, 1964

Superfamily ATHYRIDOIDEA Davidson, 1881

Family ATHYRIDIDAE Davidson, 1881

Subfamily ATHYRIDINAE Davidson, 1881

Genus *Athyris* M'Coy, 1844

TYPE SPECIES. — *Terebratula concentrica* von Buch, 1834, by subsequent designation (King 1850: 136).

*Athyris oehlerti* Rigaux, 1908

(Figs 24A-J; 25; 26)

*Athyris oehlerti* Rigaux, 1908: 13, pl. 1, fig. 2. — Asselberghs 1912: 14, 43, pl. 1, fig. 12 (?). — Brice 1988: 354, 355, pl. 43, figs 6-10, text-fig. 2D.

*Athyris davidsoni* Rigaux 1908 (e.p.): 13, pl. 1, fig. 3.

MATERIAL EXAMINED. — BM-2001-1 (two articulated specimens); BM-2002-8 (48 articulated specimens); BM-2003-3 (83 articulated specimens, one ventral valve); BM-2003-4 (18 articulated specimens, one ventral valve); BM-2003-10 (40 articulated specimens); BM-2004-1 (10 articulated specimens); BM-2004-5 (two articulated specimens).

#### DESCRIPTION

Shell small-sized, wider than long (width/length ratio: 0.91-1.31), ventribiconvex, rounded subpentagonal in outline; widest at about mid-length or close to the posterior margin; anterior commissure uniplicate or, more rarely, parasulcate.

Ventral valve regularly curved in lateral profile except in the umbonal area (slight accentuation), with top flattened in posterior view; flanks sloping

moderately towards lateral commissure; beak erect or weakly curved; foramen large, permesothyrid; sulcus absent or originating generally in the posterior half of the valve, wide (sulcus width/width ratio: 0.39-0.45), delimited by two ridges in parasulcate shells; tongue 1.91-3.16 times wider than high, rounded to subtrapezoidal, almost perpendicular to the commissural plane; shoulder lines concave, more rarely subrectilinear; shoulder and apical angles between 124-132° and (87°) 93-112° (120°), respectively; palintropes small, poorly differentiated.

Dorsal valve highest at about midvalve (curving or maintaining anteriorly); flanks sloping moderately towards lateral commissure; fold only developed close to anterior margin of adult shells, with top rounded.

Distance between the distal margins of two successive growth lamellae varying between 1 and 2.5 mm in the median part of the valves; more closely spaced near lateral and anterior commissures.

Ventral interior with lateral apical cavities poorly developed, delimited by short dental plates; teeth small, subrectangular in transverse section.

Dorsal interior with hinge plate apically perforated by dorsal foramen, relatively flat or concave in its posterior part and convex in its anterior one; dental sockets moderately deep; short septum developed in the umbonal region, but quickly giving rise to myophragm; spiral cones laterally oriented, comprising at least nine whorls.

#### DISCUSSION

The specimen identified as *Athyris davidsoni* by Rigaux (1908, pl. 1, fig. 3) displays widely spaced growth lamellae, that leads me to assign it rather to *A. oehlerti* Rigaux, 1908. Moreover, it has been designated as the paralectotype of *A. davidsoni* by Brice (1988) who considered this specimen as exceptional because of the unusual development of its sulcus ridges. Maillieux (1933) mentioned the species as occurring in the Frasnian of southern Belgium but not in his later publications (Maillieux 1940, 1941b). Specimens of *A. oehlerti* from the cemetery quarry in Boussu-en-Fagne (BM-2003-10) have been identified under five different names by Maillieux according to their labels: *A. davidsoni* (Rigaux, 1873), *A. bayeti* Rigaux, 1908, *A. bisinuata*

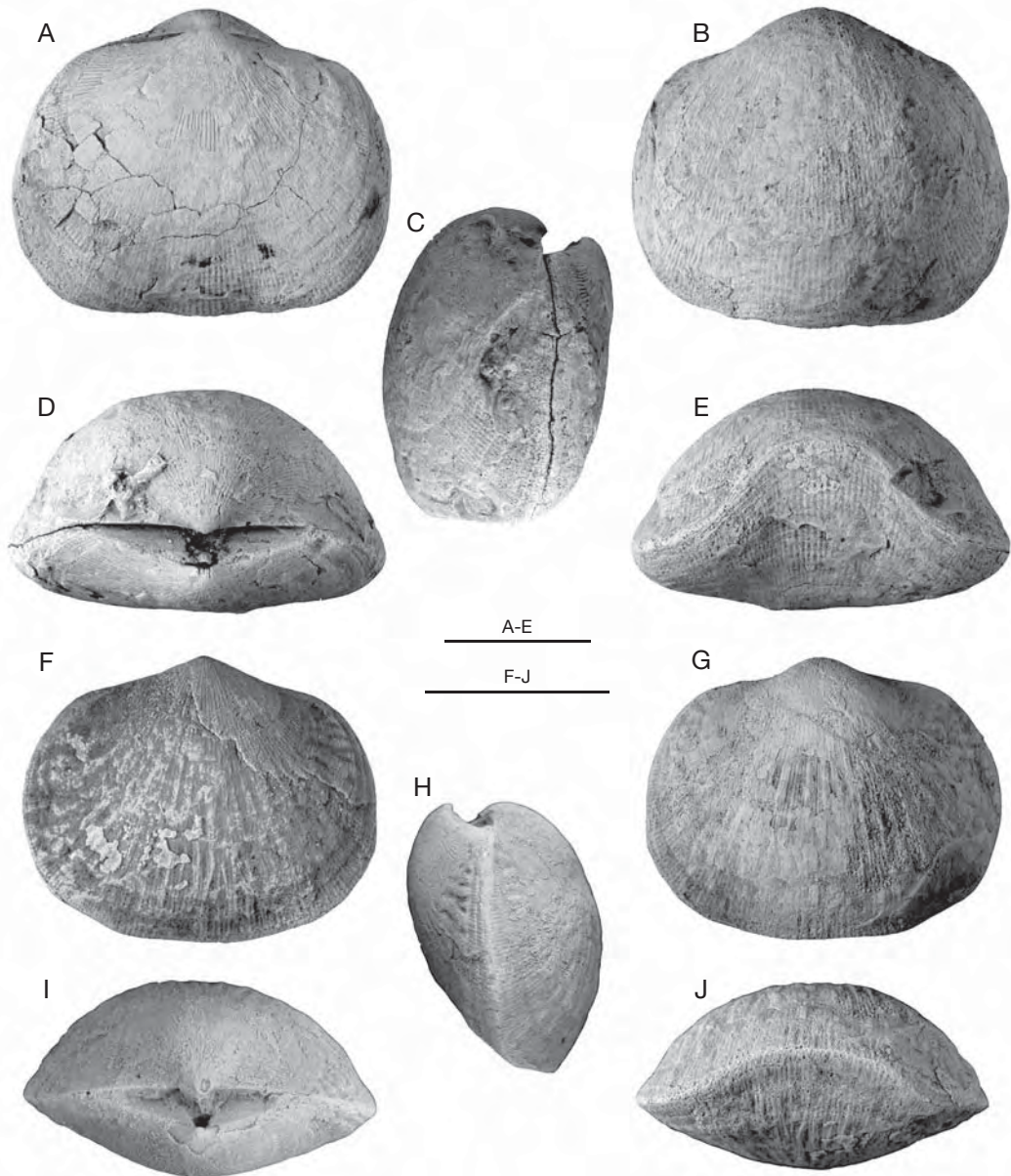


FIG. 23. — *Schizophoria* cf. *simpsoni* Merriam, 1940, loc. BM-2003-2, Famenne Group ("Senzeille Formation"): **A-E**, complete shell (IRScNB a12367); **F-J**, complete shell (IRScNB a12368); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bars: 10 mm.

Frech, 1891, *A. communis* (Gosselet, 1877) and *A. globularis* (Phillips, 1836). The specimen illustrated by Asselberghs (1912: pl. 1, fig. 1) must be re-examined.

#### DISTRIBUTION

Presently, *Athyris oehlerti* is recognized from the Boussu-en-Fagne Member up to the Les Valisettes Formation. In the Dinant Synclinorium, the species is present

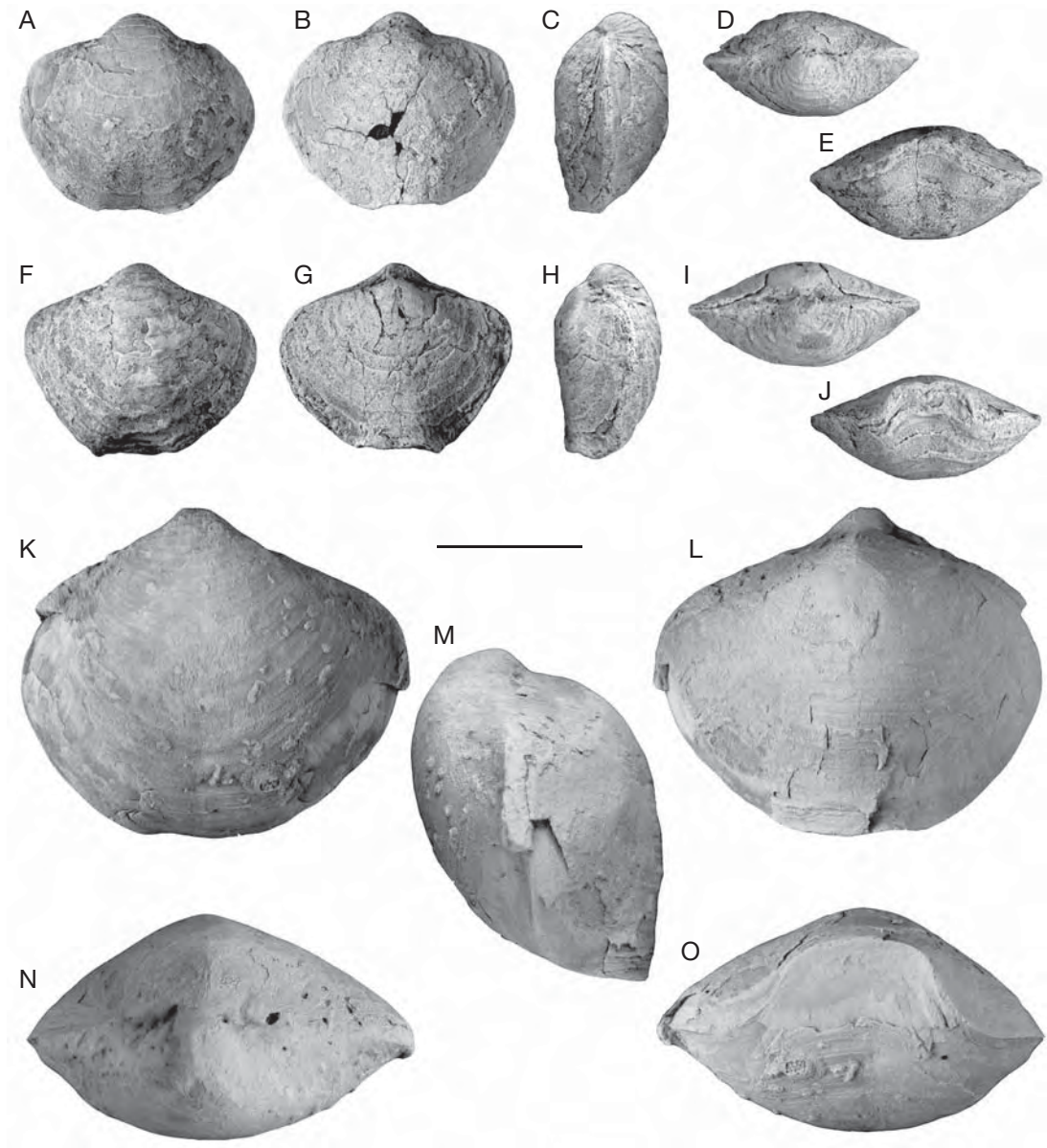


FIG. 24. — **A-J**, *Athyris oehlerti* Rigaux, 1908, loc. BM-2003-3, Les Valisettes Formation; **A-E**, complete shell (IRScNB a12315); **F-J**, complete shell (IRScNB a12316); **K-O**, *Athyris* cf. *murchisoni* Brice, 1988, complete shell (IRScNB a12319), BM-2002-7, Grands Breux Formation (Boussu-en-Fagne Member); **A, F, K**, ventral views; **B, G, L**, dorsal views; **C, H, M**, lateral views; **D, I, N**, posterior views; **E, J, O**, anterior views. Scale bar: 10 mm.

from “les schistes à *Receptaculites*” up to the “schistes de la Zone à *Spirifer pachyrhynchus*” according to Mailieux (1909b: 138, 139). Asselberghs (1912, 1936)

reported it within the Frasnian of the northern border of the Namur Synclinorium. In this area, the species is known presently in the Aisemont Formation.

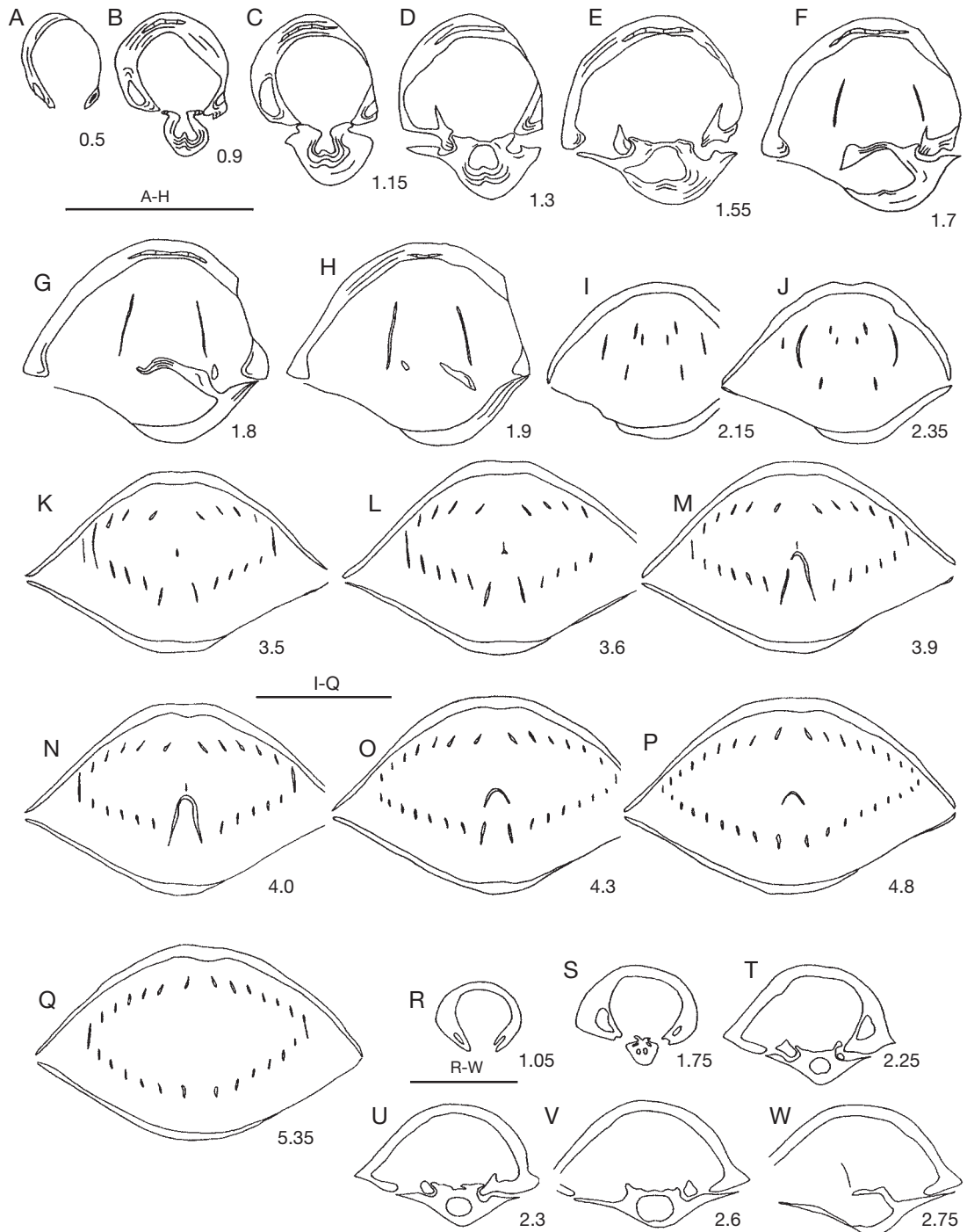


FIG. 25. — Transverse serial sections of *Athyris oehlerti* Rigaux, 1908, loc. BM-2003-3, Les Valisettes Formation: **A-Q**, IRScNB a12317; **R-W**, IRScNB a12318. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

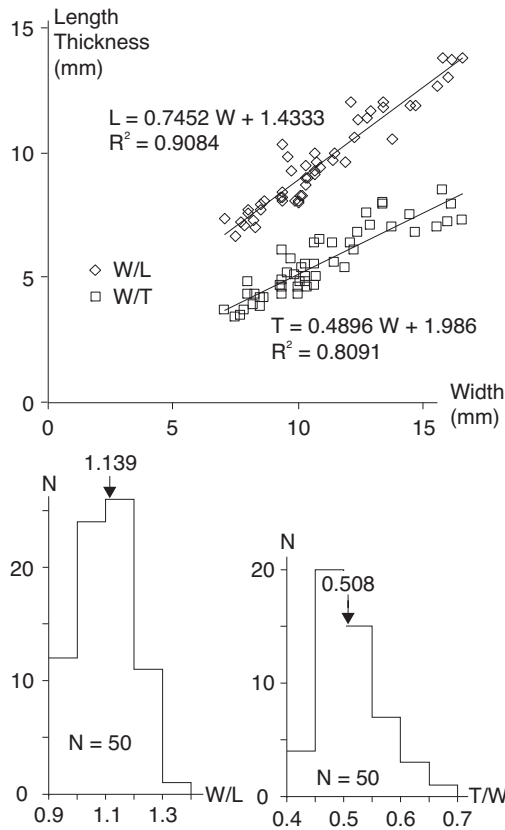


FIG. 26. — *Athyris oehlerti* Rigaux, 1908 (loc. BM-2003-2, Les Valisettes Formation). Scatter diagrams of shell width (**W**) to shell length (**L**), shell width to shell thickness (**T**); frequency diagrams of **W/L** and **T/W**. Arrows indicate the means.

*Athyris* cf. *murchisoni* Brice, 1988  
(Fig. 24K-O; Table 3)

*Athyris concentrica murchisoni* Brice, 1988: 348, 350, pl. 42, figs 14-16, text-fig. 2A.

MATERIAL EXAMINED. — BM-2002-8 (one articulated specimen); BM-2003-7 (six articulated specimens, one dorsal valve); BM-2003-11 (three articulated specimens).

REMARKS

These specimens are characterized by a medium-sized, wider than long and dorsibiconvex shell with a rounded subpentagonal outline, a suboval tongue perpendicular to the commissural plane, 9 or 10 growth lamellae per 5 mm in the median part of the

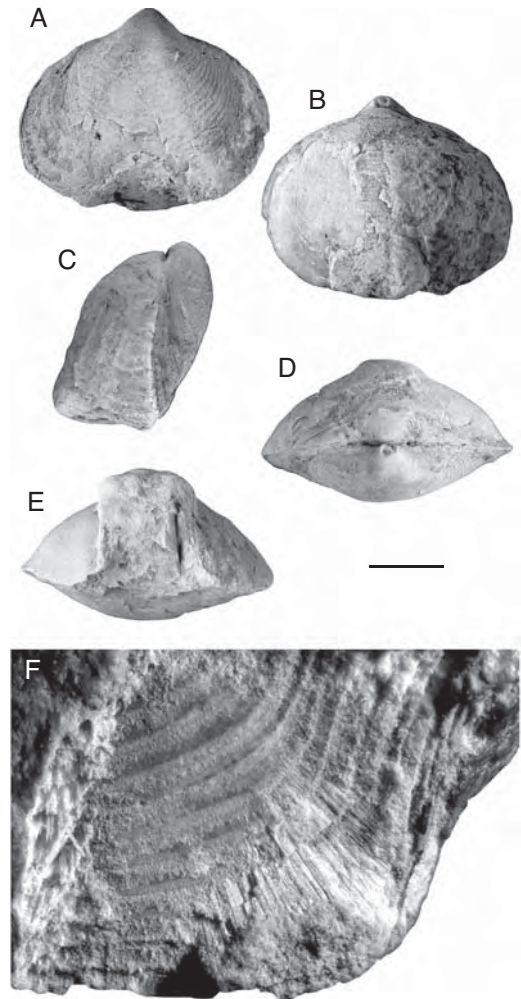


FIG. 27. — *Cleiothyridina davidsoni* (Rigaux, 1873), loc. BM-2003-2, Famenne Group ("Senzeille Formation"): **A-E**, complete shell (IR-ScNB a12266), **F**, complete shell (IRScNB a12478); **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view; **F**, detail of ornamentation. Scale bar: A-E, 5 mm; F, 1 mm.

valves. The small amount of material does not allow a more precise identification of these specimens although they are close to *A. murchisoni* but smaller.

Asselberghs (1912: 13, 1923: 33) discussed the status of the Boulonnais species identified as "*Terebratulina concentrica* de Buch" by Murchison (1840: 251). He pointed out that *A. concentrica* Murchison was a separate species which could not be assigned to *T. concentrica* von Buch. Asselberghs (1923: 33)

proposed the name *A. buchi* for von Buch's specimens and suggested that the name *concentrica* should be reserved for Murchison's taxon. However, as mentioned by Alvarez *et al.* (1996: 67), the substitution name *A. buchi* Asselberghs, 1923 is not available because it concerns a case of (primary) objective synonymy. Brice (1988: 348) placed the three varieties described by Murchison in her new subspecies *A. concentrica murchisoni*. The latter has been promoted to a specific rank by Brice (2003: 415). Alvarez *et al.* (1996: 80) chose a neotype for *A. concentrica concentrica* (von Buch, 1834), but Grunt & Weyer (2002: 39) subsequently designated a lectotype after the discovery of specimens that they consider as von Buch's types at the MB but the designation of a lectotype by the latter would not respect the *International Code of Zoological Nomenclature* (ICZN, 1999) according to Alvarez & Brunton (2005).

#### DISTRIBUTION

*Athyris* cf. *murchisoni* is recognized within the Grands Breux Formation (Boussu-en-Fagne Member) and at the base of the Neuville Formation (southeastern border of the Dinant Synclinorium, Philippeville Anticlinorium).

Subfamily CLEIOTHYRIDININAE  
Alvarez, Rong & Boucot, 1998

Genus *Cleiothyridina* Buckman, 1906

TYPE SPECIES. — *Atrypa pectinifera* Sowerby, 1840 in 1840-1846, validated by ICZN Opinion 1041 (ICZN 1976: 210).

*Cleiothyridina davidsoni* (Rigaux, 1873)  
(Fig. 27)

*Spirigera Davidsoni* Rigaux, 1873: 48, figs 10a-c.

*Cleiothyridina davidsoni* – Mottequin 2008: 1062, 1063, figs 13, 14.

*Athyris davidsoni* – Rigaux 1908 (e.p.): 13, non pl. 1, fig. 3 (= *Athyris oehlerti*). — Maillieux 1909b: 122, 138, 139; 1922b: 18; 1933: 81; 1940: 27; 1941b: 12. — Maillieux in Kaisin *et al.* 1922 (e.p.): 23. — Maillieux in Asselberghs &

Maillieux 1925: 166. — Brice 1988: 352, 353, pl. 43, figs 1, 3, 4, non pl. 43, fig. 2 (= *Athyris oehlerti*).

MATERIAL EXAMINED. — BM-2003-8 (31 articulated specimens); JG-1995-5 (12 articulated specimens).

#### REMARKS

The Belgian material assigned to Rigaux's species has been described and discussed by Mottequin (2008). These specimens display thin spine-like outgrowths anteriorly or anterolaterally directed from the growth lamellae. This taxon occurs within the Neuville Formation as well as in the lowermost part of the Famenne Group on the southern flank of the Dinant Synclinorium.

*Cleiothyridina* sp. A  
(Figs 28; 29; Table 3)

*Athyris communis* – Maillieux 1933: 83; 1939: 4, 5; 1941b (e.p.): 12.

MATERIAL EXAMINED. — BM-2001-2 (three articulated specimens); BM-2001-3 (six articulated specimens); BM-2001-4 (six articulated specimens); BM-2001-5 (two articulated specimens); BM-2002-6 (14 articulated specimens).

#### DESCRIPTION

Shell medium-sized, wider than long (width/length ratio: 1.09-1.39), dorsibiconvex to ventribiconvex, elliptical in outline; anterior commissure uniplicate to parasulcate.

Ventral valve regularly curved in lateral profile; flanks sloping moderately towards lateral commissure; beak curved; foramen permesothyrid; sulcus wide (sulcus width/width ratio: 0.42-0.52), poorly defined, shallow to moderately deep; tongue 1.25-2.73 times wider than high, semi-oval, more or less perpendicular to commissural plane; shoulder lines subrectilinear to concave; shoulder and apical angles between 119-137° and 91-123° respectively; palintropes small, poorly defined.

Dorsal valve regularly convex in posterior view; highest at about midvalve or at the front (in the first case, the height is maintained anteriorly or decreases progressively with sometimes a weakly inflexion near the anterior margin); fold with top

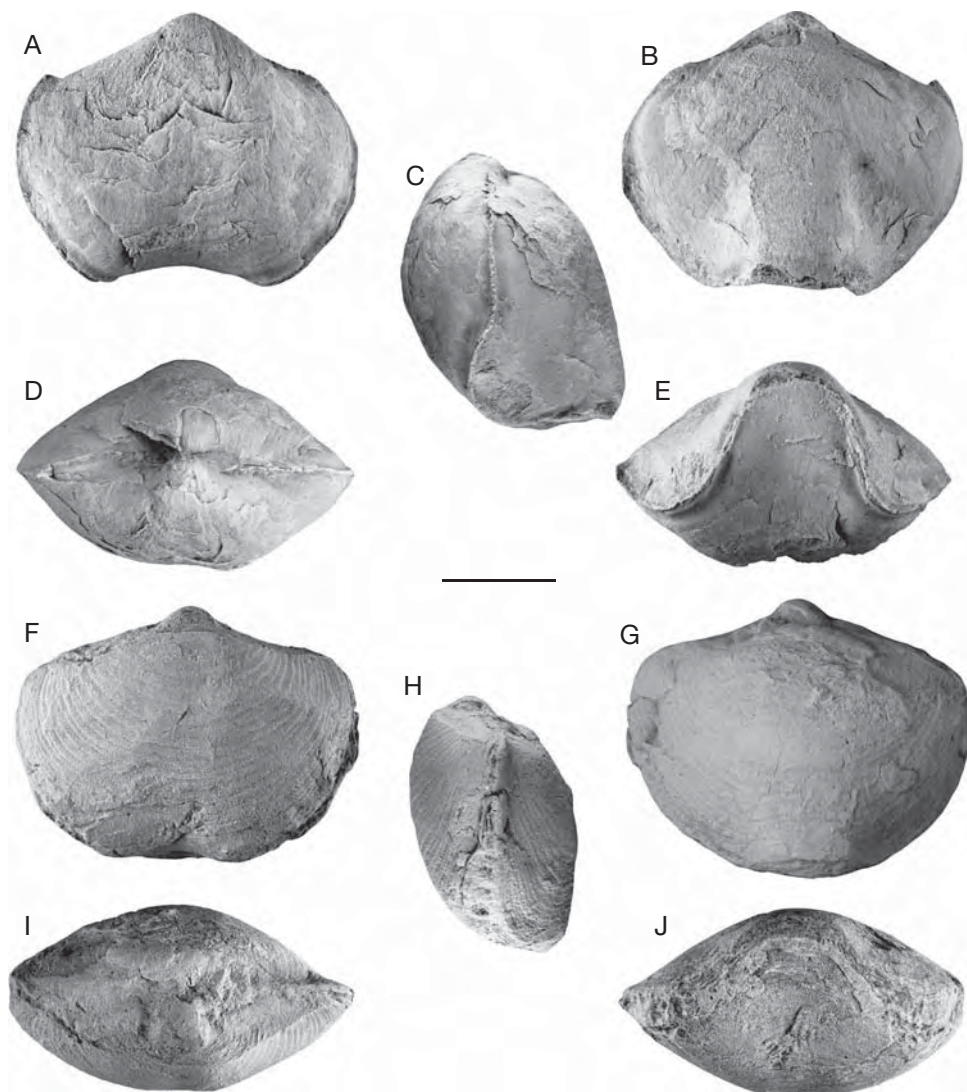


FIG. 28. — *Cleiothyridina* sp. A, loc. BM-2001-3, Barvaux Formation: **A-E**, complete shell (IRScNB a12320); **F-J**, slightly deformed complete shell (IRScNB a12328); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 10 mm.

rounded or slightly flattened, low to moderately high, only well-defined near the front.

In the plane of symmetry, five growth lamellae per 5 mm; more closely spaced near the commissure; spine-like outgrowths anteriorly or anterolaterally directed from the growth lamellae (shells frequently encrusted).

Ventral interior with wide and poorly filled apical lateral cavities; dental plates posteriorly thickened; teeth suboval in transverse section.

Dorsal interior with cardinal plate apically perforated by dorsal foramen, relatively flat, thickened; myophragm not very prominent; at least nine whorls by spiral cone.



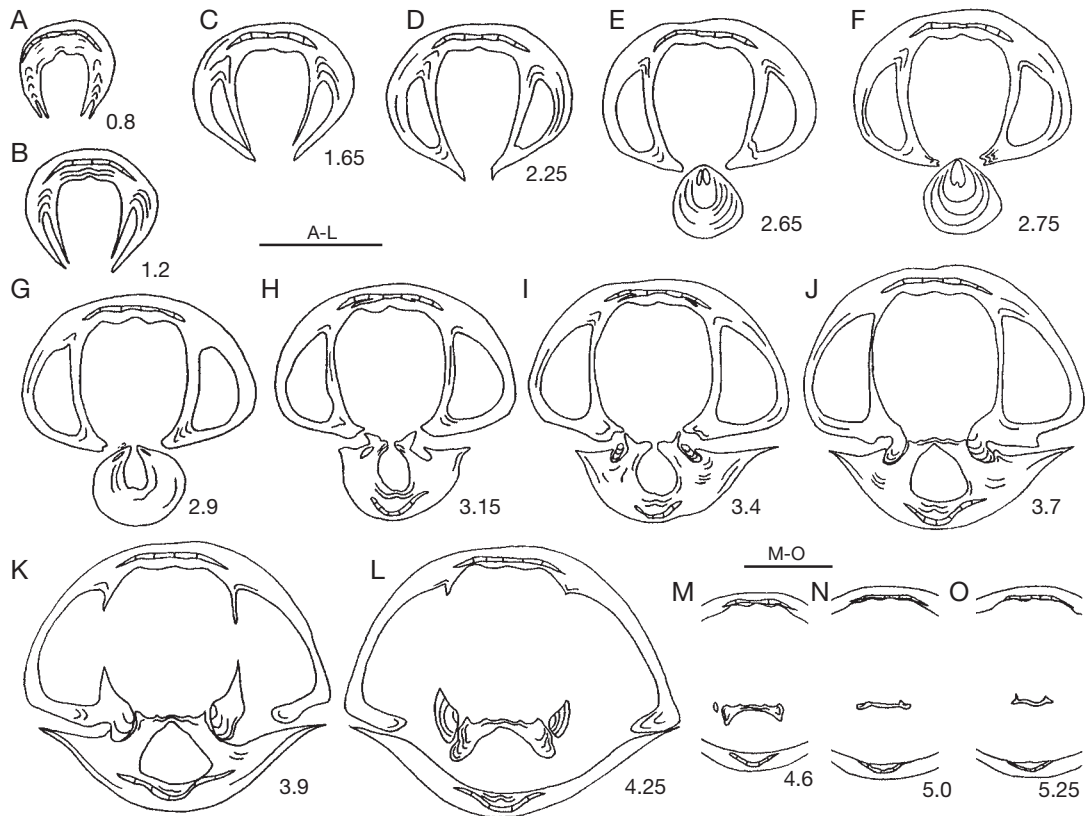


FIG. 29. — Transverse serial sections of *Cleiothyridina* sp. A (IRScNB a12329), loc. BM-2002-6, Barvaux Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

#### DISCUSSION

*Cleiothyridina* sp. A has been previously assigned to *Spirigera concentrica* var. *communis*, a variety introduced by Gosselet (1877: 312). The types of this variety correspond to both specimens of “*Terebratula concentrica* de Buch” illustrated by Murchison (1840: pl. 2, fig. 1a-e). They are probably lost according to Brice (1988: 348) who transferred them to *A. murchisoni* Brice, 1988. *Cleiothyridina* sp. A differs from the latter in its wider cardinal margin, its different outline as well as by its more spaced growth lamellae with spine-like outgrowths. Furthermore, it never displays a globose appearance.

#### DISTRIBUTION

*Cleiothyridina* sp. A occurs at the top of the Barvaux (southeastern border of the Dinant Synclinorium)

and Les Valisettes (Philippeville Anticlinorium) formations, but also in the Frasnian part of the Lambermont Formation (northern border of the Dinant Synclinorium and Vesdre area).

#### Subfamily HELENATHYRIDINAE Dagys, 1974

##### Genus *Biernatella* Baliński, 1977

TYPE SPECIES. — *Biernatella polonica* Baliński, 1977, by monotypy.

##### *Biernatella abunda* Mottequin, 2004

*Biernatella abunda* Mottequin, 2004b: 50-52, 55, 56, figs 2-7.

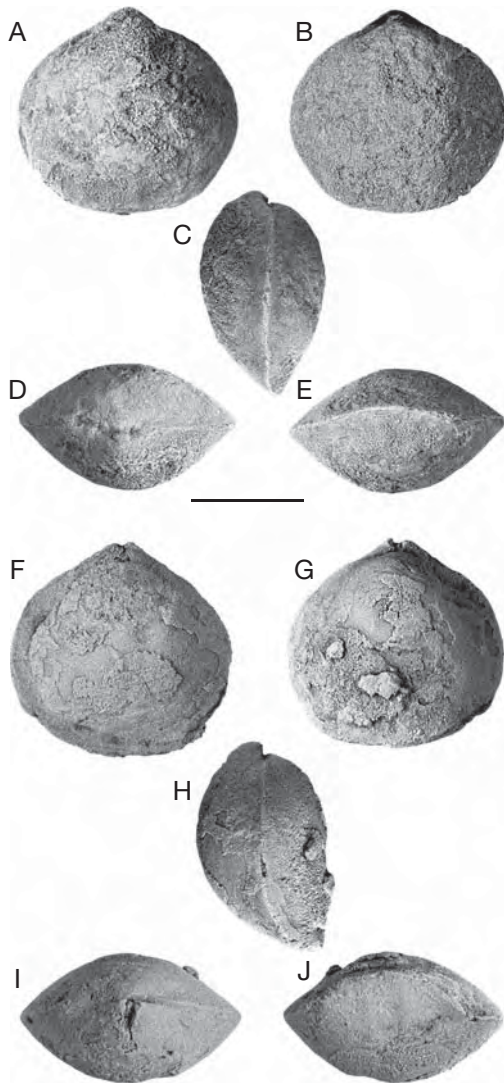


FIG. 30. — *Neptunathyris buxi* n. gen., n. sp.: **A-E**, loc. BM-2003-8, Neuville Formation, complete shell (holotype IRScNB a12330); **F-J**, loc. JG-1995-5, Neuville Formation, complete shell (IRScNB a12331); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 5 mm.

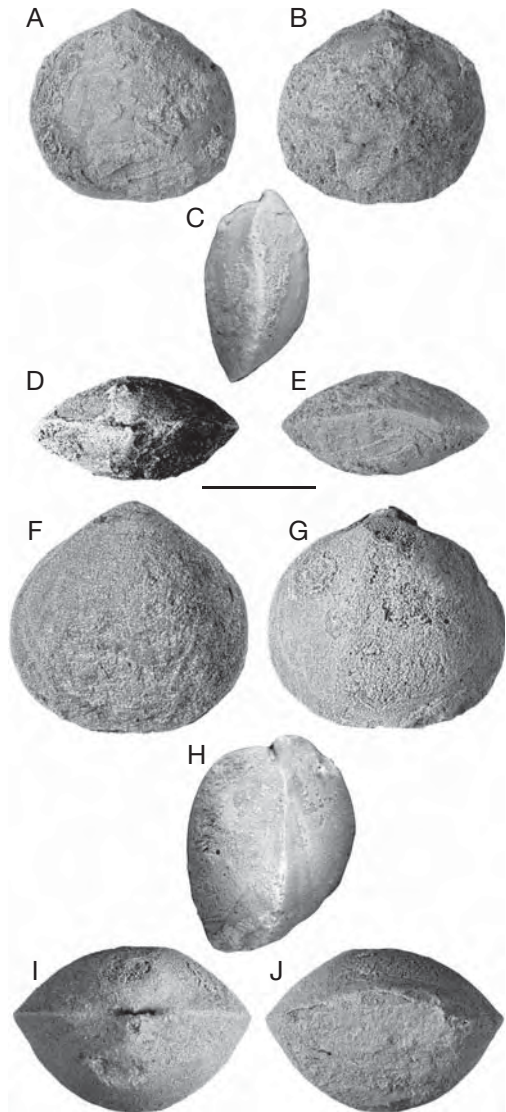


FIG. 31. — *Neptunathyris buxi* n. gen., n. sp.: **A-E**, loc. BM-2003-8, Neuville Formation, complete shell (IRScNB a12332); **I-J**, loc. JG-1995-5, Matagne Formation, complete shell (IRScNB a12333); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 5 mm.

REMARKS

The species has been described in detail by Mottequin (2004b). At the southern flank of the Dinant Synclinorium, *Biernatella abunda* occurs within the Neuville Formation. It is also present in the Philippeville Anticlinorium within the Neuville and Les Valisettes formations (see Mottequin [2004b:

55-57]) as well as within the lowermost part of the Matagne Formation. A single specimen of an unidentified species of *Biernatella* has been collected within the lower limestone unit of the Aisemont Formation on the northern border of the Dinant Synclinorium (BM-2004-4).

Genus *Neptunathyris* n. gen.

TYPE AND ONLY SPECIES. — *Neptunathyris buxi* n. gen., n. sp., by present designation.

ETYMOLOGY. — Combination of *Neptunus* (Latin), the god of water in Roman mythology and of *Athyris*, a generic name. Allusion to the Neptune cave in Nismes, where the Eau Noire disappears.

OCCURRENCE. — Nismes (BM-2003-8), Neuville and Matagne formations, Lower to Upper *Palmatolepis rhenana* zones, Late Frasnian.

DIAGNOSIS. — Shell small-sized, dorsibiconvex to ventribiconvex; ventral sulcus absent or only perceptible near the frontal margin; fold absent; anterior commissure slightly undulating to uniplicate; ventral beak erect to weakly incurved (not in contact with the dorsal umbo); ventral area small, concave, apsacline; pedicle opening hypothryidid; deltidial plates absent; growth lamellae rare. Dental plates thin; teeth short and massive; central apical cavity wide; lateral apical cavities narrow; dental socket moderately deep with inner socket ridges slightly developed; dorsal myophragm absent; spiral cones ventrolaterally oriented; jugum with jugal stem; accessory lamellae stretching from the posterior part of the jugum towards the end of the main spires.

## DISCUSSION

The external and internal features of *Neptunathyris* n. gen. such as the presence of a well-developed diplospirium place it within the subfamily Helenathyridinae as stated by Alvarez & Rong (2002: 1522) though the growth lines are weak.

*Neptunathyris* n. gen. is distinguished from *Helenaathyris* Alekseeva, 1969 by the absence of spines disposed on the growth lamellae and by its less developed inner socket ridges.

*Neptunathyris* n. gen. differs from *Biernatella* Baliński, 1977 by the presence of dental plates and of a cardinal plate.

*Neptunathyris* n. gen. is separable from *Sphaerathyris* Baranov, 1994 by the absence of deltidial plates and the development of a jugal stem.

*Neptunathyris* n. gen. has dental plates like *Eobiernatella* Baliński, 1995 but in the latter, they are stronger and longer. Moreover, *Eobiernatella* displays a rectimarginate anterior commissure, thin growth

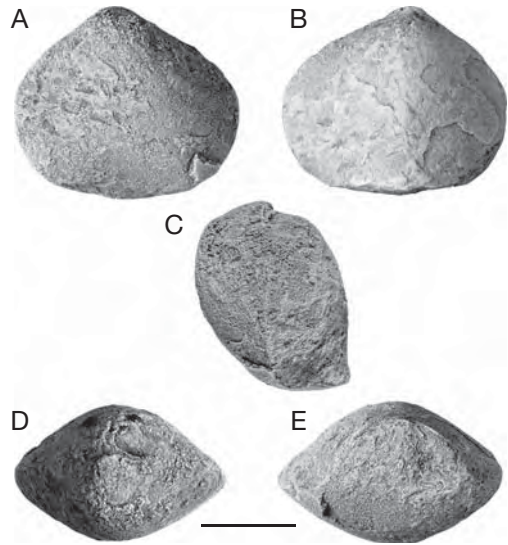


FIG. 32. — *Neptunathyris buxi* n. gen., n. sp., slightly deformed complete shell (IRScNB a12334), loc. JG-1995-5, Neuville Formation: A, ventral view; B, dorsal view; C, lateral view; D, posterior view; E, anterior view. Scale bar: 5 mm.

lamellae, a thick cardinal plate and the inner socket ridges are more developed.

*Neptunathyris* n. gen. resembles *Pygmis* Baliński, 2002, but the latter does not possess a diplospirium.

*Neptunathyris buxi* n. sp.  
(Figs 30-35)

HOLOTYPE. — IRScNB a12330.

ETYMOLOGY. — From *buxus* (Latin), boxwood, in reference to the “Tiène aux Pauquis” (hill covered in boxwood in Walloon) which lines the *locus typicus* in the north.

LOCALITY AND AGE. — Nismes railway section (BM-2003-8), upper part of the Neuville Formation (Early *Palmatolepis rhenana* Zone).

DIAGNOSIS. — As for the genus.

MATERIAL EXAMINED. — BM-2003-8 (21 articulated specimens); JG-1995-5 (19 articulated specimens).

## DESCRIPTION

Shell small-sized, longer than wide to wider than long (width/length ratio: 0.86-1.15), ventribiconvex,

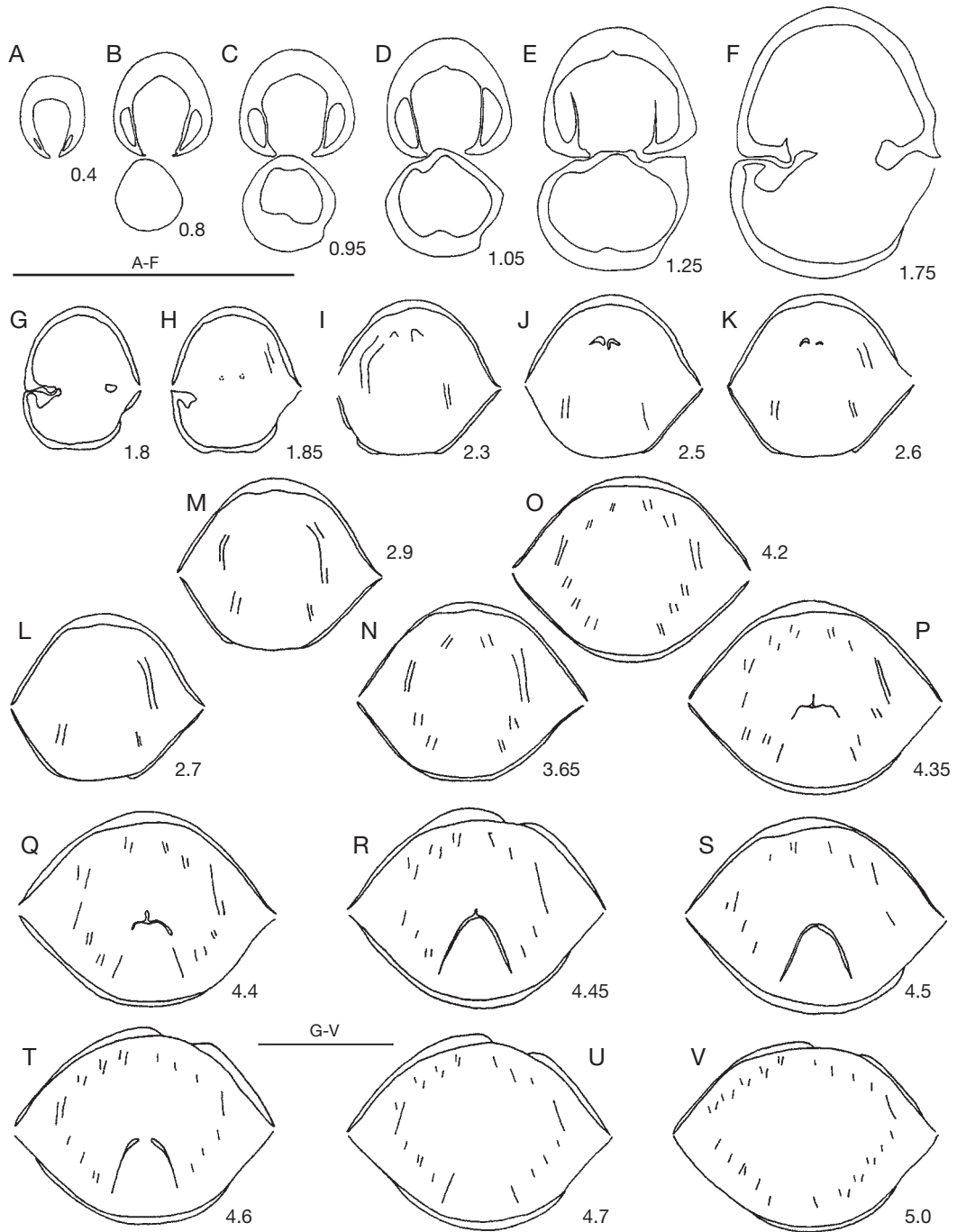


FIG. 33. — Transverse serial sections of *Neptunathyris buxi* n. gen., n. sp. (IRScNB a12335), loc. JG-1995-5, Matagne Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

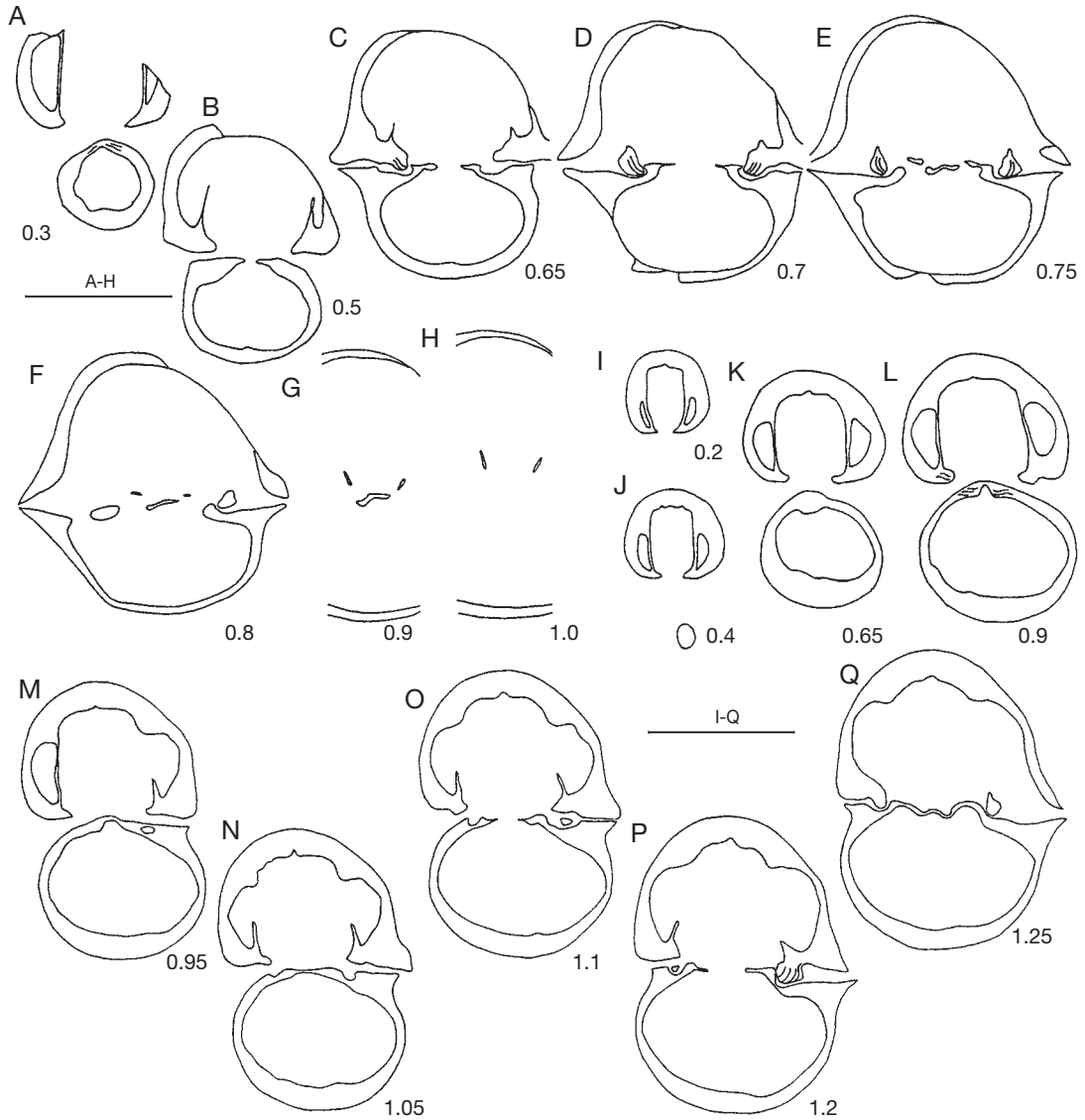


FIG. 34. — Transverse serial sections of *Neptunathyris buxi* n. gen., n. sp., loc. JG-1995-5, Matagne Formation: **A-H**, IRScNB a12336; **I-Q**, IRScNB a12337. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

rounded in outline; widest at about mid-length; anterior margin rounded to straight; anterior commissure vaguely undulating to uniplicate.

Ventral valve dome-shaped in posterior view, regularly convex in lateral profile; flanks sloping slightly to moderately towards lateral commissure; beak erect to slightly incurved, never in contact with the dorsal

umbo; sulcus exceptionally present (only perceptible near the anterior margin); tongue 2.16-3.29 times wider than high, semicircular, sometimes perpendicular to commissural plane; shoulder lines weakly concave; shoulder and apical angles between 111-129° and 93-122°, respectively; interarea small, concave, apsacline.

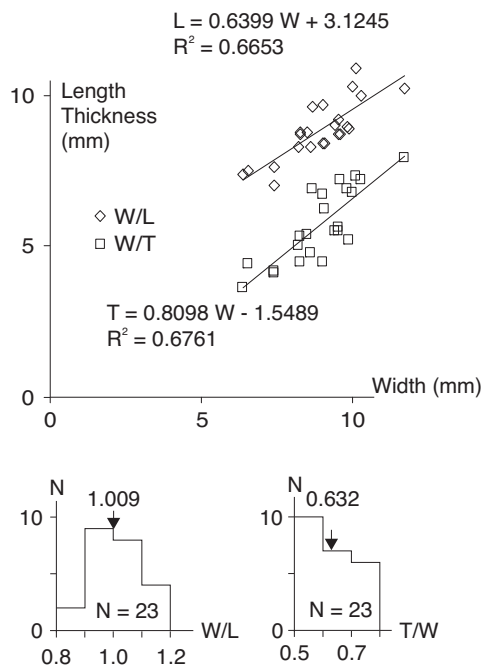


FIG. 35. — *Neptunathyris buxi*, n. gen., n. sp. (loc. BM-2003-9 and JG-1995-5, Neuville and Matagne formations). Scatter diagrams of shell width (W) to shell length (L), shell width to shell thickness (T); frequency diagrams of W/L and T/W. Arrows indicate the means.

Dorsal valve rounded to suboval in outline; highest at about midvalve or more posteriorly (height decreasing more or less sharply towards anterior margin); no fold.

Growth lamellae rare; average distance between two successive growth lamellae about 0.5 mm (only observed close to the commissure).

Ventral interior with thin and short dental plates supporting teeth subrectangular in transverse section; lateral apical cavities not filled in, narrow; no myophragm; median depression in the posterior part of the valve.

Dorsal interior with cardinal plate pierced in its posterior part; anteriorly, it extends in the manner of thin inner hinge plates; inner socket ridges poorly developed; spiral cones ventrolaterally oriented, with at least five whorls per cone.

DISTRIBUTION

To date, *Neptunathyris buxi* n. sp. is only recognized at the southern border of the Dinant Synclinorium,

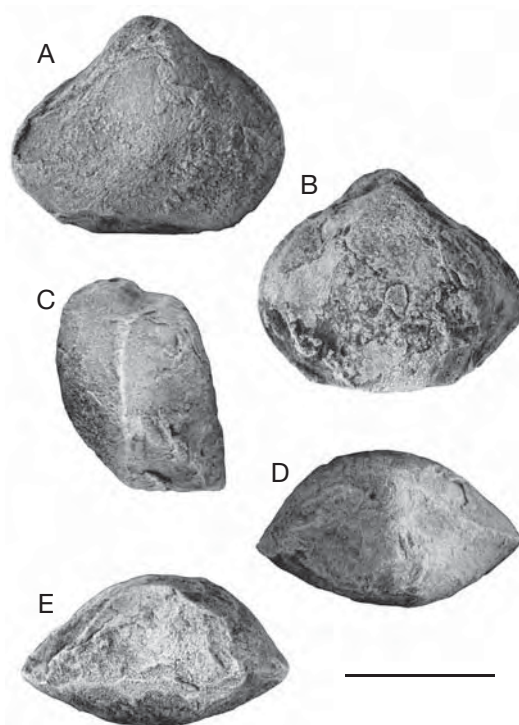


FIG. 36. — *Camarium* sp., complete shell (IRScNB a12338), loc. JG-1996-3, Les Valisettes Formation: A, ventral view; B, dorsal view; C, lateral view; D, posterior view; E, anterior view. Scale bar: 10 mm.

within the top of the Neuville Formation and the lowermost part of the Matagne Formation.

Superfamily MERISTELLOIDEA Waagen, 1883

Family MERISTIDAE Hall & Clarke, 1895

Subfamily MERISTINAE Hall & Clarke, 1895

Genus *Camarium* Hall, 1859

TYPE SPECIES. — *Camarium typum* Hall, 1859, by monotypy.

*Camarium* sp.

(Figs 36, 37; Table 3)

MATERIAL EXAMINED. — BM-2002-8 (one articulated specimen); BM-2004-1 (one articulated specimen); JG-1996-3 (one articulated specimen); Senzeille 6854 (one articulated specimen).

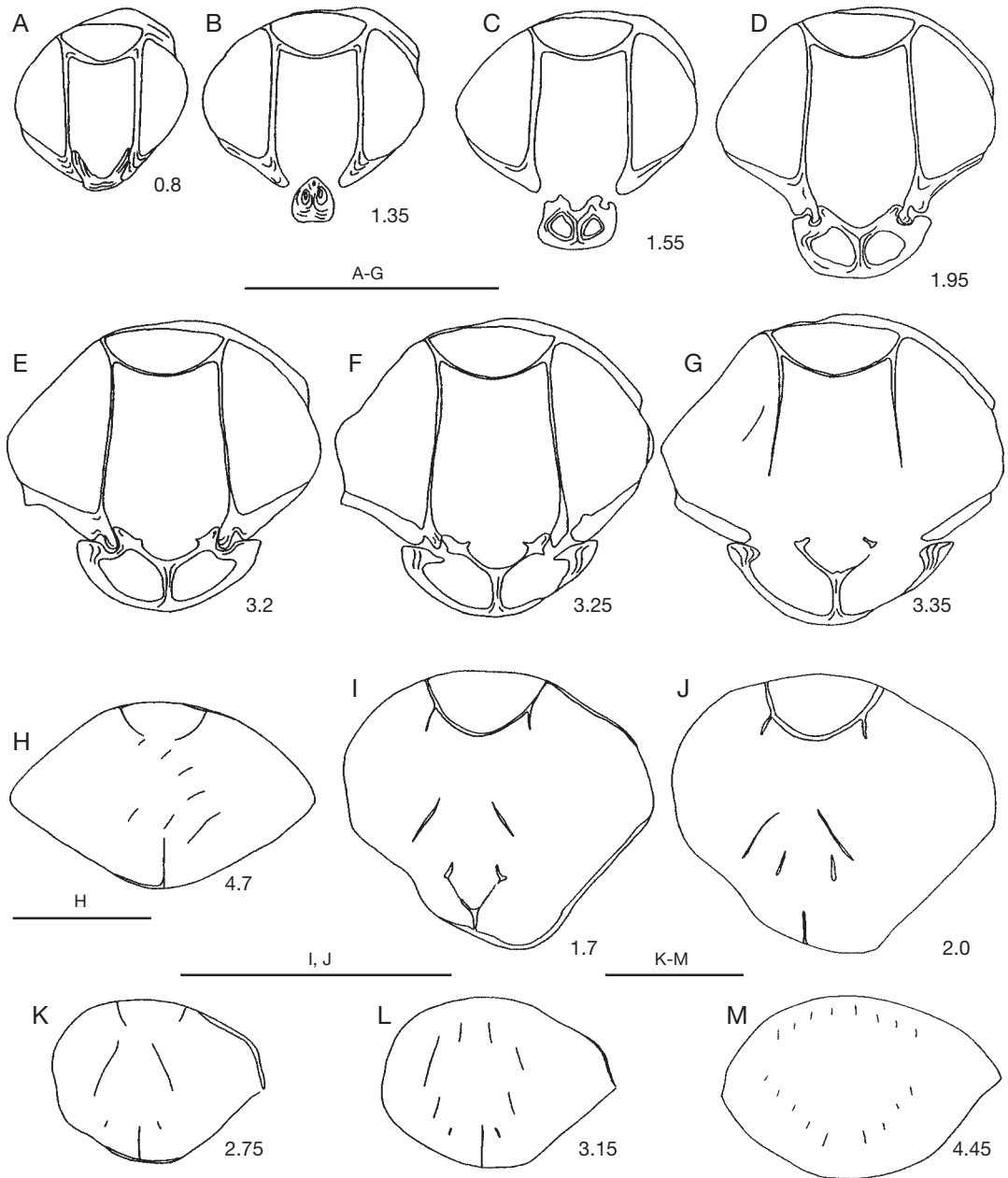


FIG. 37. — Transverse serial sections of *Camarium* sp.: **A-H**, IRScNB a12339, loc. Senzeille 6854, Les Valisettes Formation; **I-M**, IRScNB a12340, loc. JG-1996-3, Les Valisettes Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

REMARKS

Shell wider than long to longer than wide, rounded subpentagonal in outline; anterior commissure

uniplicate; sulcus and fold absent; tongue semicircular, high, almost perpendicular to commissural plane. The absence of mystrochial plates in the ventral valve

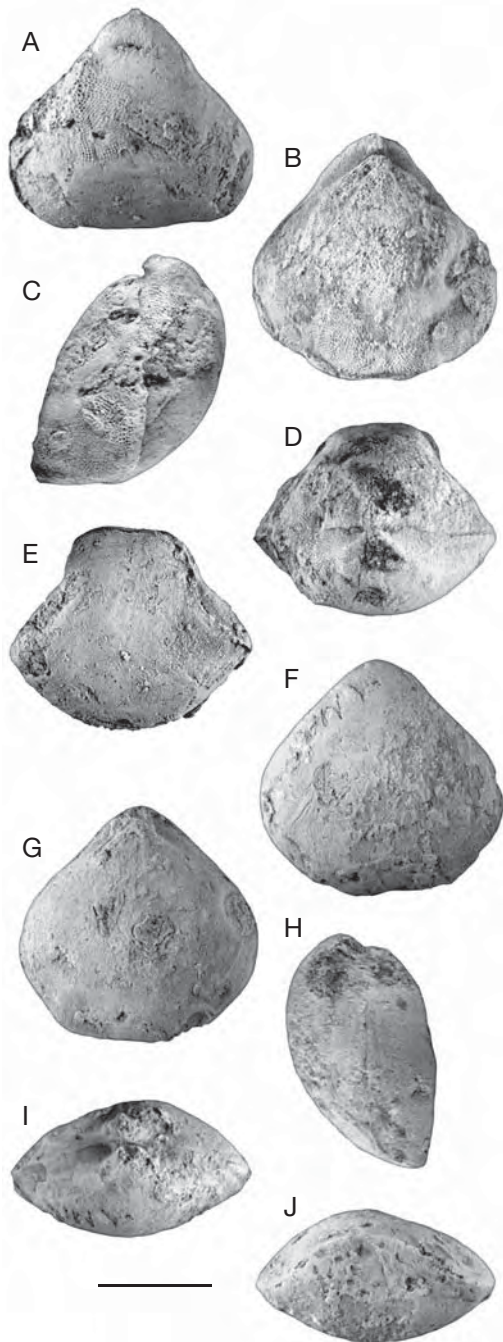


FIG. 38. — *Dicamara plutonis* n. sp., loc. Couvin 6158p., Grands Breux Formation (Boussu-en-Fagne Member): **A-E**, complete shell (holotype IRSnb a12341); **F-J**, complete shell (IRSnb a13342); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 10 mm.

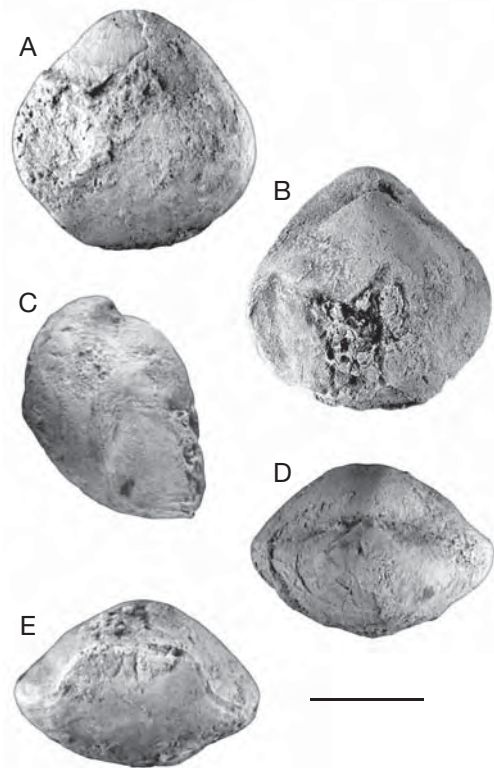


FIG. 39. — *Dicamara plutonis* n. sp., complete shell (IRSnb a12343), loc. Couvin 6158p., Grands Breux Formation (Boussu-en-Fagne Member): **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view. Scale bar: 10 mm.

and of shoe-lifter process in the dorsal one led me to assign these specimens to the genus *Camarium* as revised by Amsden (1968) rather than to *Merista* Suess, 1851. The limited number of specimens does not permit a more detailed description or a worthwhile comparison with other species of *Camarium* such as *C. rhenanensis* (Grunt in Grunt & Racki, 1998).

DISTRIBUTION

*Camarium* sp. is known within the Les Valisettes Formation (Philippeville Anticlinorium).

Genus *Dicamara* Hall & Clarke, 1893

TYPE SPECIES. — *Atrypa plebeia* Sowerby, 1840, by subsequent designation (Hall & Clarke 1894: 966).



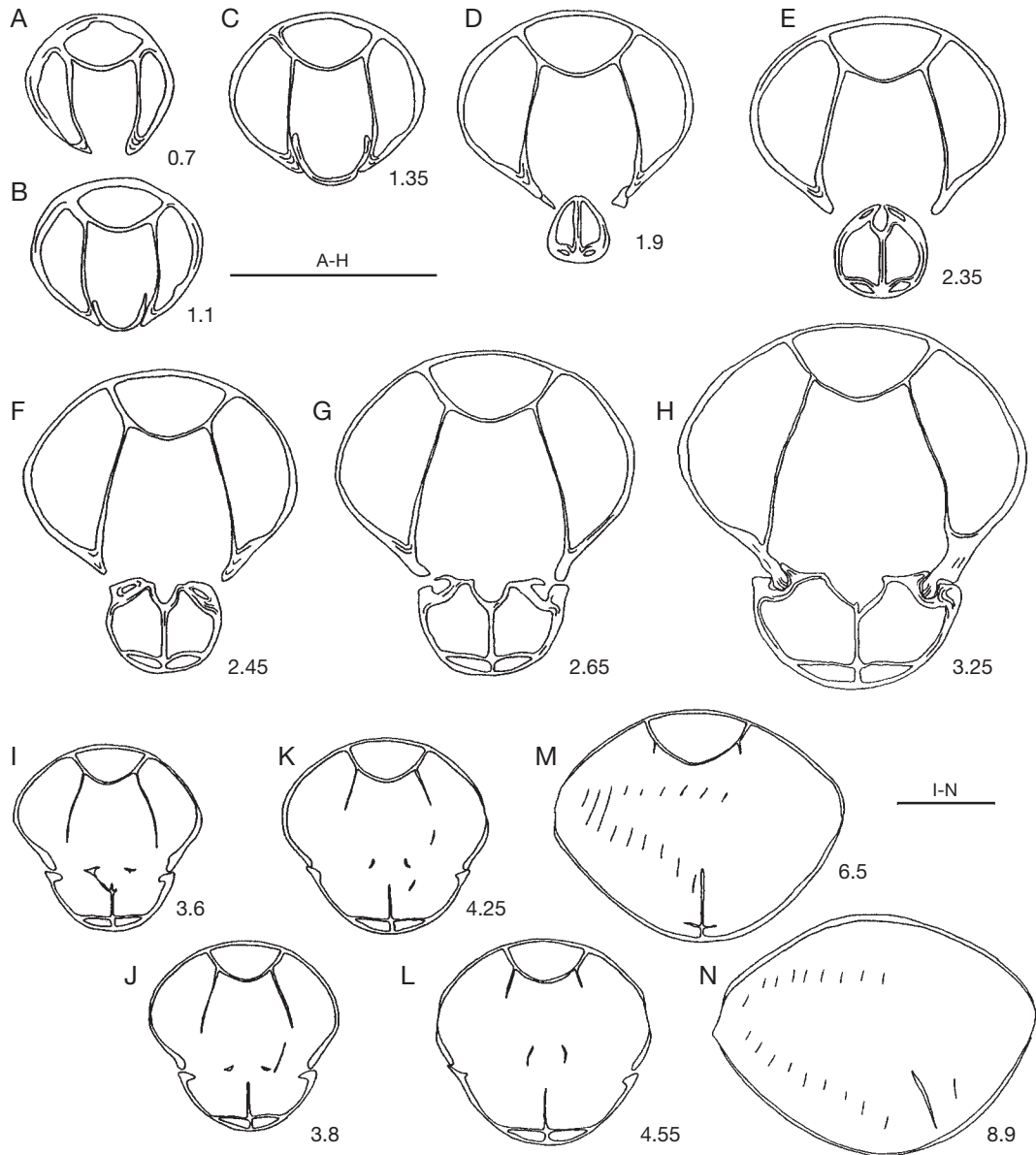


FIG. 40. — Transverse serial sections of *Dicamara plutonis* n. sp. (IRScNB a12344), loc. Couvin 6158p., Grands Breux Formation (Boussu-en-Fagne Member). Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

*Dicamara plutonis* n. sp.  
(Figs 38–41)

*Merista plebeia* — Maillieux 1909b: 122, 138, 139.

*Merista plebeja* — Maillieux 1922b (e.p.): 18. — Maillieux in Kaisin *et al.* 1922: 23.

*Dicamara plebeja* — Maillieux 1933 (e.p.): 81; 1940: 27; 1941b (e.p.): 11. — Maillieux in Asselberghs & Maillieux 1925: 166. — Dumon 1929: 164.

HOLOTYPE. — IRScNB a12341.

ETYMOLOGY. — *Pluto, onis* (Latin): Pluto, king of hell

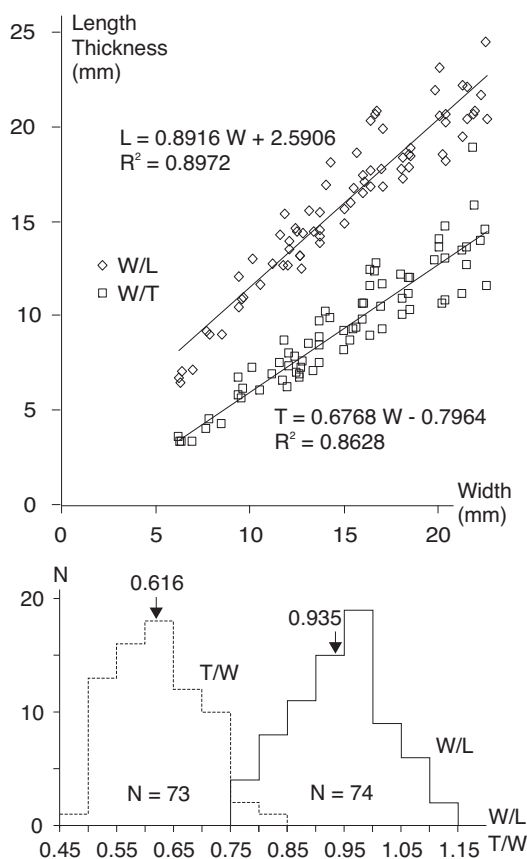


FIG. 41. — *Dicamara plutonis* n. sp. (loc. BM-2003-10, JG-1995-4, Couvin 6158p., Grands Breux Formation [Boussu-en-Fagne Member]). Scatter diagrams of shell width (**W**) to shell length (**L**), shell width to shell thickness (**T**); frequency diagrams of **W/L** and **T/W**. Arrows indicate the means.

and god of the dead, with reference to the Boussu-en-Fagne cemetery located near the *locus typicus*.

LOCALITY AND AGE. — Boussu-en-Fagne, cemetery quarry (BM-2003-10 = Couvin 6158p. and JG-1995-4). Grands Breux Formation (Boussu-en-Fagne Member, in the vicinity of the Lion Member carbonate mounds).

MATERIAL EXAMINED. — BM-2003-10 (15 articulated specimens); JG-1995-4 (six articulated specimens); Couvin 6158p. (99 articulated specimens).

DIAGNOSIS. — Shell medium-sized (maximum width: 22.5 mm; maximum length: 24.5 mm; maximum thickness: 18.9 mm), generally longer than wide (width/length ratio: 0.77-1.12), dorsibiconvex to ventribiconvex, rounded subpentagonal in outline; sulcus and fold rarely

developed; tongue present; shoulder and apical angles identical, between 69-103°.

#### DESCRIPTION

Shell medium-sized, generally longer than wide (width/length ratio: 0.77-1.12), dorsibiconvex to ventribiconvex, rounded subpentagonal in outline; anterior margin usually straight, sometimes rounded; widest in the anterior half of the shell; anterior commissure uniplicate.

Ventral valve regularly curved in posterior view; flanks sloping moderately towards lateral commissure; in lateral profile, anterior part of the valve forming a quarter of an ellipse, whereas curvature is strongly marked in umbonal area; slight, poorly defined median depression close to anterior margin in some specimens; tongue 1.75-2.89 times wider than high, subrounded to subtrapezoidal, sometimes perpendicular to commissural plane; shoulder lines rectilinear; shoulder and apical angles identical, between 69 and 103° (most common values between 79 and 99°); beak erect to incurved, not in contact with dorsal umbo; foramen small, permesothyrid.

Dorsal valve rounded subpentagonal in outline; highest at about midvalve or at the anterior margin (in the first case, the height of the valve decreases gradually or maintains its height towards the anterior margin); umbo prominent; fold occurring rarely, moderately high, only perceptible near the front, with top flattened.

Shell smooth; no growth lamella observed (possibly as a result of poor preservation).

Ventral interior with thin and long dental plates with a weak thickening in their posterior part; dental plates fused with a shoe-lifter process delimiting a broad cella; cella roughly subpyramidal, widening anteriorly along an angle of 20-36° (11 specimens observed); teeth subrectangular in transverse section.

Dorsal interior with shoe-lifter process divided by a long and thin median septum supporting the septalium; dental sockets deep, relatively long, with internal crests well-developed; spiral cones comprising at least 10 whorls (brachidium of the sectioned specimen distorted!).

#### DISCUSSION

*Dicamara plutonis* n. sp. has commonly been misidentified with *D. plebeia* (Sowerby, 1840) from the Middle

Devonian from which it can be distinguished by its more elongated outline, its more acute apical angle and its less prominent fold (where it is developed). *Dicamara scalprum* (Roemer, 1844) has been placed in synonymy with *D. plebeia* (Sowerby, 1840) by several authors, notably by Davidson (1865: 20), Torley (1934: 116), Comte (1938: 76), Boucot *et al.* (1965: H658) and Alvarez & Rong (2002: 1572). Nevertheless, Roemer's species is maintained by Struve (1964: 518, 519) who subdivided it into two subspecies: *D. scalprum scalprum* (Roemer, 1844) and *D. scalprum antescalprum* Struve, 1964. From both subspecies, *D. plutonis* n. sp. is distinguished by its larger size, its more elongated outline and by its more acute apical angle. *Dicamara plutonis* n. sp. displays a subpentagonal outline completely different from that of *D. prunulum* (Schnur, 1851). *Dicamara plutonis* n. sp. differs from *D. pertinax* Ficner & Havlíček, 1978 by its clearly larger size and a narrow apical angle.

#### DISTRIBUTION

*Dicamara plutonis* n. sp. occurs within the Grands Breux Formation (Boussu-en-Fagne Member), near the Lion Member mounds (southern flank of the Dinant Synclinorium). Maillieux (1926, 1940) listed "*Dicamara plebeja* (Sowerby)" (*sic*) in several stratigraphic levels of the Frasnian from the Philippeville Anticlinorium as well as from the Dinant and Namur synclinoria but the verification of all these records is beyond the scope of this paper.

Order SPIRIFERIDA Waagen, 1883  
Suborder SPIRIFERIDINA Waagen, 1883  
Superfamily ADOLFIOIDEA Sartenaer, 1967  
Family ADOLFIIDAE Sartenaer, 1967  
Subfamily ADOLFIINAE Sartenaer, 1967

#### Genus *Adolfia* Gürich, 1909

TYPE SPECIES. — *Spirifer deflexus* Roemer, 1843, by subsequent designation (Schuchert 1929: 27).

#### REMARKS

The two types of micro-ornament observed in the Devonian "Guerichellinae" from Belgium led Vandercammen (1966: 266) to reserve the genus *Adolfia* for

the species whose micro-ornament is characterized by simple or dichotomous subradial capillae, on which spine bases are regularly or irregularly distributed. On the other hand, he assigned those displaying subradial and discontinuous alignments of spine bases to the genus *Guerichella* Paeckelmann, 1913. According to Vandercammen (1967: 7), the micro-ornament of the type of *Spirifer deflexus* Roemer, 1843 consists of "microcostules (= capillae) pseudoradiaires fines et continues portant de petites épines". The maintenance of *Guerichella* is unacceptable as discussed by Sartenaer (1967) in accordance with the *International Code of Zoological Nomenclature* (ICZN 1999). As suggested by Gourvenec (1989: 174), a new subgenus could be erected for grouping the species previously assigned to *Guerichella* by Vandercammen (1966).

Vandercammen (1957d: 47) reported the following species in the upper part of the Frasnian of southern Belgium: *A. pseudomultifida* (Vandercammen, 1955) ("F2i", "F2j", "F2IIDb" [*sic*], "F2IIDc", "F2IINb", "F2IIIB", "F2IIIC"), *A. biverrucosa* (Vandercammen, 1955) ("F2i", "F2IIIB"), *A. deflexa* (Roemer, 1843) ("F2i", "F2IIDb" [*sic*], "F2IIDc", "F2IIIC"), *A. rarispinosa* (Vandercammen, 1955) ("F2i", "F2IIDb" [*sic*]). *Adolfia faniensis* Vandercammen, 1966 ("F2j") and *Adolfia trelonensis* (Le Maître, 1961) ("F2j") have been added later by Vandercammen (1966: 274, 279). However, the detailed revision of these taxa is beyond the scope of this paper.

#### *Adolfia* cf. *pseudomultifida*

(Vandercammen, 1955)  
(Fig. 42)

*Gürichella pseudomultifida* Vandercammen, 1955: 2, 3; 1957d: 15-24, 26-31, 47, pl. 1, figs 1-4, 5-8 (?), 9, 10, non 11, 12 (= *A. biverrucosa*), 13, text-figs 4-23; 1966: 275, 284, pl. 3, fig. 9.

*Guerichella pseudomultifida* – Sartenaer 1967: 386.

MATERIAL EXAMINED. — BM-2002-8 (eight articulated specimens).

#### REMARKS

These relatively small-sized specimens display the following characters: widest at the posterior margin, acute cardinal extremities, well-developed ventral

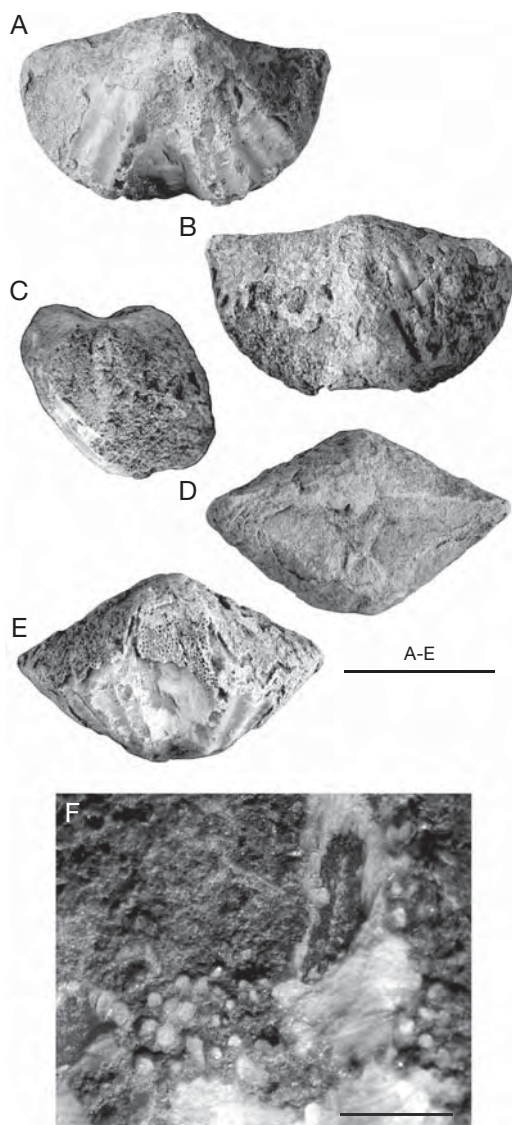


FIG. 42. — *Adolfia* cf. *pseudomultifida* (Vandercammen, 1955), almost complete shell (IRScNB a12283), loc. BM-2002-8, Les Valisettes Formation: **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view; **F**, detail of micro-ornament. Scale bars: A-E, 10 mm; F, 1 mm.

interarea, a relatively narrow sulcus, high tongue, 6-7 low and rounded costae per flank, separated by similar grooves. Micro-ornament composed of large spine bases aligned subradially. These specimens, recovered in the Neuville and Les Valisettes

formations, may represent immature forms of *A. pseudomultifida*, but in the absence of specimens of comparable size to the holotype (IRScNB a7978), they are tentatively compared to this species.

*Adolfia biverrucosa* (Vandercammen, 1955)  
(Figs 43A-F; 44; Table 4)

*Gürichella biverrucosa* Vandercammen, 1955: 3; 1957d: 24, 25, 30-37, 47, pl. 1, figs 14-20, text-figs 24-39; 1966: 275, 284, pl. 3, fig. 8.

*Gürichella pseudomultifida* – Vandercammen 1957d (e.p.): pl. 1, figs 11, 12.

*Guerichella biverrucosa* – Sartenaer 1967: 386.

MATERIAL EXAMINED. — BM-2003-8 (nine articulated specimens, one ventral valve); Olloy 575 (10 articulated specimens, one ventral valve).

DESCRIPTION

Shell medium-sized, wider than long (width/length ratio: 1.35-1.53), dorsibiconvex to slightly ventribiconvex, rounded subpentagonal in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.64-0.90); widest at about mid-length or posteriorly; anterolateral margins outlining a curve variably excavated by the sulcus in its median part; cardinal extremities rounded.

Ventral valve regularly curved in lateral profile except in beak area; flanks sloping moderately towards lateral commissure; sulcus wide (sulcus width/width ratio: 0.43-0.56), originating at beak, moderately deep, relatively well-delimited, with bottom flattened at anterior margin; tongue 1.22-1.62 times wider than high, subtrapezoidal to subrectangular, perpendicular to commissural plane (in some specimens, distal part of tongue bent dorsally); shoulder lines concave; shoulder and apical angles between 102-112° and 146-(146°+) respectively; interarea concave, high (interarea height/hinge line width ratio: 0.17-0.28), cata-apsacine; delthyrium wide, closed by relatively convex pseudodeltidium.

Dorsal valve wider than long (width/dorsal valve length ratio: 1.32-1.53), subtrapezoidal in outline; posterolateral areas tending to become flat; highest at front or about midvalve (in the second case, it curves progressively or maintains its height); fold

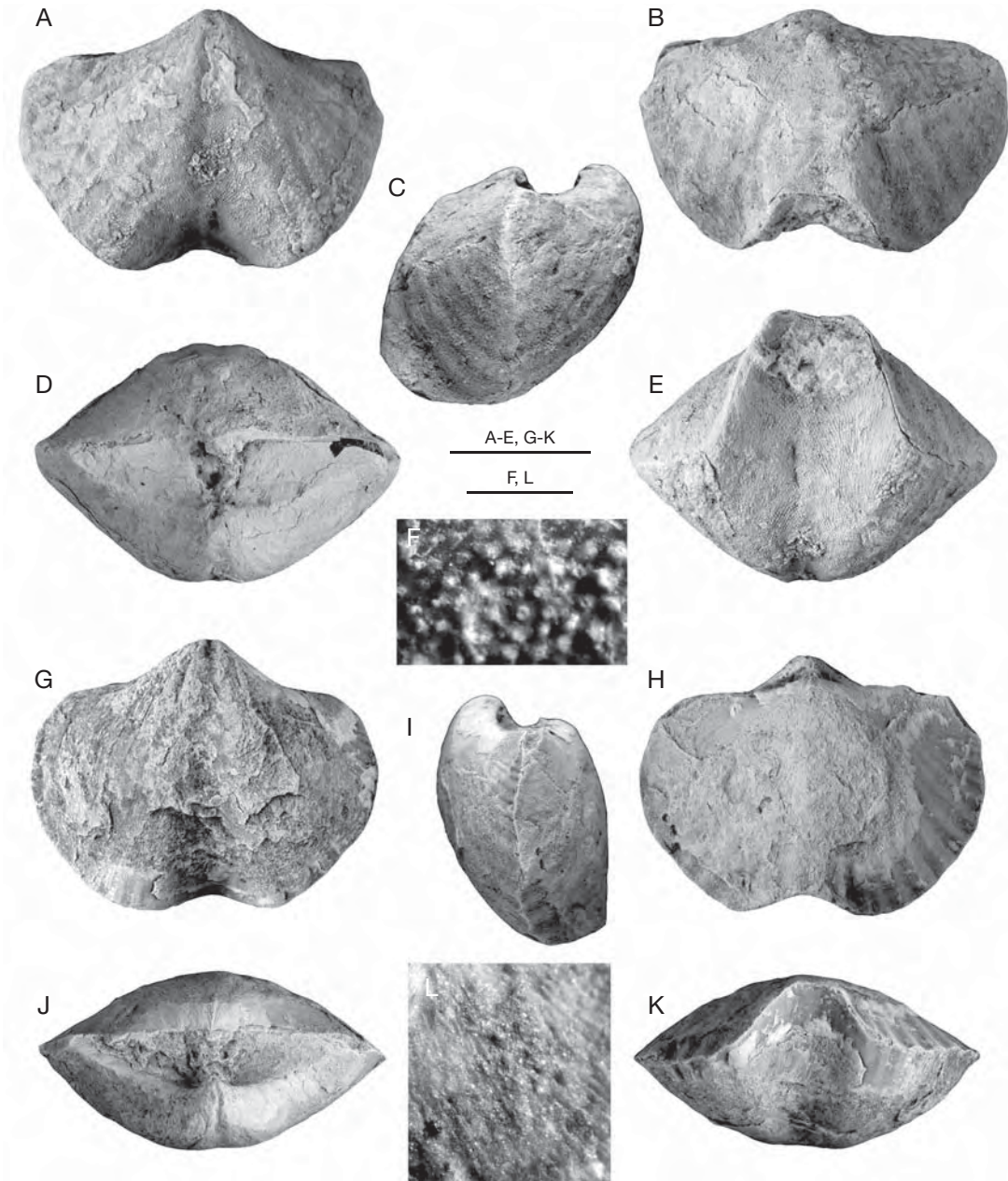


FIG. 43. — **A-F**, *Adolfia biverrucosa* (Vandercammen, 1955), almost complete shell (IRScNB a12285), loc. BM-2003-8, Neuville Formation; **G-L**, *Adolfia* sp., complete shell (IRScNB a12288), loc. BM-2002-7, Neuville Formation; **A, G**, ventral views; **B, H**, dorsal views; **C, I**, lateral views; **D, J**, posterior views; **E, K**, anterior views; **F, L**, detail of micro-ornament. Scale bars: A-E, G-K, 10 mm; F, L, 1 mm.

originating at beak, moderately high, with top rounded at anterior margin; interarea orthocline, plane, linear.

Flanks covered by at least nine rounded costae, separated by similar grooves; sulcus with a median costa and 1-3 additional costae; fold with 2 or 3 costae;

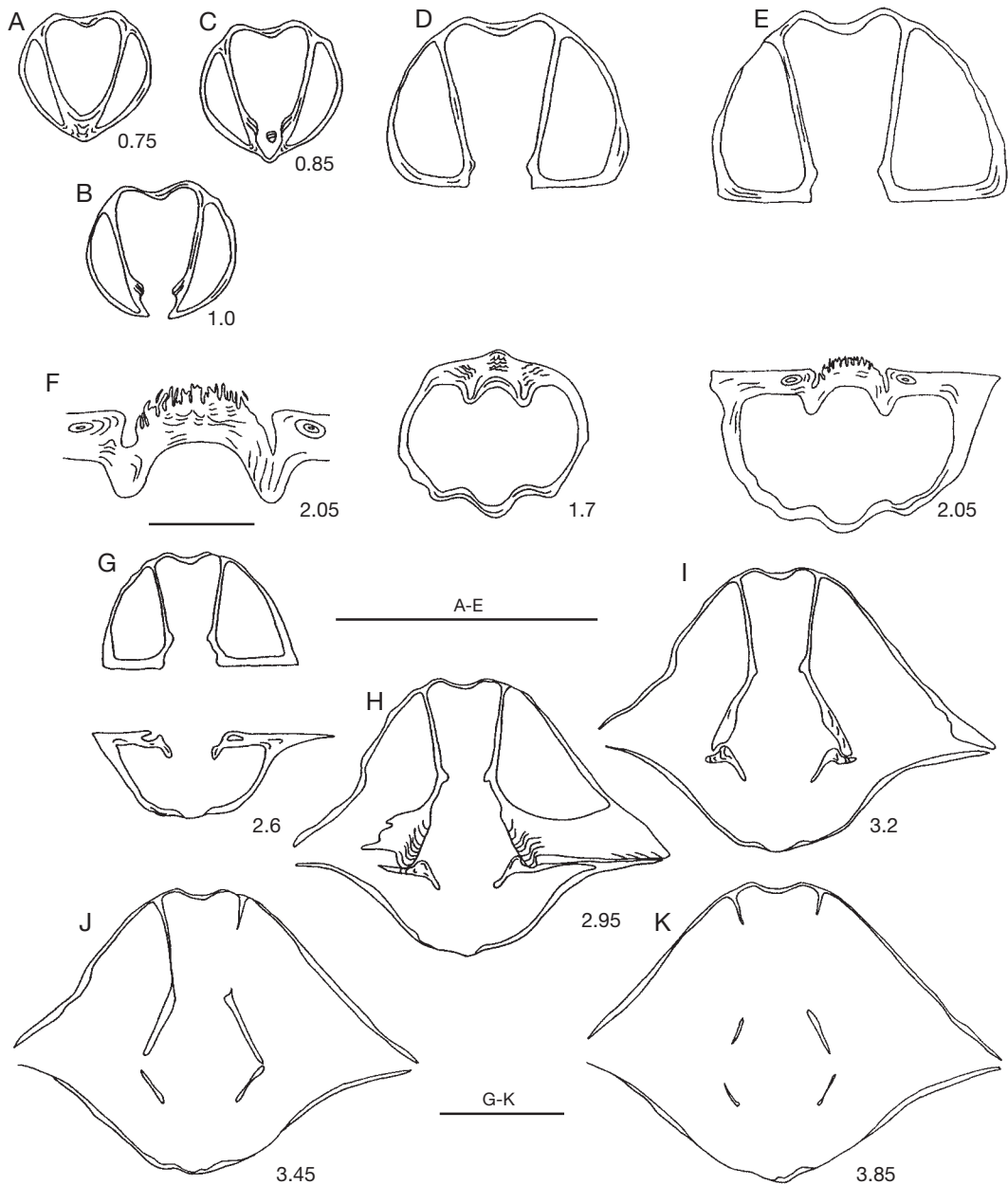


FIG. 44. — Transverse serial sections of *Adolfia biverrucosa* (Vandercammen, 1955) (IRScNB a12287), loc. BM-2003-8, Neuville Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: A-E, G-K, 5 mm; F, 1 mm.

micro-ornament consisting of subradial alignments composed of small and big spine bases principally on the top of costae; growth lamellae irregularly spaced (see

Vandercammen [1957d: 31, 32, pl. 1, figs 19, 20]).

Ventral interior with extrasinal thin dental plates supporting small and rounded teeth; delthyrial plate

absent (or very short?); lateral and central apical cavities not filled in.

Dorsal interior with ctenophoridium including more or less 15 thickened plates (some with dichotomous distal extremities); dental sockets moderately deep; spiral cones not observed.

#### DISCUSSION

*Adolfia biverrucosa* differs from *A. pseudomultifida* by its less transverse outline, its narrower sulcus and by its micro-ornament including small and large spine bases.

#### DISTRIBUTION

Vandercammen (1957d: 34) reported *Adolfia biverrucosa* within "F2b", "F2i" and "F2IIIb". The specimens presently studied originate from the top of the Neuville Formation in the railway section between Mariembourg and Nismes (BM-2003-8; southern border of the Dinant Synclinorium), i.e. the *locus typicus* of the species.

*Adolfia* sp.  
(Fig. 43G-L)

MATERIAL EXAMINED. — BM-2002-7 (five articulated specimens, one ventral valve, one dorsal valve).

#### REMARKS

Seven poorly preserved specimens of which the micro-ornament consists of long subradial capillae with spine bases are left in open nomenclature. They have been collected in the upper part of the Neuville Formation on the southeastern margin of the Dinant Synclinorium. They are close to *Adolfia deflexa* (Roemer, 1843) *sensu* Vandercammen and *A. rarispinosa* (Vandercammen, 1955), but both species need to be revised.

*Adolfia* cf. *treilonensis* (Le Maître, 1961)  
(Fig. 45; Table 4)

*Gürichella treilonensis* Le Maître, 1961: 115-120, pl. 8, figs 1-14. — Vandercammen 1966: 276-279, 284, pl. 2, figs 1-10, pl. 3, fig. 7.

*Gürichella treilonensis* – Sartenaer 1967: 386.

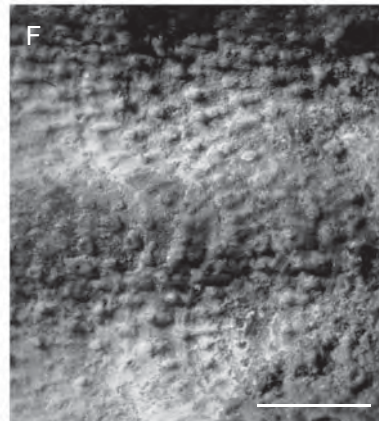
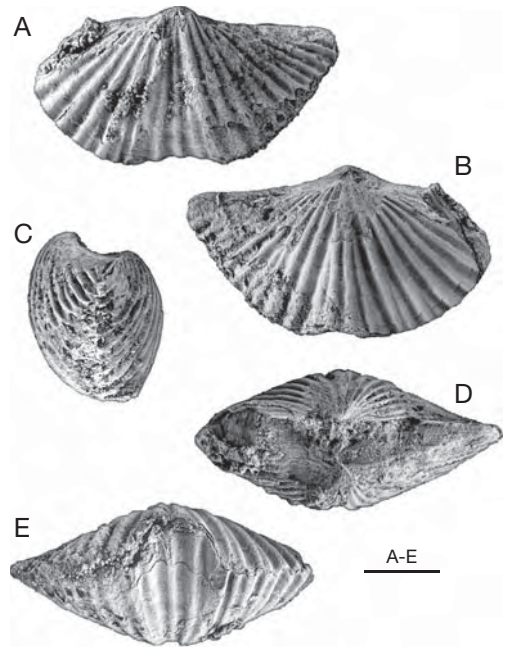


FIG. 45. — *Adolfia* cf. *treilonensis* (Le Maître, 1961), almost complete shell (IRScNB a12289), loc. BM-2001-2, Lambermont Formation: **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view; **F**, detail of micro-ornament with anterior margin to the left of the photograph. Scale bars: A-E, 10 mm; F, 1 mm.

MATERIAL EXAMINED. — BM-2001-2 (one articulated specimen).

#### REMARKS

Only one specimen has been recovered. It displays the following external characters: shell wider than long,

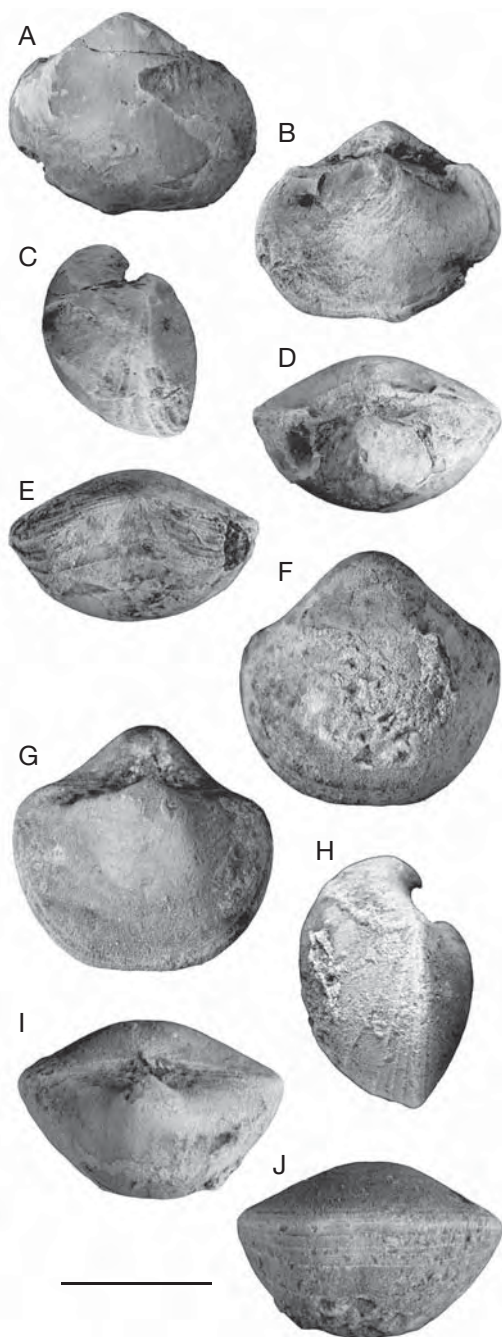


FIG. 46. — *Emanuella* sp., Grands Breux Formation (Boussu-en-Fagne Member): **A-E**, complete shell (IRScNB a12293), loc. BM-2003-7; **F-J**, complete shell (IRScNB a12292), loc. Bm-2003-10; **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: A-E, 10 mm; F-J, 5 mm.

ventribiconvex, subpentagonal in outline; lateral and anterior margins outlining a curve slightly excavated medially by the sulcus; sulcus wide, well-delimited, shallow, with bottom flattened at front; tongue 1.85 times wider than high, subtrapezoidal, perpendicular to the commissural plane; ventral interarea slightly concave, (6.25) times wider than high, cata-apsacline; delthyrium not observed; dorsal valve wider than long, subtrapezoidal in outline; dorsal posterolateral areas inclined to become flat; fold originating at beak, low, clearly delimited, with top flattened; dorsal interarea not observed; 12 sharp and rounded costae per flank, separated by similar grooves; most internal costae with bifurcation; sulcus with one central and two lateral costae; fold with four costae increasing by intercalation; subcylindrical spine bases arranged along subradial alignments; growth lamellae rare. The specimen is close to Le Maître's species in the bifurcations of the most internal costae on the flanks, the profile of its interarea, its shallow sulcus and low fold, as well as its transverse outline. However, it does not display rounded cardinal extremities. It originates from the base of the Lambermont Formation (northern border of the Dinant Synclinorium). Some badly preserved specimens collected in the upper part of the Aisemont Formation could be assigned to this taxon.

#### Genus *Acutatheca* Stainbrook, 1945

TYPE SPECIES. — *Acutatheca propria* Stainbrook, 1945, by monotypy.

#### *Acutatheca rigauxi* (Maillieux, 1909)

*Cyrtina Rigauxi* Maillieux, 1909a: 10, 11, figs a-c.

*Acutatheca rigauxi* – Mottequin 2005a: 56-58, figs 3, 4, 9, table 1.

#### REMARKS

The species has been described in detail by Mottequin (2005a). *Acutatheca rigauxi* occurs at the southern border of the Dinant Synclinorium (Neuville Formation). Representatives of the genus *Acutatheca* have been also collected within the Les Valisettes Formation (BM-2002-8; Philippeville Anticlinorium) as well as in the Frasnian beds of the Lambermont Formation (BM-



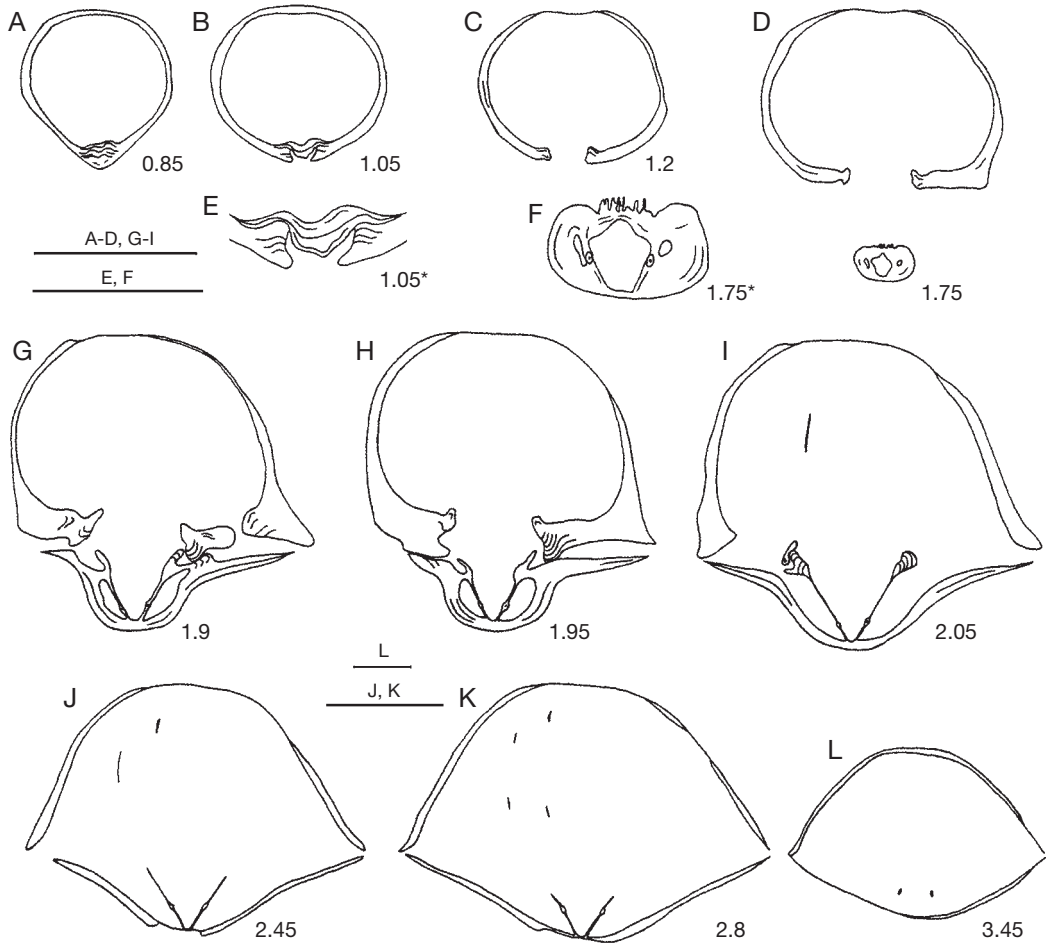


FIG. 47. — Transverse serial sections of *Emanuella* sp. (IRScNB a12290), loc. BM-2003-7, Grands Breux Formation (Boussu-en-Fagne Member). Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: A-D, G-L, 2.5 mm; E, F, 1 mm.

2002-1; northern border of the Dinant Synclinorium). However, additional material is needed to confirm if they belong to *A. rigauxi* or to another species.

Superfamily AMBOCOELIOIDEA George, 1931  
 Family AMBOCOELIIDAE George, 1931  
 Subfamily RHYNCHOSPIRIFERINAE Paulus, 1957

Genus *Emanuella* Grabau, 1923

TYPE SPECIES. — *Nucleospira takwanensis* Kayser, 1883, by original designation.

*Emanuella* sp.  
 (Figs 46; 47; Table 4)

MATERIAL EXAMINED. — BM-2003-7 (two articulated specimens); BM-2003-10 (two articulated specimens).

DESCRIPTION

Shell small-sized, wider than long (width/length ratio: 1.02-1.23), ventribiconvex, rounded sub-pentagonal in outline; hinge line shorter than greatest width (hinge line width/width ratio: 68-0.74); widest at about mid-length; anterior margin straight; anterior commissure rectimarginate to slightly uniplicate.

Ventral valve clearly curved in lateral profile, especially in the umbonal area; beak curved on the interarea; largest specimen displaying a shallow median depression near anterior margin; shoulder lines concave; shoulder and apical angles between 99-119° and 90-105°, respectively; interarea 3.70-6.25 times wider than high, concave, cata-apsaline; fragments of deltidial plates observed.

Dorsal valve wider than long (width/dorsal valve length ratio: 1.40-1.46), rounded subtrapezoidal to elliptic in outline; highest in its posterior part curving progressively towards the front; no fold or groove; interarea linear, anacline, plane.

In the middle part of the valves, distance between two successive growth lamellae between 2.4-2.7 mm (more closely spaced near the commissure); spine bases of variable diameter arranged in discontinuous subradial alignments.

Ventral interior devoid of dental plates; teeth relatively strong; dental ridges strong; "pedicle collar" *sensu* Veevers (1959a) (= "delthyrial plate" of Ma *in* Ma *et al.* 2006) dorsally directed, closing delthyrium apex.

Dorsal interior with ctenophoridium separated from the valve floor by a broad central apical cavity (number of lamellae unknown); lateral apical cavities poorly filled in; dental sockets laterally connected to the valve floor (intermediate-type dental sockets *sensu* Goldman & Mitchell [1990: 92, fig. 17]); spiral cones not observed in the sectioned specimen.

#### DISCUSSION

Some specimens identified as *Crurithyris inflata* (Schnur, 1853) by Vandercammen (1956: 11-19) could be included with those identified here as *Emanuella* sp. They cannot be assigned to *Crurithyris* because the latter does not have well-developed crural plates as in the transverse sections of *Crurithyris urii* (Fleming, 1828) illustrated by Veevers (1959a: text-fig. 4B). They display the main characteristics of the genus *Emanuella* itemised by Goldman & Mitchell (1990: 90), but they do not display a narrow furrow at the dorsal valve. The lectotype of *Emanuella takwanensis* (Kayser, 1883) has been designated by Veevers (1959a: 904) and illustrated by Dürkoop (1970: pl. 17: 1a-e). Both authors presented transverse serial sections of specimens of this species, coming from Kayser's collection (MB). The specimen sectioned by Veevers (1959a:

text-fig. 4A) displays a cardinal process fixed to the valve floor whereas this structure is apparently raised in the other representatives of the genus *Emanuella*, i.e. separated from the valve floor by a central apical cavity (Crickmay 1967: pl. 2, figs 1, 4; Goldman & Mitchell 1990: figs 8, 9). This cavity is present in the specimen sectioned by Dürkoop (1970: pl. 56, fig. 1) as well as in the one illustrated by Grabau (1931: fig. 46d); so, it is possible that the specimen sectioned by Veevers belongs to another genus on the basis of the layout of the cardinal process, unless this is only an intraspecific variation. The resolution of this question requires further study.

#### DISTRIBUTION

*Emanuella* sp. occurs within the Grands Breux Formation (Boussu-en-Fagne Member) on the southern flank of the Dinant Synclinorium. Similar specimens originate from the top of the Les Valisettes Formation (Philippeville Anticlinorium).

#### Rhynchospiriferinae gen. and sp. indet. (Figs 48; 49; Table 4)

MATERIAL EXAMINED. — BM-2003-9 (two articulated specimens, one ventral valve); JG-1996-1 (four articulated specimens).

#### DESCRIPTION

Shell small-sized, longer than wide to wider than long (width/length ratio: 0.96-1.23), ventribiconvex, rounded subpentagonal in outline; hinge line straight but shorter than greatest width (hinge line width/width ratio: 0.61-0.72); widest at about mid-length; anterior margin straight; anterior commissure rectimarginate (sulcus and fold absent).

Ventral valve regularly convex in lateral profile (except in the beak area); dome-shaped in posterior view; flanks sloping moderately towards the lateral commissure; beak strongly curved on the interarea; umbo prominent; shoulder lines concave; shoulder and apical angles between 96-102° and 77-86°, respectively; interarea 2.85-5.26 times wider than high, concave, cata-apsaline to apsacaline; delthyrium partially closed by deltidial plates.

Dorsal valve wider than long (width/dorsal valve length ratio: 1.23-1.53); highest posteriorly, curving

progressively in anterior direction; interarea anacline, flat, less developed than the ventral one.

Broad spine bases observed only in a single specimen; growth lamellae close to the commissure.

Ventral interior devoid of dental plates; teeth simple, small; “pedicle collar” dorsally directed, closing the delthyrium apex (not represented in Fig. 49).

Dorsal interior with cardinal process fixed to the valve floor; crural plates dorsomedially oriented, splitting off from the valve floor at some distance from their posterior margin; spiral cones laterally oriented, with at least three whorls.

#### DISCUSSION

By their micro-ornament and internal characters (sessile cardinal process, slight individualization of the crural plates...), these specimens differs clearly from those identified as *Emanuella* sp. Internally, they present similarities with the specimen sectioned by Veevers (1959a: text-fig. 4A) and assigned to *Emanuella takwanensis* such as the absence of central apical cavity as well as the layout of the dental sockets. However, they display an apparently bilobed cardinal process (defective preservation?).

These specimens cannot be assigned to the genus *Crurispina* Goldman & Mitchell, 1990 because they are devoid of ventral sulcus and their anterior commissure is rectimarginate, contrary to what occurs in the representatives of the genus *Crurispina*.

#### DISTRIBUTION

These unidentified Rhynchospiriferinae have been collected at the top of the Neuville Formation (southern border of the Dinant Synclinorium).

#### REMARK

Vandercammen (1956: 42) quoted the following ambocoeliid species in the late Mid- to Late Frasnian of southern Belgium (using stratigraphical notation of the time): *Ambothyris infima* (Whidborne, 1893) (“F2i”, “F2IIIb”, “F2IINb”), *Crurithyris inflata* (Schnur, 1853) (“F2i”, “F2j”, “F3”), *Thomasaria gibbosa* Vandercammen, 1956 (“F2i”, “F2j”, “F3”), *T. parallela* Vandercammen, 1956 (“F2i”), *Echino-coelia* cf. *incurva* Cooper & Williams, 1935 (“F2j”), *E. rigauxi* (Maillieux, 1909a) (“F2j”), *Emanuella volhynica* Kelus, 1939 (“F2i”, “F3”). Ambocoeliidae

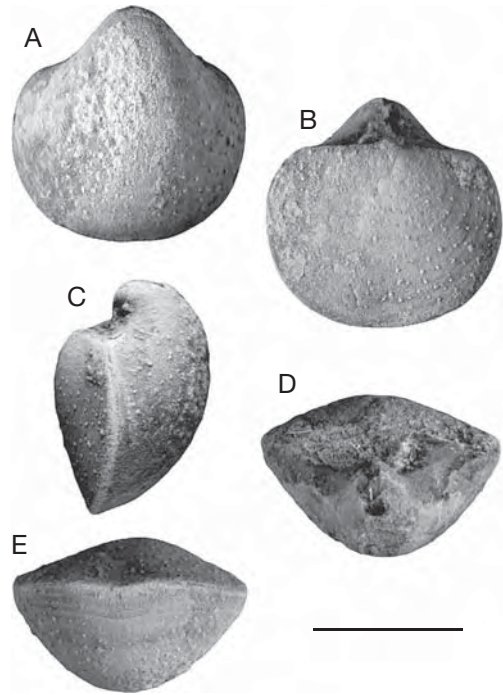


FIG. 48. — Rhynchospiriferinae gen. et sp. indet., complete shell (IRScNB a12294), loc. BM-2003-9, Neuville Formation: **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view. Scale bar: 5 mm.

are not frequent in the investigated outcrops. They seem more abundant in the carbonate mudmounds, but the latter have not been studied in detail. Most of the specimens previously identified as *Echino-coelia rigauxi* have been transferred to *Dionacoelia secessus* by Mottequin (2005a).

Suborder DELTHYRIDINA Ivanova, 1972  
Superfamily RETICULARIOIDEA Waagen, 1883

Family RETICULARIIDAE Waagen, 1883

Subfamily RHENOTHYRIDINAE

Gourvenec (*in Carter et al.* 1994)

Genus *Warrenella* Crickmay, 1953

Subgenus *Warrenella* (*Warrenella*)  
Crickmay, 1953

TYPE SPECIES. — *Warrenella eclecticæ* Crickmay, 1953, by monotypy.

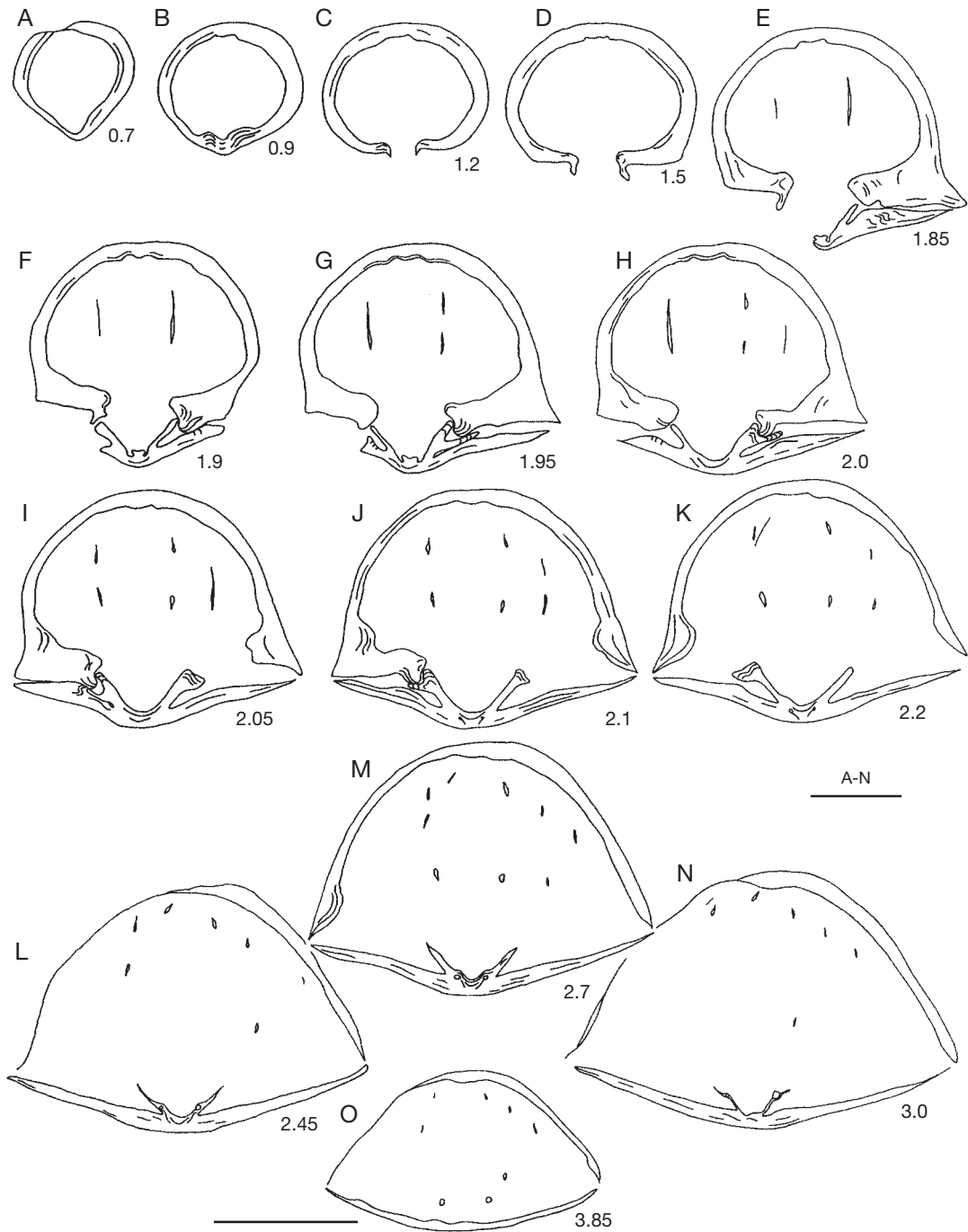


FIG. 49. — Transverse serial sections of *Rhynchospiriferinae* gen. et sp. indet. (IRScNB a12296), loc. BM-2003-9, Neuville Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 2.5 mm.

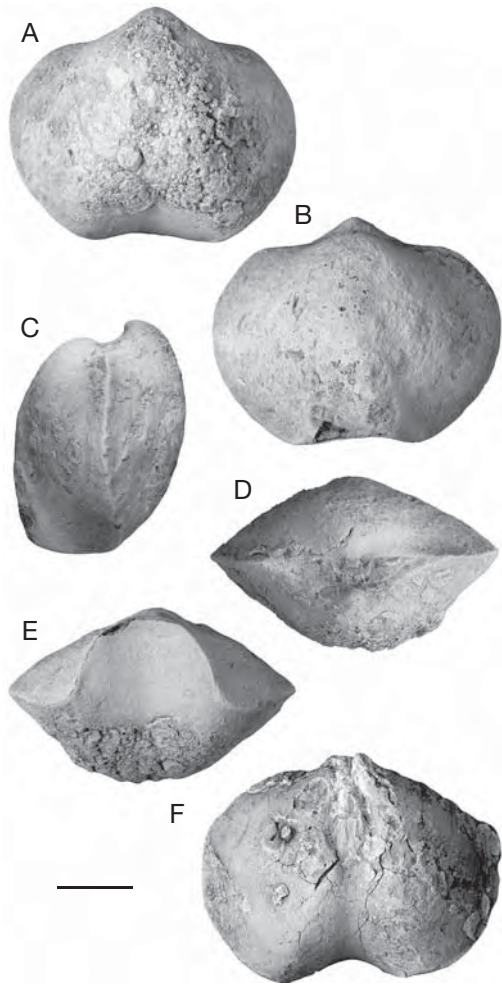


FIG. 50. — *Warrenella (Warrenella) aquaealbae* n. sp., loc. Olloy, Neuville Formation, 575: **A-E**, complete shell (holotype IRScNB a12299); **F**, internal mould of a complete shell (IRScNB a12300); **A, F**, ventral views; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view. Scale bar: 10 mm.

*Warrenella (Warrenella) aquaealbae* n. sp.  
(Figs 50-54)

*Spirifer pachyrhynchus* – Maillieux 1909b (e.p.): 122, 136, 137 (only those from the “schistes de la Zone à *Spirifer pachyrhynchus*”); 1914: 90; 1922a (e.p.): 56; 1922b (e.p.): 18; 1933: 81, non pl. 6, fig. 105 [copy of Schnur (1853) = *Warrenella (W.) eryglossa* (Schnur, 1851)]; 1940: 26; 1941a: 4. — Maillieux in Kaisin *et al.* 1922: 23. — Maillieux in Asselberghs & Maillieux 1925: 166. — Dumon 1929: 164, fig. 12; 1964: fig. 9.

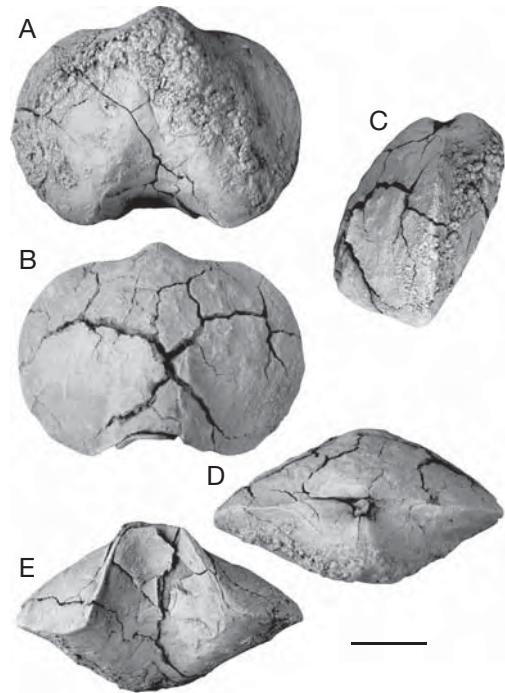


FIG. 51. — *Warrenella (Warrenella) aquaealbae* n. sp., complete shell (IRScNB a12301), loc. BM-2003-8, Neuville Formation; **A**, ventral view; **B**, dorsal view; **C**, lateral view; **D**, posterior view; **E**, anterior view. Scale bar: 10 mm.

*Minatothyris maureri* – Vandercammen 1957a (e.p.): 184; 1957b: 7-17, figs 1-9, pl. 2, figs 1-11, pl. 3, figs 1-13; 1959: 10.

*Warrenella (sic)* – Helsen & Bultynck 1992: table 3b.

HOLOTYPE. — IRScNB a12299.

ETYMOLOGY. — Latin, *aqua*, water and *alba*, white, in reference to the “Eau Blanche” whose channel is located close to the *locus typicus*.

LOCALITY AND AGE. — Nismes railway section (BM-2003-8), upper part of the Neuville Formation (Lower *Palmatolepis rhenana* Zone).

DIAGNOSIS. — Shell medium-sized (maximum width: 45.6 mm; maximum length: 33.7 mm; maximum thickness: 28 mm), wider than long (width/length ratio: 1.04-1.44), dorsibiconvex to ventribiconvex; sulcus and fold little or moderately developed; tongue wide, high, suboval to subtrapezoidal in outline; 4 or 5 growth lamellae per mm.

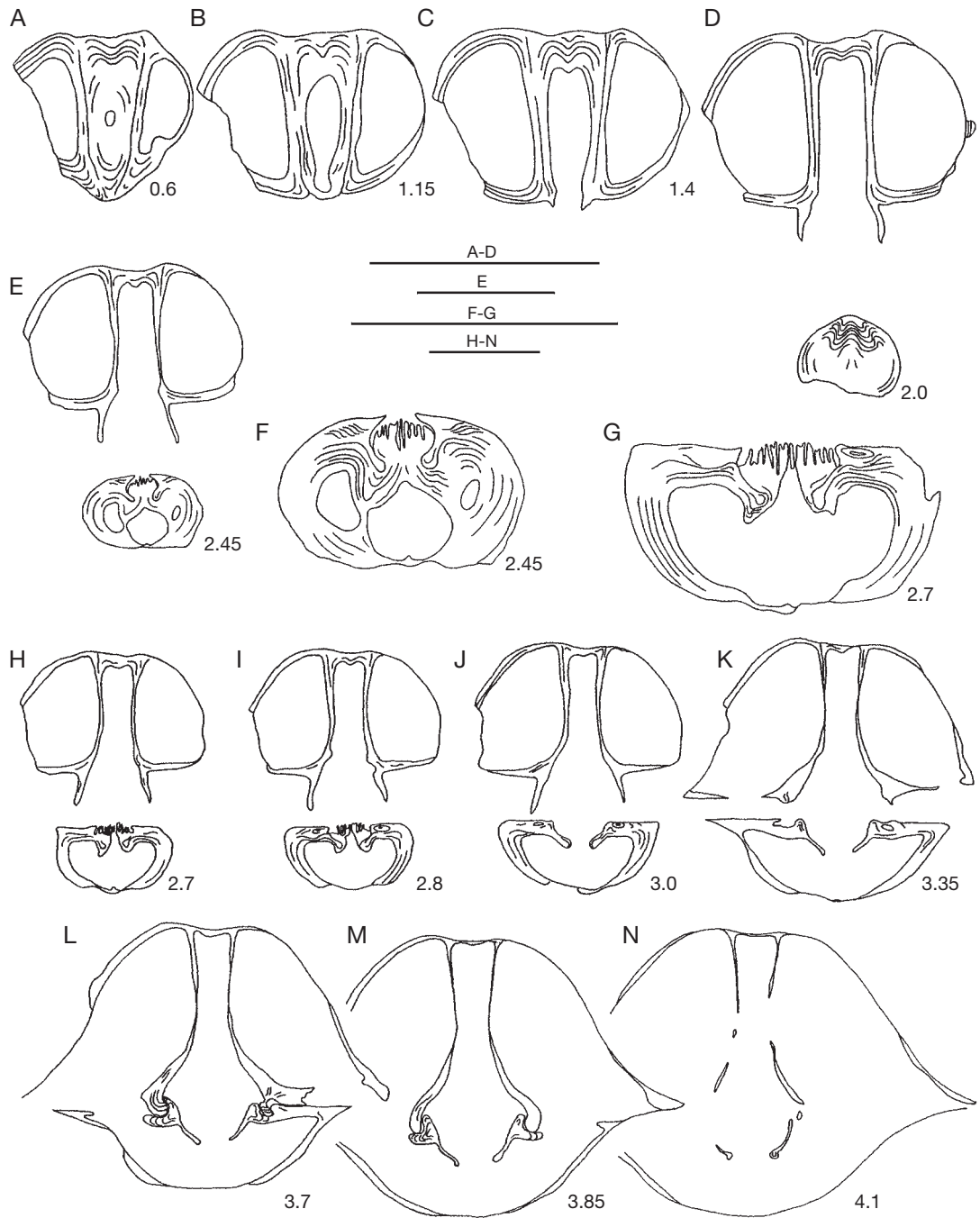


FIG. 52. — Transverse serial sections of *Warrenella (Warrenella) aquaealbae* n. sp. (IRScNB a12302), loc. Olloy 575, Neuville Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

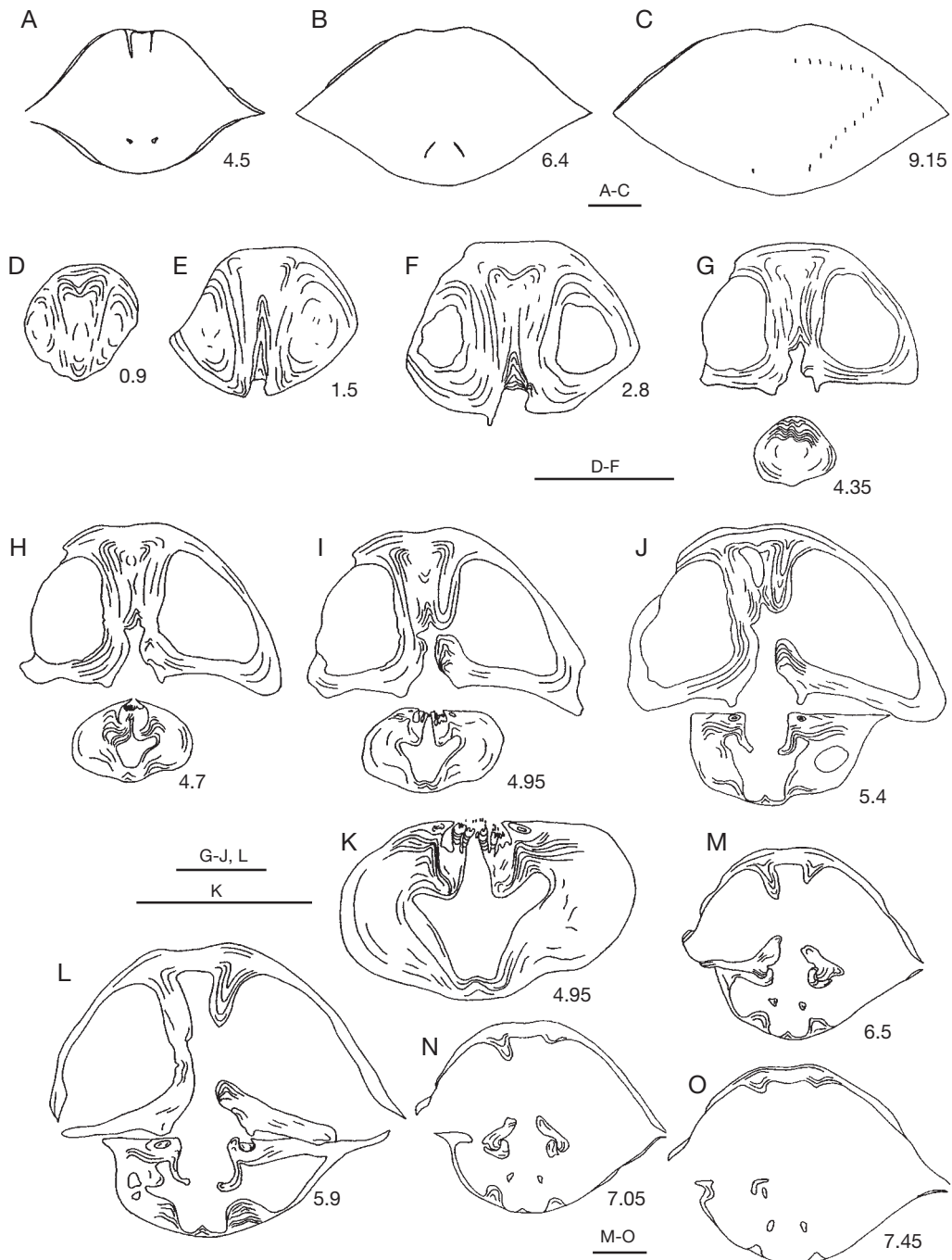


FIG. 53. — Transverse serial sections of *Warrenella (Warrenella) aquaealbae* n. sp., loc. Olloy 575, Neuville Formation: **A-C**, IRScNB a12302; **D-O**, IRScNB a12303. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: 5 mm.

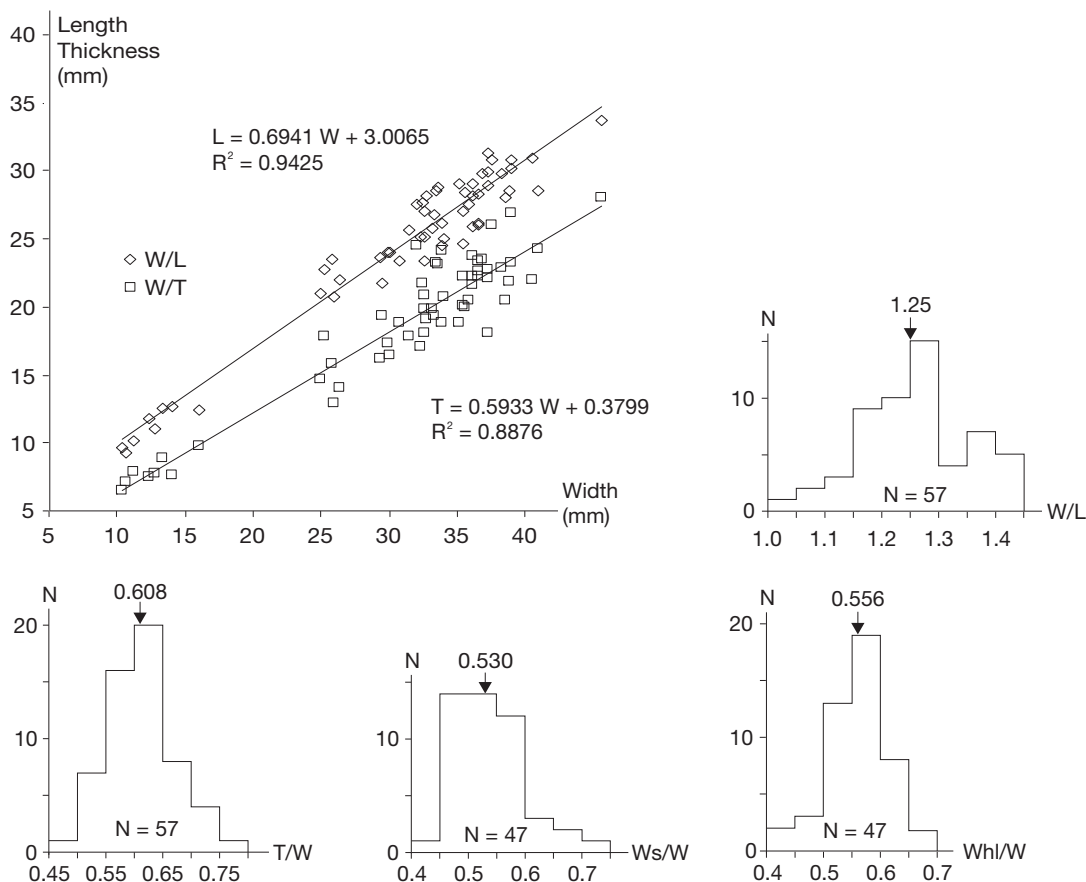


FIG. 54. — *Warrenella (Warrenella) aquaealbae* n. sp. (loc. BM-2003-8, JG-1995-5, Olloy 575, Neuville Formation). Scatter diagrams of shell width (**W**) to shell length (**L**), shell width to shell thickness (**T**); frequency diagrams of **W/L**, **T/W**, **Ws/W** (sulcus width)/**W**, and **Whl/W** (hinge line width)/**W**. Arrows indicate the means.

**MATERIAL EXAMINED.** — BM-2003-8 (14 articulated specimens, three ventral valves, one dorsal valve); JG-1995-5 (25 articulated specimens); Olloy 575 (45 articulated specimens).

**DESCRIPTION**

Shell medium-sized, wider than long (width/length ratio: 1.04-1.44), dorsibiconvex to ventribiconvex, oval in outline; hinge line shorter than greatest width (hinge line width/width ratio: 0.44-0.69); widest at mid-length; lateral margins rounded; anterior margin variably excavated by the sulcus; anterior margin uniplicate.

Ventral valve regularly curved with an accentuation in the umbonal area in lateral profile; flanks sloping

gently to moderately towards lateral commissure; sulcus not originating at beak, wide (sulcus width/width ratio: 0.41-0.71), with bottom rounded to flat at front, with blunt margins; tongue 1.03-2.06 times wider than high, perpendicular to the commissural plane or bent dorsally, trapezoidal to suboval in outline; shoulder lines broken to concave; shoulder and apical angles between 118-145° and 92-114°, respectively; beak curved, overhanging the interarea; interarea 3.45-7.69 wider than high, concave, well-delimited, cata-apsaline to apsaline; delthyrium narrow, partially closed by deltidial plates.

Dorsal valve wider than long (width/dorsal valve length ratio: 1.31-1.47); dome-shaped in posterior



view; highest at front or posteriorly (curving or maintaining anteriorly); fold originating at about midvalve or more anteriorly, with top rounded to flattened at the front (median depression rare on the fold); interarea flat, orthocline, linear.

Radial ornamentation absent although some specimens display slightly undulose anterolateral commissure; 4 or 5 growth lamellae per mm with spine bases (Vandercammen 1957b: 9, text-fig. 4, pl. 3, fig. 12).

Ventral interior with dental plates intrasinal, slightly divergent, thin, with length corresponding more or less to the third of the unrolled length of the valve (measured on the internal mould); large specimens with umbonal callus produced by thickening of dental plates from their internal face; teeth small, simple; central apical cavity poorly filled in, except for the large specimens; lateral apical cavities poorly filled in; muscle field diamond-shaped, not excavated, divided by a myophragm (muscle scars obtained by calcining specimens are insufficiently well-displayed for detailed description).

Dorsal interior with ctenophoridium consisting of parallel thickened plates whose distal extremities divided generally in two or three; crural plates short, converging towards the plane of symmetry but not attaining the valve floor; myophragm prominent; large specimens with muscle field delimited laterally by two prominent curved ridges; spiral cones ventrolaterally oriented, comprising at least 10 whorls.

#### DISCUSSION

In southern Belgium, this species was frequently misidentified as *Spirifer pachyrhynchus* de Verneuil, 1845 whose type material originating from the Ural has been revised by Vandercammen (1959a: 2-10, pl. 1, figs 1-4) and assigned by him to *Emanuella* Grabau, 1923 (Ambocoeliidae). According to Vandercammen (1957b: 17), in Belgium, *Spirifer pachyrhynchus* de Verneuil, 1845 would encompass both following species: *Minatothyris euryglossus* (Schnur, 1851) and *M. maureri* (Holzapfel, 1895). The genus *Minatothyris* Vandercammen, 1957 (type species: *Spirifer euryglossus* Schnur, 1851) has been placed in synonymy with *Warrenella* (*Warrenella*) Crickmay, 1953 by several authors, e.g., Pitrat (1965: H721), Johnson (1966:

175), Biernat (1971: 156), Ludvigsen & Perry (1975: 64), Baliński (1979: 72), Brice (1982: 86), Drot (1982: 77) and Gourvenec (*in Carter et al.* [1994: 352]). However, it was maintained by Struve (1970: 539, 540, 1992: 572). *Warrenella* (*W.*) *aquaealbae* n. sp. has been misidentified as *W.* (*W.*) *maureri*. The latter is conspecific with *W.* (*W.*) *concentrica* (Schnur, 1851), but can be distinguished at a subspecific level by biostatistics according to Struve (1970: 539). After Scupin (1900: 245), Holzapfel's species should be restricted to the "Stringocephalenkalk" while *W.* (*W.*) *concentrica* is an Eifelian species (Struve 1970: table 11). However, *W.* (*W.*) *maureri* has not been revised recently. *Warrenella* (*W.*) *aquaealbae* n. sp. differs from *W.* (*W.*) *euryglossa* (Schnur, 1851) by its larger size, its narrow hinge line (hinge line width/width ratio: 0.44-0.69 vs 0.64-0.76 for the type material of the German species according to Vandercammen's [1957a: 184] measurements), the absence of foraminate deltidium, a less well-defined sulcus, a less curved beak and a ventral muscle field not excavated (see Vandercammen [1957a: pl. 1, fig 10, pl. 3, fig. 14]). The internal characters of *W.* (*W.*) *euryglossa* from the Eifel are not known in detail because Vandercammen (1957a) used Belgian specimens assigned to that species to illustrate using serial section its internal morphology. *Warrenella* (*W.*) *aquaealbae* n. sp. is distinguished from *W.* (*W.*) *concentrica* (Schnur, 1851) by its proportionally wider sulcus (sulcus width/width ratio: 0.41-0.71 vs 0.34-0.55 for Schnur's species according to Struve [1970: 541]), a tongue more developed in height, and a lower maximum size. After study of specimens labelled *Spirifer maureri* from the "Massenkalken der Frettermühle und Bilveringsgr" housed at the ULP and probably belonging to Holzapfel's collections, it is clear that *W.* (*W.*) *aquaealbae* n. sp. differs from *W.* (*W.*) *maureri* (Holzapfel, 1895) by its smaller size, a sulcus more defined at the front and a more developed tongue. *Warrenella* (*W.*) *aquaealbae* n. sp. is distinguished from *W.* (*W.*) *laevis* (Hall, 1843a) by its greater size, the absence of costae close to the anterior margin and by its ventral muscle field which is not excavated. *Warrenella* (*W.*) *aquaealbae* n. sp. is separated from *W.* (*W.*) *electea* Crickmay, 1953 by its greater size, a less defined sulcus and a more prominent dorsal myophragm [see Crickmay

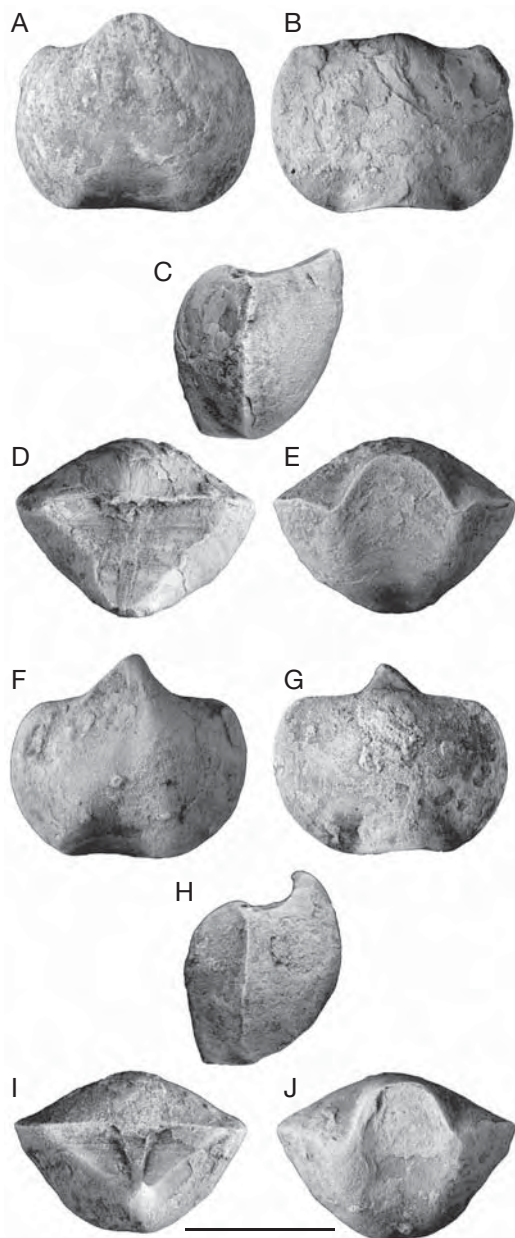


FIG. 55. — *Thomasaria cf. altumbona* Stainbrook, 1945, loc. BM-2003-9, Neuville Formation: **A-E**, complete shell (IRScNB a12304); **F-J**, complete shell (IRScNB a12305); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 10 mm.

(1968: pl. 5, figs 5-15)]. *Warrenella (W.) aquaealbae* reaches a size clearly superior to the one of *W. (W.) adopecta* Crickmay, 1953 and displays a wider sulcus

as well as a more inflated dorsal valve. Furthermore, the filling of the lateral and central apical cavities is clearly less developed within the latter.

#### DISTRIBUTION

*Warrenella (W.) aquaealbae* n. sp. occurs in the upper part of the Neuville Formation as well as the extreme base of the Matagne Formation on the southern flank of the Dinant Synclinorium. Incomplete valves collected within the Les Valisettes Formation (Philippeville Anticlinorium) have been assigned to *Warrenella (W.)* sp.

Family THOMASARIIDAE Cooper & Dutro, 1982

Genus *Thomasaria* Stainbrook, 1945

TYPE SPECIES. — *Thomasaria altumbona* Stainbrook, 1945, by monotypy.

*Thomasaria cf. altumbona* Stainbrook, 1945  
(Figs 55-58)

*Spirifer simplex* – Dumon 1929: 164.

*Reticularia simplex* – Maillieux 1933 (e.p.): 81.

*Reticularia (Eoreticularia) simplex* – Maillieux 1940: 27.

*Eoreticularia simplex* – Maillieux 1941a (e.p.): 6.

*Thomasaria altumbona* Stainbrook, 1945: 58, 59, pl. 4, figs 22-30, text-figs 2, 14.

*Plectospirifer simplex* – Vandercammen 1957c (e.p.): 12-20, pl. 2, figs 7-15, 17, non pl. 2, figs 3-6, 16.

*Thomasaria* sp. – Mottequin 2004b: 52.

MATERIAL EXAMINED. — BM-2003-6 (one articulated specimen, one ventral valve); BM-2003-8 (six articulated specimens); BM-2003-9 (25 articulated specimens, seven ventral valves); JG-1996-1 (30 articulated specimens, two ventral valves).

#### DESCRIPTION

Shell medium-sized, wider than long (width/length ratio: 1.13-1.57), ventribiconvex, rounded subpentagonal (those with an apsacline ventral area) to semi-elliptical (those with a procline ventral area); hinge line shorter

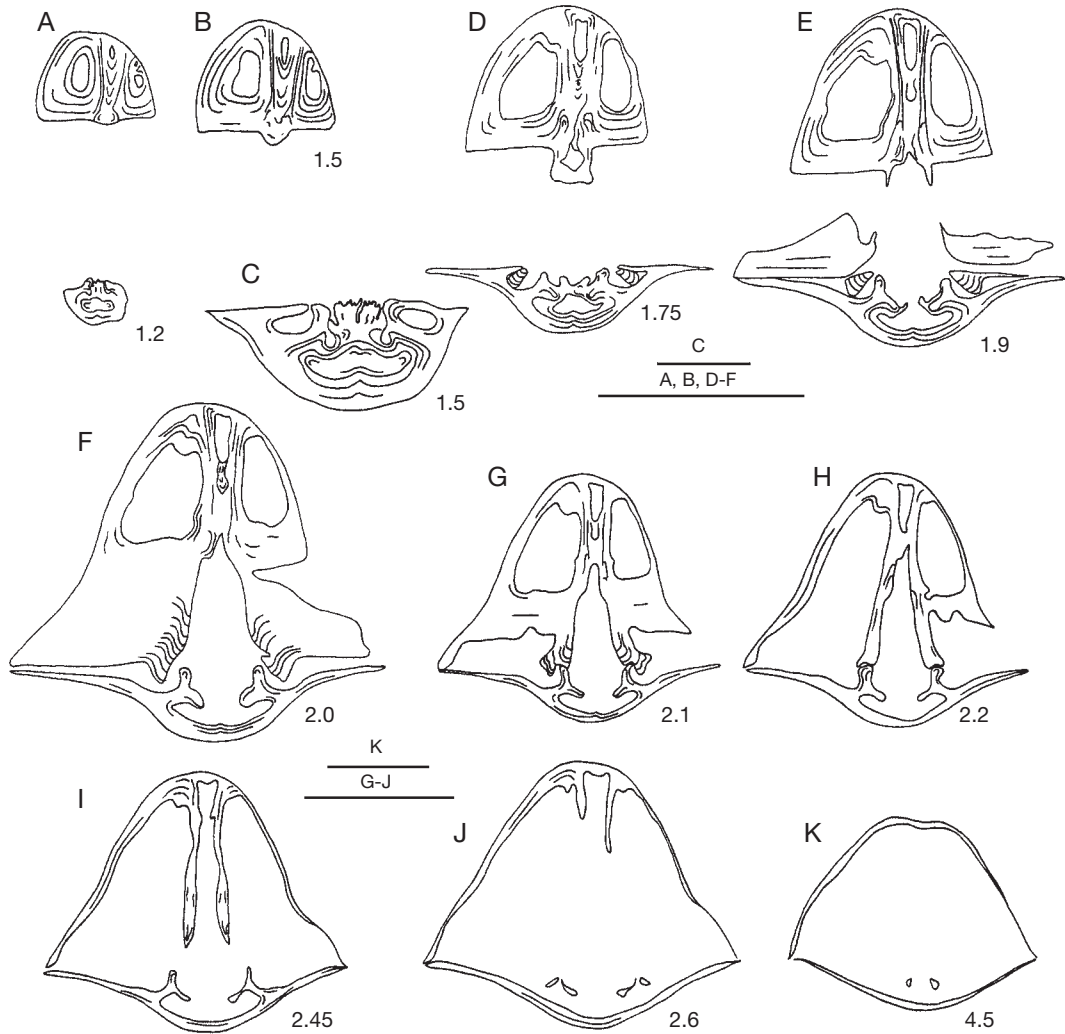


FIG. 56. — Transverse serial sections of *Thomasaria* cf. *altumbona* Stainbrook, 1945 (IRScNB a12306), loc. BM-2003-9, Neuville Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: A, B, D-F, 5 mm; C, 1 mm

than greatest width (hinge line/width ratio: 0.68-0.91); widest at about mid-length; cardinal extremities rounded; anterior commissure uniplicate.

Ventral valve hemipyramidal, in lateral profile, regularly and moderately curved or nearly flat in the case of the specimens with a procline interarea; flanks sloping moderately or strongly towards the lateral commissure; sulcus originating close to beak, either well-defined, relatively wide (sulcus width/width ratio: 0.35-0.57), deep with a flattened

bottom or corresponding to a shallow and poorly defined groove; tongue 1.56-2.45 times wider than high, rounded to subtrapezoidal, perpendicular to commissural plane or bent dorsally; shoulder lines straight or concave; apical angle between 82-96°; beak straight or moderately curved; interarea 1.45-3.37 times wider than high, clearly defined, flat to concave, procline or pro-apsaline to cata-apsaline; delthyrium partially closed by a convex pseudodeltidium.

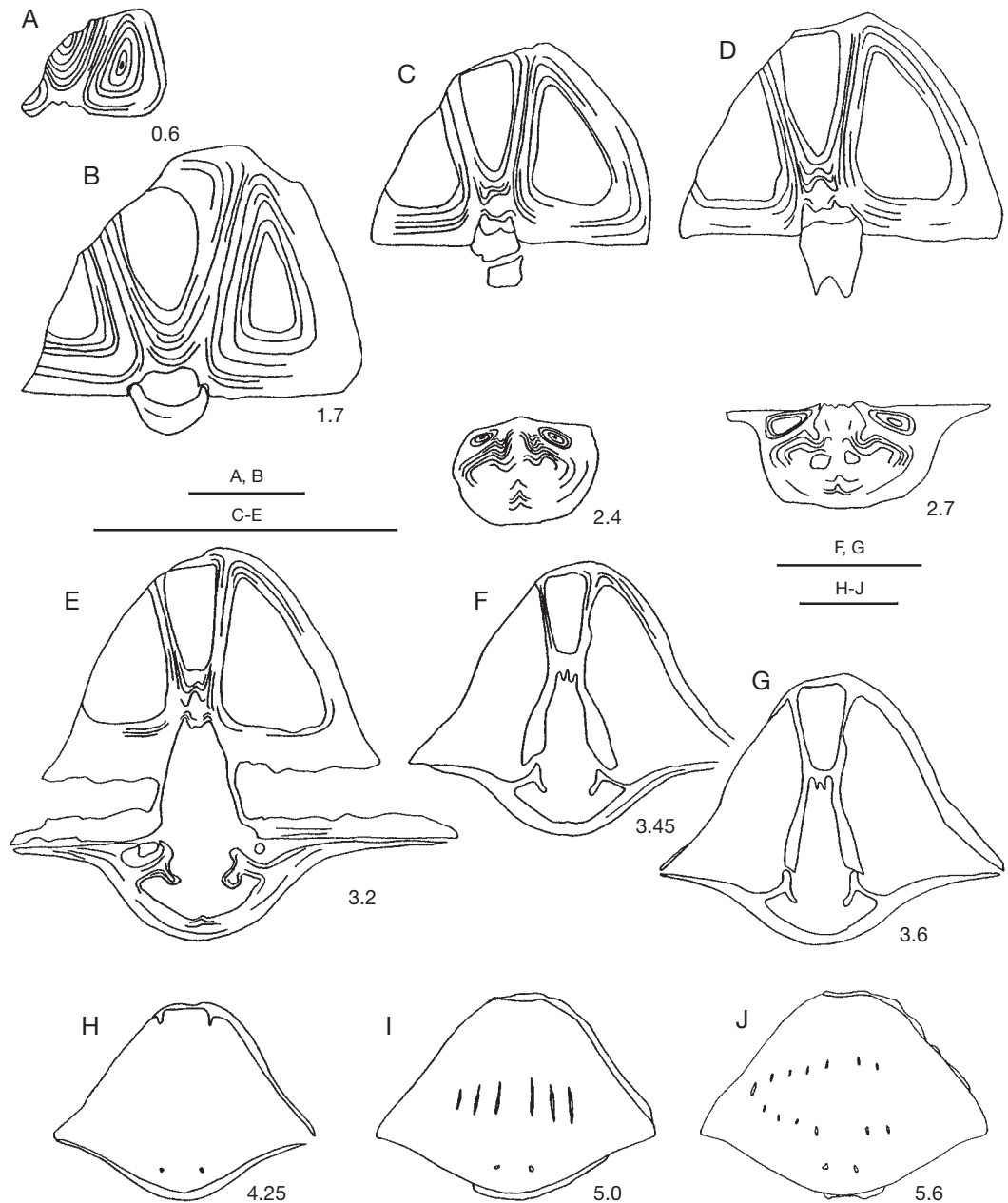


FIG. 57. — Transverse serial sections of *Thomasaria* cf. *altumbona* Stainbrook, 1945 (IRScNB a12307), loc. BM-2003-9, Neville Formation. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars: A, B, 1 mm; C-J, 5 mm.

Dorsal valve wider than long (width/dorsal valve length: 1.23-1.57), semi-elliptical in outline; postero-lateral extremities inclined to become flat; fold

originating at about midvalve or close to the anterior margin (absent in juvenile forms), rounded at top; interarea flat, orthocline, linear.

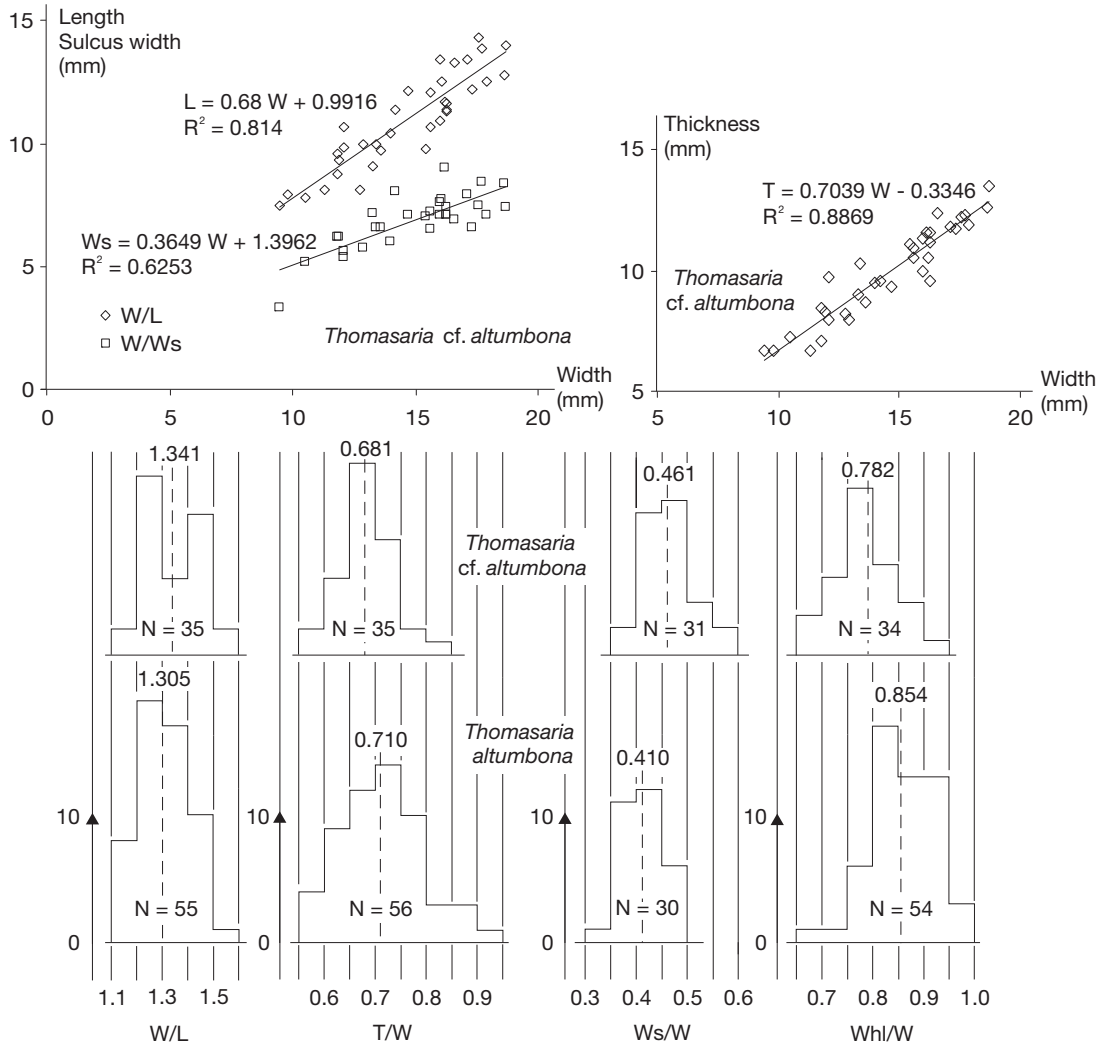


FIG. 58. — Comparison between *Thomasaria cf. altumbona* Stainbrook, 1945 (loc. BM-2003-9, Neuville Formation) and *Thomasaria altumbona* (Independence Shale, Brandon, Iowa, SU). Scatter diagrams of shell width (**W**) to shell length (**L**), shell width to shell thickness (**T**); frequency diagrams of **W/L** and **T/W**. Dotted lines indicate the means.

Flanks generally devoid of costae but up to three in some specimens; most internal costae better defined and originating in the anterior half of the shell (external ones only perceptible near anterior margin); growth lamellae close to the commissure; no spine base observed (poor preservation).

Ventral interior with relatively long dental plates supporting teeth of small dimensions; pair

of apical plates originating from the internal face of dental plates and dividing the post-delthyrial cavity; lateral and central apical cavities poorly filled in.

Dorsal interior with ctenophoridium composed of more or less 10 thickened plates; dental sockets shallow with internal crests well-developed; myophragm short and slightly prominent; spiral cones laterally oriented with at least five whorls.

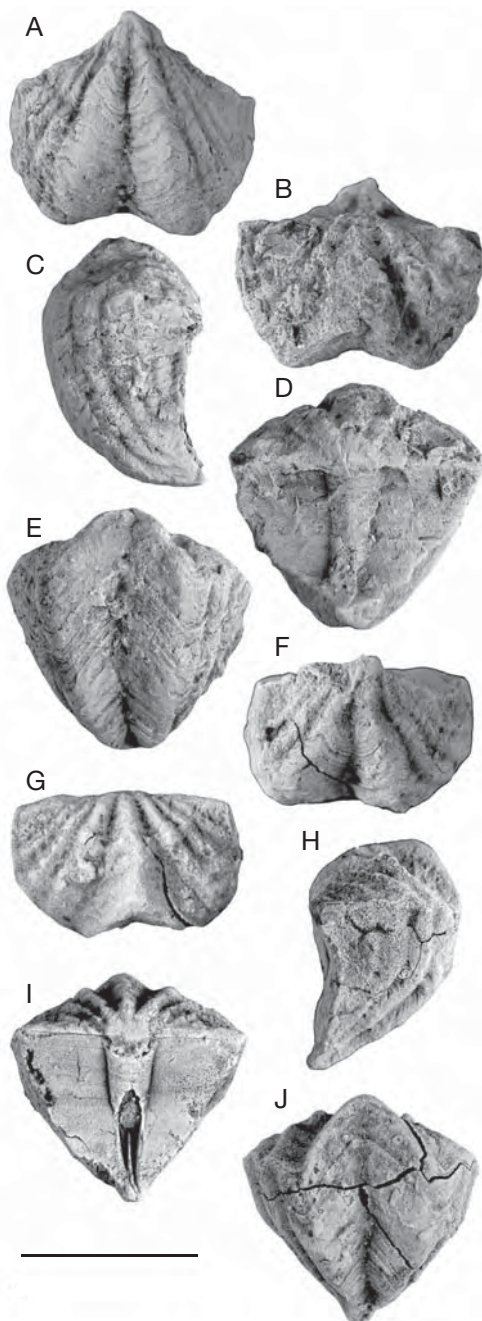


FIG. 59. — *Cyrtina douvillei* Rigaux, 1908, loc. Couvin 6158p., Grands Breux Formation (Boussu-en-Fagne Member): **A-E**, complete shell (IRScNB a12310); **F-J**, complete shell (IRScNB a12308); **A, F**, ventral views; **B, G**, dorsal views; **C, H**, lateral views; **D, I**, posterior views; **E, J**, anterior views. Scale bar: 10 mm.

## DISCUSSION

These specimens are close to *T. altumbona* Stainbrook, 1945 on the basis of their similar size and outline as well as the development of the tongue and of the ventral area. Nevertheless, the specimens from the Namur-Dinant Basin display a generally wider sulcus (sulcus width/width ratio: 0.35-0.57 vs 0.28-0.49 in *T. altumbona*) and a convex pseudodeltidium. The latter has not been observed in the type material of Stainbrook's species housed at the SUI.

In Belgium, these smooth spiriferids have always been misidentified with *Spirifera simplex* Phillips, 1841, the type species of *Pyramidalia* Nalivkin, 1947. The validity of the latter genus is not clear because it has been considered as a doubtful synonym of *Cyrtinaella* Frederiks, 1916 by Pitrat (1965: H678), synonym of *Thomasaria* by Baliński (1979: 71) or more recently, a synonym of *Squamulariina* Frederiks, 1916 by Carter *et al.* (1994: 361) and Johnson (2006: 1882). However, it was maintained as a distinct genus by Drot (1964: 78, 79) and Biernat (1966: 136). *Cyrtinaella* and *Squamulariina* have been assigned to the Cyrtinidae which implies that *Spirifera simplex* has a punctate shell. However, the shell structure has never been described in the English species which is very close to *Spirifer pyramidalis* Schnur, 1853 and *Spirifer nudus* Schnur, 1853 from the Eifel. A revision of Phillips' species is urgently needed but it is beyond the scope of this work.

Vandercammen (1956: 29, pl. 1, figs 28-44, pl. 2, figs 1-6) described two Frasnian species that he assigned to *Thomasaria* (*T. gibbosa* and *T. parallela*), an opinion followed by Oleneva (2006: 421) but they have nothing in common with this genus and need to be revised.

## DISTRIBUTION

*Thomasaria* cf. *altumbona* occurs in the upper part of the Neuville Formation on the southern flank of the Dinant Synclinorium. Representatives of the genus *Thomasaria* are known in the uppermost part of the Les Valisettes Formation as well as in the basal part of the Matagne Formation, but their poor state of preservation does not permit to identify them at the specific level.

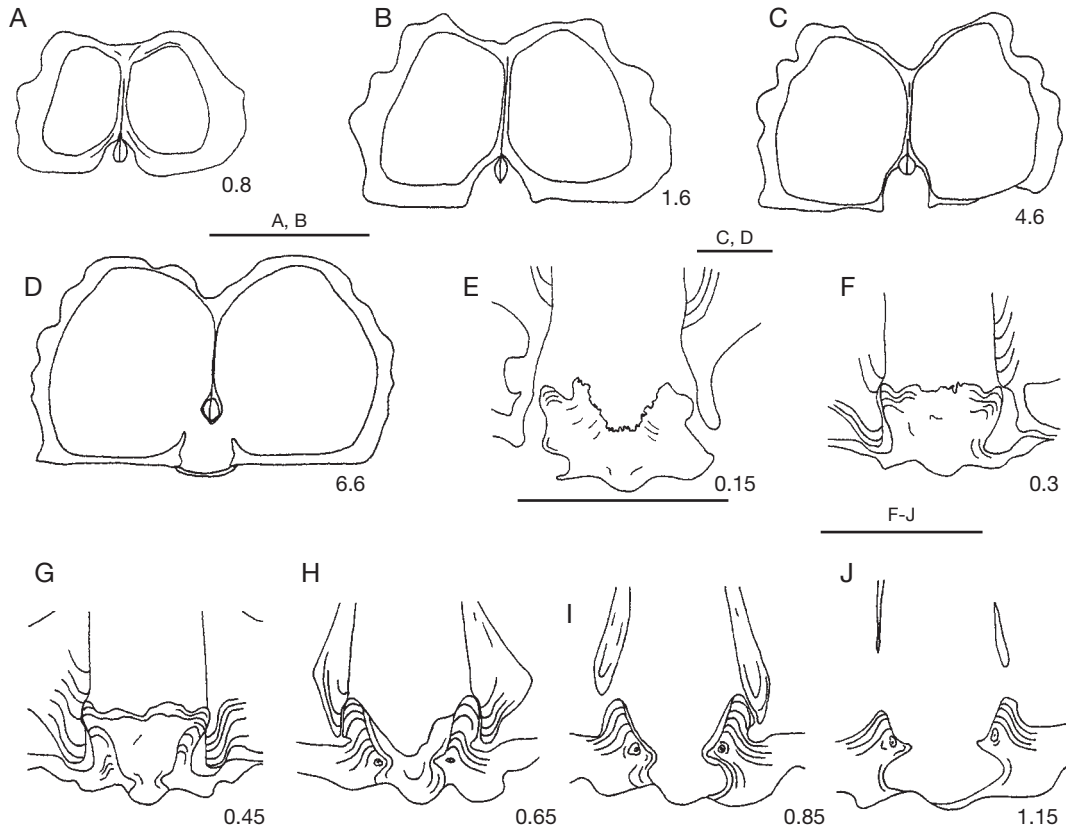


FIG. 60. — Transverse serial sections of *Cyrtina douvillei* Rigaux, 1908 (IRScNB a12314), loc. Couvin 6158p., Grands Breux Formation (Boussu-en-Fagne Member). Numbers refer to distances in mm from the top of the ventral umbo (A–D) and the dorsal one (E–J). Scale bars: 2.5 mm.

Order SPIRIFERINIDA Ivanova, 1972  
 Suborder CYRTINIDINA  
 Carter & Johnson (*in* Carter *et al.* 1994)  
 Superfamily CYRTINOIDEA Frederiks, 1911  
 Family CYRTINIDAE Frederiks, 1911

Genus *Cyrtina* Davidson, 1858

TYPE SPECIES. — *Calcolea heteroclita* DeFrance, 1828, by subsequent designation (Oehlert 1887b: 40).

*Cyrtina douvillei* Rigaux, 1908  
 (Figs 59; 60; Table 4)

*Cyrtina Douvillei* Rigaux, 1908: 20, 21, pl. 1, fig. 9. — Maillieux 1909a: 10; 1909b: 120, 122, 136, 137; 1909c:

259, 260; 1933 (e.p.): 81; 1940: 27; 1941a (e.p.): 6. — Maillieux *in* Asselberghs & Maillieux 1925: 166. — Dumon 1929: 164. — Brice 1988: 358, 359, pl. 43, figs 14–16.

MATERIAL EXAMINED. — BM-2003-6 (one articulated specimen); BM-2003-7 (three articulated specimens, one dorsal valve); BM-2003-10 (three articulated specimens, two ventral valves); Couvin 6158p. (14 articulated specimens).

#### DESCRIPTION

Shell medium- to large-sized for the genus; generally wider than long (width/length ratio: 0.99–1.50), ventribiconvex; hinge line generally shorter than greatest width (hinge line width/width ratio: 0.85–1); cardinal extremities in some specimens mucronate.

Ventral valve hemipyramidal, more or less strongly curved in lateral profile; flanks sloping strongly towards lateral commissure; sulcus originating at beak, wide (sulcus width/width ratio: 0.53-0.59), subangular, deep, sharply delimited; tongue 1.20-2.14 times wider than high, perpendicular to commissural plane or bent dorsally, subtriangular to suboval in outline; shoulder lines slightly concave to subrectilinear; shoulder and apical angles identical, between 80-97°; beak little to moderately curved, sometimes twisted; interarea triangular, very high, well-defined, pro-apsacine to apsacine; delthyrium narrow, closed by a thin pseudodeltidium pierced by a wide foramen.

Dorsal valve wider than long (width/dorsal valve length ratio: 1.47-1.69), semi-oval to subtrapezoidal in outline; fold originating at beak, high, clearly delimited by two wide grooves; interarea flat, orthocline, linear.

Flanks with 5 or 6 and 4 or 5 rounded to subangular costae on ventral and dorsal valves, respectively; grooves similar but narrower; sulcus and fold smooth; growth lamellae prominent, sometimes very crowded, irregularly spaced.

Ventral interior with short dental plates converging towards the plane of symmetry to fuse to a septum and forming a spondylium; teeth small and rounded; tichorhinum with median partition; lateral apical cavities not filled in.

Dorsal interior with bilobed cardinal process bearing small protuberances on their internal face; dental socket moderately deep with internal crests particularly well-developed; shelly deposits in the posterocentral part of the valve; brachial apparatus not observed in the sectioned specimen.

#### DISCUSSION

These specimens are identical to those identified as *Cyrtina douvillei* by Brice (1988: 358, 359).

#### DISTRIBUTION

*Cyrtina douvillei* is recognized within the Grands Breux Formation (Boussu-en-Fagne Member) on the southern border of the Dinant Synclinorium. Specimens assigned to *Cyrtina* and distinct from *C. douvillei* have been collected within the Neuville, Aisemont, Les Valisettes and Barvaux formations

as well as in the Frasnian part of the Lambermont Formation. They will be described in detail when sufficient material becomes available.

#### STRATIGRAPHIC SUMMARY

The geographic and stratigraphic distributions of the brachiopod species across the Namur-Dinant Basin are presented in Figures 61-63.

#### PALAEOGEOGRAPHIC AFFINITIES

Relationships between the Namur-Dinant Basin and adjacent areas have been well known for a long time. Maillieux (1909b) has already reported numerous analogies between various fossil groups from the Frasnian of the Namur-Dinant Basin and the Boulonnais (Northern France), which is its western prolongation. More recently, similar observations have been made by Coen-Aubert (1994) on the Frasnian rugose corals. Several species described in this paper are recognized in the Boulonnais or are close to those from that area (e.g., *Athyris cf. murchisoni*). The Grands Breux Formation is correlated with the Ferques Formation by Brice *et al.* (1979: fig. 1), Lafuste & Tourneur (1988: fig. 3) and Coen-Aubert (1994: table 1). More particularly, the Boussu-en-Fagne Member corresponds to the two upper members of the Ferques Formation, i.e. the La Parisienne and Gris members. The species in common are, among others, *Cyrtospirifer verneuili* (Murchison, 1840), *Athyris oehlerti* Rigaux, 1908, *Douwillina dutertrei* (Murchison, 1840) and *Productella subaculeata* (Murchison, 1840). On the other hand, no atrypid species from the Boulonnais (Godefroid 1988) has been reported in the Frasnian units investigated in this work. The Hydrequent Formation, which caps the Ferques Formation, corresponds notably to the Neuville, Aisemont, Les Valisettes and Matagne formations of the Namur-Dinant Basin, but it is poorly fossiliferous (Brice 1988: table 2).

The brachiopods from the Late Frasnian and Early Famennian from the Namur-Dinant Basin display similarities with those reported and/or illustrated



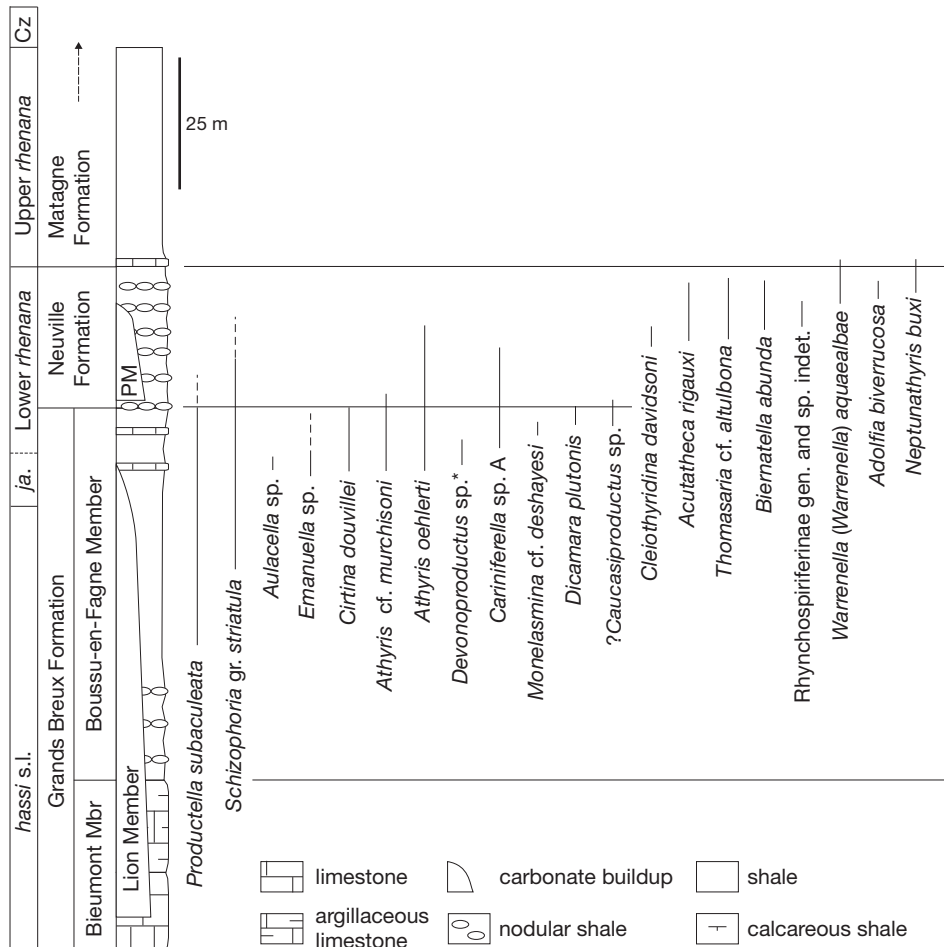


FIG. 61. — Distribution of the studied Frasnian brachiopods at the southern border of the Dinant Synclinorium. See Figure 62 for the stratigraphic ranges of the Famennian species from that area. The species with an asterisk has only been cited in the text. Abbreviations: **CZ**, conodont zones; **ja.**, *Palmatolepis jamieae* Zone; **PM**, Petit-Mont Member.

(e.g., Klähn 1912; Wulff 1923; Paeckelmann 1942) in the Aachen Basin (Germany) which is the eastern prolongation of the Belgian basin. More recently, Sartenaer & Hartung (1992) reported the presence of *Navalicia compacta* Sartenaer, 1989 in the Aachen Basin, a rhynchonellid characteristic of the Neuville and the Aisemont formations. In the Eifel (Reichle quarry), the atrypid fauna collected within the Ooser Plattenkalk and described by Godefroid & Hauser (2003) is very close to that of the Neuville Formation. Grunt (*in* Grunt & Racki 1998: 370, figs 7, 8) described from the same locality a new

athyridid species *Pachyplaxoides postgyralea*, which is also recognized in the Holy Cross Mountains (Poland), but this taxon is absent from the Namur-Dinant Basin.

As the Frasnian was characterized by the highest sea-levels of the Devonian (Johnson *et al.* 1985) permitting exchanges between distant basins, it could be anticipated that the brachiopods investigated would show also similarities at the generic level with more distant areas such as Poland (e.g., Baliński 1979, 2002), Iowa (Stainbrook 1945), Hunan (e.g., Ma *et al.* 2002; see also the strong

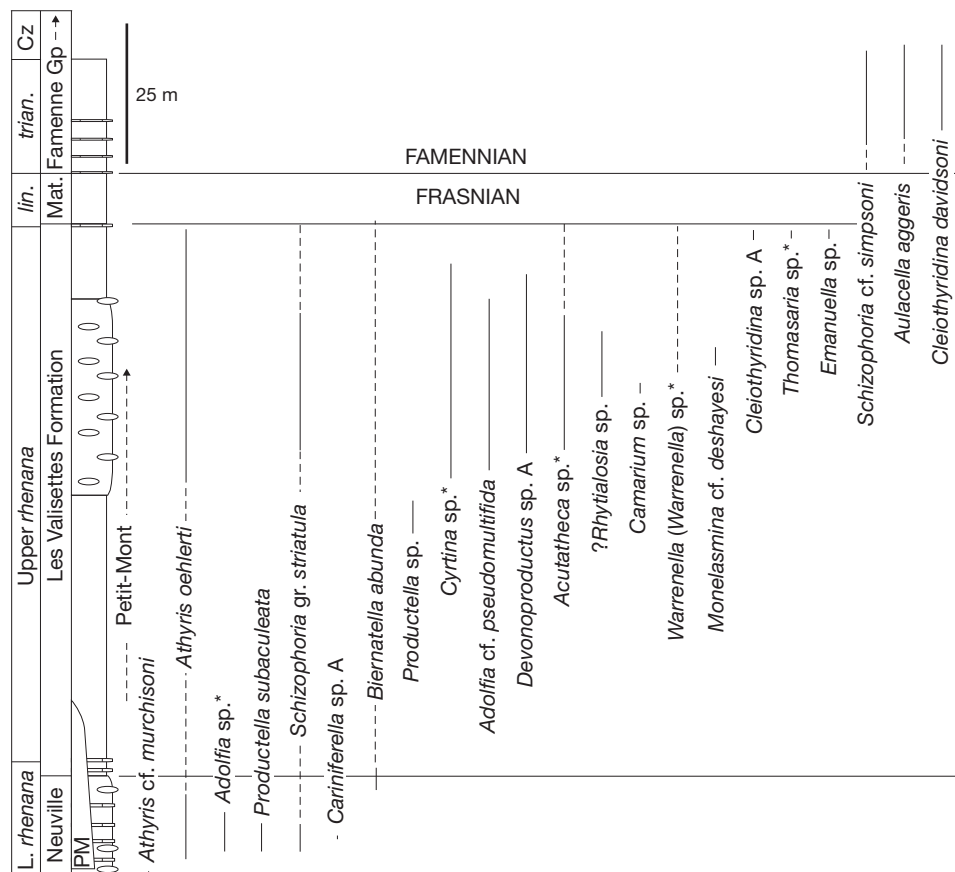


FIG. 62. — Distribution of the studied Frasnian brachiopods in the Philippeville Anticlinorium and those of the Famennian at the southern flank of the Dinant Synclinorium. The species with an asterisk have only been cited in the text. Abbreviations: Cz, conodont zones; L., Lower; lin., *Palmatolepis linguiformis* Zone; Mat., Matagne Formation; PM, Petit-Mont Member; trian., *P. triangularis* Zone.

resemblance between *Athyris oehlerti* and *A. superavitata* Tien, 1938 illustrated by these authors) and the Russian platform (e.g., Liashenko 1959).

### CONSEQUENCES OF THE LATE FRASNIAN BIOLOGICAL CRISIS ON THE BRACHIOPODS OF THE NAMUR-DINANT BASIN

The time interval between the upper part of mid-Givetian and the Devonian/Carboniferous boundary includes a complex sequence of events; the most significant ones are the Taghanic (latest Middle

Givetian), Upper Kellwasser (latest Frasnian) and Hangenberg events (latest Famennian). The Late Frasnian crisis, culminating during the Upper Kellwasser Event, caused the disappearance of more or less 70 to 80% of the marine species (Jablonski 1994). It is ranked among the five most important mass extinctions of the Phanerozoic (Sepkoski 1986). In the course of the Frasnian, the shallow waters of the platforms and continental slopes were frequently oxygen-depleted as shown by numerous occurrences of black shales (Algeo *et al.* 1995) but, according to McGhee (1996), most of them were not related to extinctions and their lateral extent is not comparable to those of the Kellwasser and Hangenberg horizons.

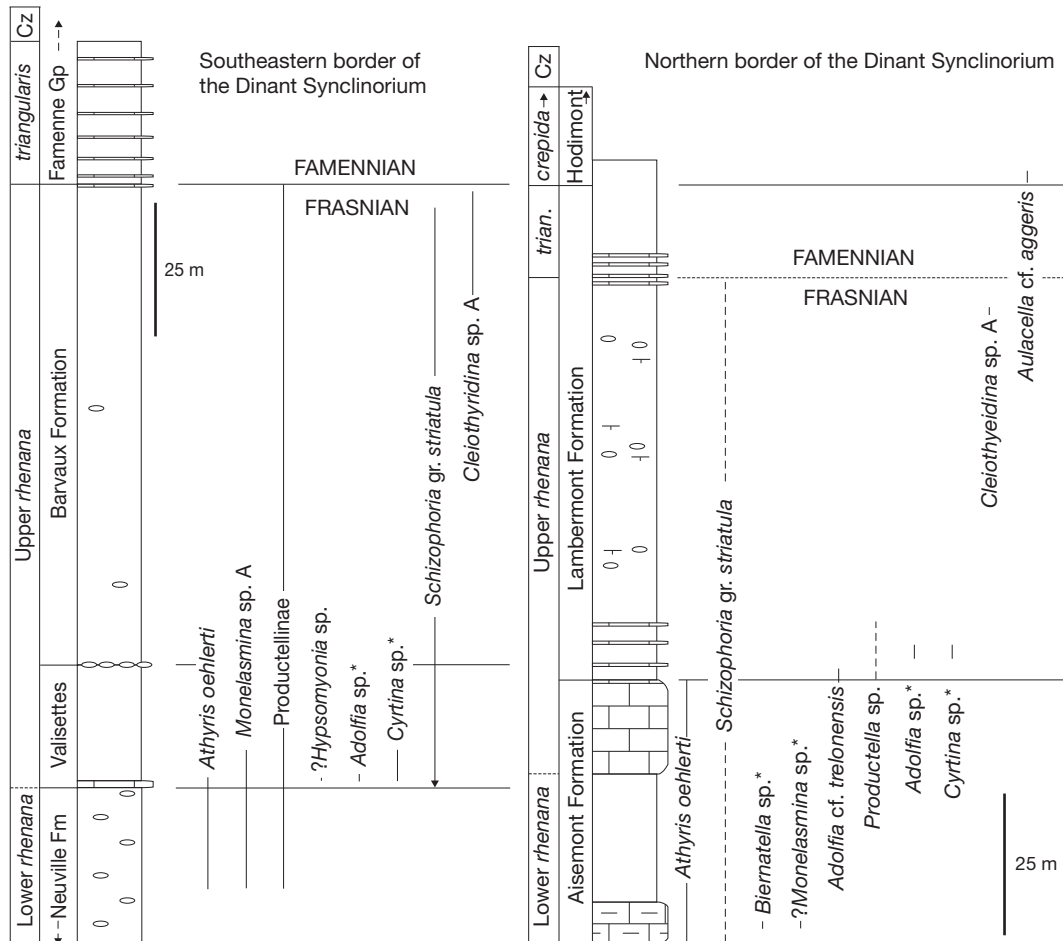


FIG. 63. — Distribution of the studied Frasnian and Famennian brachiopods at the southeastern and northern borders of the Dinant Synclinorium. The *Palmtolepis linguiformis* Zone has not been indicated because of the absence of the index species. The species with an asterisk have only been cited in the text. Abbreviations: **Cz**, conodont zones; **trian.**, *Palmtolepis triangularis* Zone.

However, according to some authors (e.g., Brett & Baird 1995; House 2002), these black shale horizons are related to minor extinctions but they have been considerably less studied than those of the Kellwasser and Hangenberg horizons. The Lower and Upper Kellwasser events, occurring respectively within the Upper *Palmtolepis rhenana* Zone and the *P. linguiformis* Zone, correspond to two distinct rises of anoxic waters onto the platform (Schindler 1993) during highstand periods (Joachimski & Buggish 1993). In the Namur-Dinant Basin, the Lower Kellwasser Event (LKW) is placed in the lowermost part of the

Matagne Formation on the southern border of the Dinant Synclinorium whereas in the Philippeville Anticlinorium, it would be situated in the basal part of the Les Valisettes Formation (Bultynck *et al.* 1998). On the southeastern margin of the Dinant Synclinorium, the fissile and azoic shales of the middle part of the Les Valisettes Formation could correspond to the LKW. Moreover, the middle part of the intermediate shales of the Aisemont Formation, i.e. the dysaerobic-anaerobic unit of Poty & Chevalier (2007), could be the record of the LKW according to these authors. The Upper Kellwasser

Event (UKW) corresponds to the Matagne Formation in the Philippeville Anticlinorium (Bultynck *et al.* 1998). The black shale horizons recognized at the top of the Frasnian part of the Lambermont Formation in the Vesdre area and on the northern margin of the Dinant Synclinorium have been correlated with the UKW by Herbosch *et al.* (1996).

The Taghanic Event, which caused extinctions among the ammonoids, trilobites and corals while radiolarians and styliolinids proliferated (Aboussalam 2003), is probably responsible for the disappearance of stringocephalids (García-Alcalde *in* Brice *et al.* 2000). The transgressions which occurred during this interval would have allowed exchanges between various palaeobiogeographic units. These would have resulted in increased competition between the organisms of analogous communities with, as a corollary, the progressive disappearance of provincialism heralding the cosmopolitanism of the Frasnian faunas to come (Johnson 1979). The Frasnian was not a major period of diversification for the atrypids (Copper 1998) and the pentamerids (Godefroid *in* Brice *et al.* 2000), which became extinct at the end of the Frasnian but this stage recorded a rapid and major period of diversification of cyrtospiriferids. Among the orders investigated, long-ranging (e.g., *Athyris*, *Schizophoria*, *Warrenella*) and typical Frasnian genera (e.g., *Cariniferella*, *Acutatheca*) have been recognized. The major brachiopod turnover occurs at the top of the *P. rhenana* Zone in the Namur-Dinant Basin, in parallel with the deterioration of the oxygenation conditions preceding the UKW. Only an impoverished fauna has been recorded in the *P. linguiformis* Zone comprising only productids (Chonetidina), rhynchonellids and lingulids. Post-extinction brachiopod recovery was rapid in the basal Famennian but, despite their great abundance, the brachiopod diversity was quite low. New cosmopolitan genera appeared at this time especially among the spiriferids, athyrids and rhynchonellids concomitantly with new species of pre-existing orthid and orthotetid genera (Mottequin 2005b).

#### PRODUCTIDA

The suborder Productidina does not seem to have suffered heavy losses at the family level in relation to the Late Frasnian mass extinction. The four

families (Araksalosiidae, Monticuliferidae, Productellidae, Sentosiidae) recognized in the Frasnian persisted in the Famennian (Brunton *et al.* 2000: fig. 236). Nevertheless, the extinction of Devonoproductinae is recorded in the Late Frasnian. In the course of the Famennian, the Productidina initiated an evolutionary radiation that reached a peak in the Carboniferous. Among the suborder Productidina, five species have been recognized in late Mid- to Late Frasnian of the Namur-Dinant Basin. Further research and additional material should allow precise identification of their genera and species. Early Famennian Productidina have not been studied due to the poor preservation of the material available.

Chonetidina did not suffer losses at the family level because the three families occurring in the Frasnian, namely the Chonostrophiidae, Anopliidae and Chonetidae, crossed the Frasnian-Famennian boundary (Racheboeuf 2000: fig. 237). In Poland (Cracow area), a species of ?*Rhyssochonetes* (Baliński 2002: 291) has been listed among the surviving taxa, just after the Frasnian/Famennian boundary. Chonetidina from the Namur-Dinant Basin have not been studied in this paper although they occur in all the investigated lithostratigraphic units. Nevertheless, *Retichonetes armatus* (Bouchard-Chantreaux *in* de Verneuil, 1845) was reported within the Matagne Formation by Maillieux (1936: 18; 1941b: 7) and Racheboeuf (1988: 399).

#### ORTHIDA

During the Frasnian, the Orthida were represented by two superfamilies, the Dalmanelloidea and Enteletoidea. On the four families of the Dalmanelloidea, only the Rhipidomellidae persisted in the Famennian. Among the two families included in the Enteletoidea, only the Schizophoriidae crossed the Frasnian/Famennian boundary (Williams & Harper 2000: fig. 522). According to Stigall Rode (2005: 164), the persistence of *Schizophoria* in the Famennian could be explained partly by the fact that it retained deep-water lineages whereas those from the shallows were severely affected by the Late Frasnian crisis. In the Namur-Dinant Basin, *Schizophoria* gr. *striatula* is the last Frasnian orthid to disappear just below the UKW or in the lowermost part of the Matagne

Formation although specimens may be reworked material as supposed for some Spiriferida collected in the same level, either at the top of the Frasnian part of the Lambermont Formation (northern flank of the Dinant Synclinorium and Vesdre area). The other Frasnian species described in this paper disappear well below the base of the Famennian. Early Famennian rocks yielded species of genera previously known (*Aulacella*, *Schizophoria*).

#### ATHYRIDIDA

The consequences of the Late Frasnian mass extinction on this order have been previously discussed, notably by Baliński (1995), Rzhonsnitskaya & Modzalevskaya (1996), Grunt & Racki (1998), Alvarez & Modzalevskaya (2001) and Alvarez (2003). In the Namur-Dinant Basin, *Cleiothyridina davidsoni* is qualified as a Lazarus taxon because its last Frasnian occurrence is recognized within the Neuville Formation (Lower *Palmatolepis rhenana* Zone) at the southern flank of the Dinant Synclinorium and it reappears in the basal part of the Famenne Group ("Senzeille Formation", Early (?)/Middle *P. triangularis* zones) in the same area. The significant development of the Helenathyridinae (*Biernatella* and *Neptunathyris*) in the upper part of the Neuville Formation on the southern flank of the Dinant Synclinorium is noteworthy. Indeed, these smooth athyridids constitute a large part of the benthos in the distal part of the Namur-Dinant Basin, just before the LKW but they became extinct by the end of the Frasnian. Moreover, *Neptunathyris buxi* is known also in the lower part of the Matagne Formation (Upper *P. rhenana* Zone). The presence of *Dicamara plutonis* n. sp. within the Grands Breux Formation (Boussu-en-Fagne Member; *P. hassi* to Lower *P. rhenana* zones) correspond to one of the more recent occurrences of this genus that is reputed to disappear in the Mid-Devonian according to Alvarez & Rong (2002: 1572). The Early Famennian (*P. triangularis* Zone) is characterized by the rapid expansion of the Cleiothyridininae (*Crinisarina*) (Mottequin 2005b).

#### SPIRIFERIDA AND SPIRIFERINIDA

In the Namur-Dinant Basin, the decimation of spiriferid brachiopods took place in two successive phases as previously reported for the Atrypida

(Godefroid & Helsen 1998). This is also the case for the other orders investigated in this paper (Mottequin 2005b). On the southern border of the Dinant Synclinorium, the last Frasnian spiriferids (*Warrenella* (*W.*) *aquaealbae*) became extinct in the lowermost part of the Matagne Formation (basal part of the Upper *Palmatolepis rhenana* Zone), i.e. lower than the LKW as it was defined by Bultynck *et al.* (1998: 53). Nevertheless, in this area, the last spiriferids disappear generally in the upper part of the Neuville Formation (top of the Lower *P. rhenana* Zone). In the Philippeville Anticlinorium (BM-2002-8), cyrtospiriferids, *Emanuella* sp. as well as fragments only identified at the generic level (*Warrenella* (*W.*), *Thomasaria*, *Acutatheca* and *Adolfia*) were recovered in the upper beds of the Les Valisettes Formations (top of the of Upper *P. rhenana* Zone). In this area, broken valves of unidentified species of *Acutatheca*, *Thomasaria* and cyrtospiriferids occur in the basal part of the Matagne Formation (*P. linguiformis* Zone) within coquina beds (reworking?).

We have only a partial view of the diversity of the Frasnian Spiriferinida of southern Belgium; they seem to be represented only by the cosmopolitan genus *Cyrtina*, at least on the basis of the available data. Maillieux (1941a) did not report it in the Famennian rocks of the Namur-Dinant Basin. In the latter, *Cyrtina* would re-occur in the Middle Viséan (Livian regional Substage) according to the last comprehensive list of Lower Carboniferous brachiopod species drawn up by Demanet (1958: 96).

#### CONCLUSIONS

This paper deals with some representatives of the brachiopod faunas occurring in the interval spanning, in terms of standard conodont zonation, the *Palmatolepis hassi* and *P. triangularis* zones (Late Middle Frasnian to Early Famennian) in the Namur-Dinant Basin (Belgium). This area, which is the historical type area of the Frasnian and Famennian stages, was located on the southeastern margin of Laurussia during the Devonian and Carboniferous. A major turnover among the brachiopods is recorded in the Upper *P. rhenana* Zone, just before the Upper

Kellwasser Event. During this major and widespread dysoxic/anoxic event (*P. linguiformis* Zone), only a small and poorly diversified brachiopod fauna was able to develop in the widespread argillaceous environments developed in the Namur-Dinant Basin. Post-extinction brachiopod recovery occurred just after the Frasnian/Famennian boundary. New cosmopolitan genera appeared at this time especially among the spiriferids, athyridids and rhynchonellids concomitantly with new species of pre-existing orthid and orthotetid genera (Mottequin 2005b). At present, only one surviving athyridid species (Lazarus taxon) is definitely recognized in the Early Famennian. Nevertheless, some productids, craniids and lingulids may have crossed the Frasnian/Famennian boundary but this still needs confirmation.

### Acknowledgements

This paper forms part of my Ph.D. thesis supervised by Jacques Godefroid (Brussels) and Édouard Poty (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. Tiffany Adrain (Iowa City), Denise Brice (Lille), Jean-Claude Horrenberger (Strasbourg), Thierry Oudoire (Lille) and Jann Thompson (Washington D.C.) kindly gave access to collections under their care. Marie Legrand-Blain (Gradignan) advised on systematics of the Productidina. Wilfried Miseur (Brussels) did the photographic work. Reviews by Denise Brice (Lille) and Patrick Racheboeuf (Brest) and the editorial revision by Annemarie Ohler (Paris) helped to improve the manuscript. George Sevastopulo (Dublin) advised on linguistic aspects of the paper. I am deeply grateful to all of them.

### REFERENCES

- ABOUSSALAM Z. S. 2003. — Das “Taghanic-Event” im höheren Mitteldevon von West-Europa und Marokko. *Münstersche Forschungen zur Geologie und Paläontologie* 97: 1-332.
- ALEKSEVA R. E. 1969. — [New and unusual Lower Devonian spiriferids (suborder Athyrididina)]. *Doklady Akademii Nauk SSSR* 187 (5): 1157-1159 (in Russian).
- ALEKSEVA R. E. & OLENEVA N. V. 2000. — Katalog kolkstii devonskikh brachiopod Vostochno-Evropeyskoy platformy (materialy A. H. Liashenko). *Byulleten' KF VNIIGNI* 2: 1-58.
- ALGEO T. J., BERNER R. A., MAYNARD J. B., SCHECKLER S. E. 1995. — Late Devonian oceanic anoxic events and biotic crises: “rooted” in the evolution of vascular land plants. *GSA Today* 5: 45, 64-66.
- 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. & BRUNTON C. H. C. 2005. — On the name-bearing type of *Athyris concentrica* (von Buch, 1834). *Lethaia* 38: 86-87.
- ALVAREZ F., BRUNTON C. H. C. & STRUVE W. 1996. — On *Athyris* (Brachiopoda) and its type species “*Terebratulula concentrica* von Buch. *Senckenbergiana lethaea* 76 (1/2): 65-105.
- ALVAREZ F. & MODZALEVSKAYA T. L. 2001. — Trends in athyrid diversity dynamics, in BRUNTON C. H. C., COCKS L. R. & LONG S. (eds), Brachiopods past and present. *The Systematics Association Special Volume Series* 63: 212-223.
- ALVAREZ F. & RONG JIA-YU 2002. — Order Athyridida, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 4. Geological Society of America, Lawrence: 1475-1583.
- ALVAREZ F., RONG JIA-YU & BOUCOT A. J. 1998. — The classification of athyridid brachiopods. *Journal of Paleontology* 72: 827-855.
- AMSDEN T. W. 1968. — Articulate brachiopods of the St. Clair Limestone (Silurian), Arkansas, and the Clarita Formation (Silurian), Oklahoma. *The Paleontological Society Memoir* 1: 1-117.
- 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.
- ASSELBERGHS E. 1923. — La faune de la Grauwacke de Rouillon (base du Dévonien moyen). *Mémoires du Musée royal d'Histoire naturelle de Belgique* 33: 1-76.
- ASSELBERGHS E. 1936. — Le Dévonien du bord nord du Bassin de Namur. *Mémoires de l'Institut géologique de l'université de Louvain* 10: 229-327.
- ASSELBERGHS E. & MAILLIEUX E. 1925. — Comptes rendus de la cinquième session extraordinaire de la Société géologique et minéralogique de Bretagne tenue dans le terrain dévonien de l'Ardenne, entre Charleville et Gembloux du 13 au 19 avril 1925. *Bulletin de la Société géologique et minéralogique de Bretagne* 6: 117-187.
- BALIŃSKI A. 1977. — *Biernatella* – a new Devonian double-spined brachiopod. *Acta Palaeontologica Polonica* 22: 175-186.
- BALIŃSKI A. 1979. — Brachiopods and conodonts from the Frasnian of the Dębnik Anticline, southern Poland. *Palaeontologia Polonica* 39: 1-95.

- BALIŃSKI A. 1995. — 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.
- BARANOV V. V. 1994. — [Palaeozoic athyridids (brachiopods) from northeast Asia]. *Paleontologicheskii Zhurnal* (4): 28-37 (in Russian).
- BAYET L. 1888. — Compte rendu de la session extraordinaire annuelle tenue dans l'Entre-Sambre-et-Meuse, du 17 au 19 septembre 1887. *Annales de la Société géologique de Belgique, Bulletins* 15: 29-54.
- BIERNAT G. 1959. — Middle Devonian Orthoidea of the Holy Cross Mountains and their ontogeny. *Palaeontographica Polonica* 10: 1-78.
- BIERNAT G. 1966. — Middle Devonian brachiopods of the Bodzentyn Syncline (Holy Cross Mountains, Poland). *Palaeontologica Polonica* 17: 1-162.
- BIERNAT G. 1971. — The brachiopods from the Kadzielnia limestone (Frasnian) of the Holy Cross Mts. *Acta Geologica Polonica* 21: 137-163.
- BOUCOT A. J., JOHNSON J. G. & STATON R. D. 1964. — On some atrypoid, retzioid, and athyridoid Brachiopoda. *Journal of Paleontology* 38: 805-822.
- BOUCOT A. J., JOHNSON, J. G. & STATON R. D. 1965. — Suborder Athyrididina, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology*, Part H, *Brachiopoda*, part 1. Geological Society of America, Lawrence: H654-667.
- 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., BULTYNCK P., COEN M., COEN-AUBERT M., LACROIX D., LALOUX M., CASIER J. G., DEJONGHE L., DUMOULIN V., GHYSEL P., GODEFROID J., HELSEN S., MOURAVIEFF N. A., SARTENAER P., TOURNEUR F. & VANGUESTAINE M. 1999. — Les formations du Frasnien de la Belgique. *Memoirs of the Geological Survey of Belgium* 44: 1-126.
- BOULVAIN F., CORNET P., DA SILVA A. C., DELAITE G., DEMANY B., HUMBLET M., RENARD M. & COEN-AUBERT M. 2004. — Reconstructing atoll-like mounds from the Frasnian of Belgium. *Facies* 50: 313-326.
- BRETT C. E. & BAIRD G. C. 1995. — Coordinated stasis and evolutionary ecology of Silurian to Middle Devonian faunas in the Appalachian Basin, in EWING D. H. & ANSTEY R. L. (eds), *New Approaches to Speciation in the Fossil Record*. Columbia University Press, New York: 285-315.
- BRICE D. 1981. — Nouvelles observations sur les Orthida et les Rhynchonellida (Brachiopodes) du Frasnien de Ferques (Boulonnais). *Annales de la Société géologique du Nord* 100: 139-153.
- BRICE D. 1982. — Brachiopodes du Dévonien inférieur et moyen des Formations de Blue Fiord et Bird Fiord des îles arctiques canadiennes. *Geological Survey of Canada, Bulletin* 326: 1-175.
- BRICE D. 1988. — Brachiopodes du Dévonien de Ferques, in BRICE D. (ed.), *Le Dévonien de Ferques*. Bas-Boulonnais (N. France). Paléontologie – Sédimentologie – Stratigraphie – Tectonique. *Biostratigraphie du Paléozoïque* 7: 323-395.
- 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., BULTYNCK P., DEUNFF J., LOBOZIAK S. & STREEL M. 1979. — Données biostratigraphiques nouvelles sur le Givétien et le Frasnien de Ferques (Boulonnais, France). *Annales de la Société géologique du Nord* 98: 325-349.
- BRICE D., CARLS P., COCKS L. R. M., COPPER P., GARCÍA-ALCALDE J. L., GODEFROID J. & RACHEBOEUF P. R. 2000. — Brachiopoda., in BULTYNCK P. (ed.), *Subcommission on Devonian Stratigraphy*. Fossil groups important for boundary definition. *Courier Forschungsinstitut Senckenberg* 220: 65-86.
- BROUSMICHE C. 1973. — Révision des Productellidae (Brachiopodes) du Dévonien de Ferques (Boulonnais, France). *Annales de la Société géologique du Nord* 93: 117-136.
- BRUNTON C. H. C., LAZAREV S. S., GRANT R. E. & JIN Y. G. 2000. — Productidina, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 3. Geological Society of America, Lawrence: 424-619.
- 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., COEN-AUBERT M. & GODEFROID J. 2000. — Summary of the state of correlation in the Devonian of the Ardennes (Belgium-NE France) resulting from the decisions of the SDS. *Courier Forschungsinstitut Senckenberg* 225: 91-114.
- BULTYNCK P. & DEJONGHE L. 2002. — Devonian lithostratigraphic units (Belgium). *Geologica Belgica* 4: 39-69.
- BULTYNCK P., HELSEN S. & HAYDUCKIEWICH J. 1998. — Conodont succession and biofacies in upper Frasnian formations (Devonian) from the southern and central parts of the Dinant Synclinorium (Belgium) – (Timing of facies shifting and correlation with late Frasnian events). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 68: 25-75.
- BULTYNCK P. & MARTIN F. 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.

- CARTER J. L., JOHNSON J. G., GOURVENNEC R. & HOU HONG-FEI 1994. — A revised classification of the spiriferid brachiopods. *Annals of Carnegie Museum* 63: 327-374.
- CHEN Y.-R. 1978. — [Paleontological Atlas of South Western China, Sichuan Province, Sinian to Devonian, vol. 1]. Geological Publishing House, Beijing: 284-381 (in Chinese).
- CHEN Y.-R. 1984. — Brachiopods from the Upper Devonian Tuqiazi Member of the Longmenshan area (Sichuan, China). *Palaeontographica*, Abteilung A 184 (5-6): 95-166.
- COEN M. 1974. — Le Frasnien de la bordure orientale du Bassin de Dinant. *Annales de la Société géologique de Belgique* 97: 67-103.
- COEN M. 1977. — La Klippe du Bois Niau. *Bulletin de la Société belge de Géologie* 86: 41-44.
- 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: 21-25.
- COEN-AUBERT M. & BOULVAIN F. 2006. — Frasnian, in DEJONGHE L. (ed.), Current status of chronostratigraphic units named from Belgium and adjacent areas. *Geologica Belgica* 9: 19-25.
- COEN-AUBERT M. & LACROIX D. 1979. — Le Frasnien dans la partie orientale du bord sud du Synclinorium de Namur. *Annales de la Société géologique de Belgique* 101: 269-279.
- COMTE P. 1938. — Brachiopodes dévoniens des gisements de Ferroñes (Asturies) et de Sabero (Léon). *Annales de Paléontologie* 27: 41-88.
- COOPER G. A. 1955. — New genera of middle Paleozoic brachiopods. *Journal of Paleontology* 29: 45-63.
- COOPER G. A. & DUTRO J. T. JR. 1982. — Devonian Brachiopods of New Mexico. *Bulletins of American Paleontology* 82-83: 1-215.
- COOPER G. A. & WILLIAMS J. S. 1935. — Tully Formation of New York. *Geological Society of America Bulletin* 46: 781-868.
- COPPER P. 1998. — Evaluating the Frasnian-Famennian mass extinction: Comparing brachiopod faunas. *Acta Palaeontologica Polonica* 43: 137-154.
- CRICKMAY C. H. 1953. — *Warrenella*, a new genus of Devonian brachiopods. *Journal of Paleontology* 27: 596-600.
- CRICKMAY C. H. 1963. — *Significant New Devonian Brachiopods from Western Canada*. Published by the Author, Calgary, 63 p.
- CRICKMAY C. H. 1967. — *The Method of Indivisible Aggregates in Studies of the Devonian*. Published by the Author, Calgary, 22 p.
- CRICKMAY C. H. 1968. — *Discoveries in the Devonian of Western Canada*. Published by the Author, Calgary, 12 p.
- DAGYS A. S. 1974. — [Triassic Brachiopods (Morphology, Classification, Phylogeny, Stratigraphical Significance and Biogeography)], vol. 214. Sibirskoe Otdelenie Izdatel'stvo "Nauka", Novosibirsk, 387 p. (in Russian).
- DAMES W. 1868. — Ueber die in der Umgebung Freiburgs in Nieder-Schlesien auftretenden devonischen Ablagerungen. *Zeitschrift der Deutschen geologischen Gesellschaft* 20: 469-508.
- DAVIDSON T. 1858. — *British Fossil Brachiopoda*, vol. 2. Carboniferous, part 5, no. 1. Palaeontographical Society Monograph, London: 1-48.
- DAVIDSON T. 1865. — *British Fossil Brachiopoda*, vol. 3. Part 6. The Devonian Brachiopoda. Palaeontographical Society Monograph, London: 1-131.
- 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* (new series, Decade II) 8 (1): 1-13.
- DEFRANCE M. J. L. 1828. — Térébratules fossiles, in CUVIER G. (ed.), *Dictionnaire des sciences naturelles*, vol. 52. F. G. Levrault, Strasbourg: 147-167.
- DEMANET F. 1958. — Contribution à l'étude du Dinantien de la Belgique. *Mémoires de l'Institut royal des Sciences naturelles de Belgique* 141: 1-152.
- DROT J. 1964. — Rhynchonelloidea et Spiriferoidea siluro-dévoniens du Maroc pré-saharien. *Notes et Mémoires du Service géologique du Maroc* 178: 1-287.
- DROT J. 1982. — Brachiopods near the Givetian-Frasnian boundary in Tafilalt and Mâder (southern Morocco), in SARTENAER P. (ed.), *Papers on the Frasnian-Givetian boundary*. Geological Survey of Belgium, Brussels: 70-84.
- DUMON P. 1929. — Étude du Frasnien en Belgique. *Publication de l'Association des Ingénieurs de l'École des Mines de Mons* 30: 119-230.
- DUMON P. 1964. — La géologie des carrières, 2<sup>ème</sup> partie. *Le Mausolée* 336: 1451-1480.
- DÜRKOOP A. 1970. — Brachiopoden aus dem Silur, Devon, Karbon in Afghanistan. *Palaeontographica*, Abteilung A 134: 153-225.
- FENTON C. L. & FENTON M. A. 1924. — The stratigraphy and fauna of the Hackberry Stage of the Upper Devonian. *Contributions from the Museum of Geology and Paleontology of Michigan* 1: 1-260.
- FICNER F. & HAVLÍČEK V. 1978. — Middle Devonian brachiopods from Čechovice, Moravia. *Paleontologie* 21: 49-104.
- FLEMING J. 1828. — *A History of British Animals, Exhibiting the Descriptive Characters and Systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom*. Bell & Bradfute, Edinburgh; James Duncan, London, 565 p.
- FRECH F. 1891. — Ueber das Devon der Ostalpen. *Zeitschrift der Deutschen geologischen Gesellschaft* 43: 672-688.



- FREDERIKS G. 1911. — Bemerkung über einige oberpalaeozoische Fossilien von Krasnoufmsk. *Kazan University, Protocols of the sessions of the Natural History Society* 269: 1-12.
- FREDERIKS G. 1916. — [Palaeontological notes. 2. On some upper Palaeozoic Brachiopoda of Eurasia]. *Comité géologique, Mémoires (new series)* 156: 1-87 (in Russian).
- GARCÍA-ALCALDE J. L. 1973. — *Braquiopódos devónicos de la cordillera cantábrica (Orden Strophomenida)*. Ph.D. thesis, University of Oviedo, Oviedo, Spain, 722 p.
- GEORGE T. N. 1931. — *Ambocoelia* Hall and certain similar British Spiriferidae. *Quarterly Journal of the Geological Society* 87: 30-61.
- GODEFROID J. 1988. — Brachiopodes Atrypida du Dévonien de Ferques (Boulonnais-France), in BRICE D. (ed.), *Le Dévonien de Ferques. Bas-Boulonnais (N. France). Paléontologie – Sédimentologie – Stratigraphie – Tectonique. Biostratigraphie du Paléozoïque* 7: 403-434.
- GODEFROID J. & HAUSER J. 2003. — The Frasnian Pentamerida and Atrypida (Brachiopoda) from the Reichle quarry (Eifel, Germany). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 73: 53-68.
- GODEFROID J. & HELSEN S. 1998. — The last Frasnian Atrypida (Brachiopoda) in southern Belgium. *Acta Palaeontologica Polonica* 43: 241-272.
- GOLDMAN D. & MITCHELL C. E. 1990. — Morphology, systematics, and evolution of Middle Devonian Ambocoeliidae (Brachiopoda), western New York. *Journal of Paleontology* 64: 79-99.
- 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. 1879. — Nouveaux documents pour l'étude du Famennien. — Tranchées de chemin de fer entre Féron et Semeries. — Schistes de Sains. *Annales de la Société géologique du Nord* 6: 389-399.
- GOSSELET J. 1880. — *Esquisse géologique du Nord de la France et des contrées voisines*. 1<sup>er</sup> fascicule. *Terrains primaires*, Imprimerie Six-Horemans, 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.
- GOURVENNEC R. 1989. — Brachiopodes Spiriferida du Dévonien inférieur du Massif Armoricain. *Systématique – Paléobiologie – Évolution – Biostratigraphie. Biostratigraphie du Paléozoïque* 9: 1-281.
- GRABAU A. W. 1923-1924. — *Stratigraphy of China*, part 1, *Palaeozoic and older*. Geological Survey of China, Beijing, 528 p.
- GRABAU A. W. 1931-1933. — Devonian Brachiopoda of China. *Palaeontologia Sinica*, series B, 3: 1-538.
- GRAY J. E. 1840. — *Synopsis of the Contents of the British Museum*, 42<sup>nd</sup> edition. British Museum, London, 370 p.
- GRUNT T. A. & RACKI G. 1998. — Late Frasnian Athyridida (Brachiopoda) from Poland and the Late Devonian biotic turnover. *Acta Palaeontologica Polonica* 43: 361-378.
- GRUNT T. A. & WEYER D. 2002. — [Revision of Leopold von Buch's type collection of athyridids from Berlin Museum of natural History]. *Paleontologicheskii Zhurnal* (4): 34-44 (in Russian).
- GÜRICH G. 1903. — Das Devon Debnik bei Krakau. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients* 15 (4): 127-164.
- GÜRICH G. 1909. — *Leitfossilien [Ein Hilfsbuch zum Bestimmen von Versteinerungen bei geologischen Arbeiten in der Sammlung und im Felde]*, vol. 2, Devon. Gebrüder Borntraeger, Berlin: 97-199.
- HALL J. 1843a. — *Survey of the Fourth Geological District*. Natural History of New York, Geology, vol. 4. Carroll & Cook, Albany, 525 p.
- HALL J. 1843b. — Notes explanatory of a section from Cleveland, Ohio, to the Mississippi River, in a south-west direction; with remarks upon the identity of the western formations with those of New York. *Association of American Geologists & Naturalists, Transactions* 1843: 267-293.
- HALL J. 1859. — Contributions to the Palaeontology of New York; being some of the results of investigations made during the years 1855, '56, '57, and '58. New York State Cabinet of Natural History, 12<sup>th</sup> Annual Report, Albany: 7-110.
- HALL J. 1867. — *Descriptions and Figures of Fossil Brachiopoda of the Upper Helderburg, Hamilton, Portage and Chemung Groups*. Natural History of New York, Palaeontology, vol. 4, part 1. New York State Geological Survey, Albany, 428 p.
- HALL J. & CLARKE J. M. 1893. — *An Introduction to the Study of the Genera of Palaeozoic Brachiopoda*. Palaeontology of New York, vol. 8, part 2. Charles van Benthuyzen & Sons, Albany, 317 p.
- HALL J. & CLARKE J. M. 1894. — *The Evolution of the Genera of the Palaeozoic Brachiopoda*. Part 2: *The Genera of Brachiopoda*. New York State Museum, 47<sup>th</sup> Annual Report, Albany: 943-1100.
- HALL J. & CLARKE J. M. 1895. — *An Introduction to the Study of the Genera of Palaeozoic Brachiopoda, Natural History of New York*, vol. 8, part 2. New York Geological Survey. Charles van Benthuyzen & Sons, Albany, 394 p. (dated 1894, published 1895).
- HARPER D. A. T. 2000. — Suborder Dalmanellidina, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 3. Geological

- Society of America, Lawrence: 782-844.
- HAVLIČEK V. 1950. — Ramenonozci Českého Ordoviku. *Rozpravy Ústředního ústavu geologického* 13: 1-72.
- HELSEN S. & BULTYNCK P. 1992. — Conodonts and megafauna from two sections at Nismes and Mariembourg (Frasnian of the southern flank of the Dinant Synclinorium, Belgium). *Annales de la Société géologique de Belgique* 115 (1): 145-157.
- HERBOSCH A., CLAEYS P. & KYTE F. T. 1996. — Étude géochimique de la limite Frasnien-Famennien à Hony (Belgique). 17th IAS Regional African-European Meeting of Sedimentology, Sfax (Tunisie), abstract: 76.
- HOLZAPFEL E. 1895. — Das Obere Mitteldevon (Schichten mit *Stringocephalus Burtini* und *Maeneceras verbratum*) im Rheinischen Gebirge. *Abhandlungen der Königlich Preussischen geologischen Landesanstalt, Neue Folge* 16: 1-459.
- HOUSE M. R. 2002. — Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 181: 5-25.
- ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) 1976. — Opinion 1041. *Bulletin of Zoological Nomenclature* 32: 210-211.
- ICZN (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE) 1999. — *International Code of Zoological Nomenclature*. 4th ed. International Trust for Zoological Nomenclature, London, 306 p.
- IVANOVA I. A. 1972. — [Main features of spiriferid evolution (Brachiopoda)]. *Paleontologicheskii Zhurnal* (3): 28-42 (in Russian).
- JABLONSKI D. 1994. — Extinction in the fossil record. *Philosophical Transactions of the Royal Society of London, Series B (Biological Sciences)*, 344: 11-17.
- JOACHIMSKI M. M. & BUGGISCH W. 1993. — Anoxic events in the late Frasnian – Causes of the Frasnian-Famennian crisis? *Geology* 21: 675-678.
- JOHNSON J. G. 1966. — Middle Devonian brachiopods from the Roberts Mountains, central Nevada. *Palaeontology* 9: 152-181.
- JOHNSON J. G. 1979. — Devonian brachiopod biostratigraphy. *Palaeontological Association, Special Papers* 23: 291-306.
- JOHNSON J. G. 2006 (†). — Superfamily Cyrtinoidea, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 5. Geological Society of America, Lawrence: 1881-1883.
- JOHNSON J. G., KLAPPER G. & SANDBERG C. A. 1985. — Devonian eustatic fluctuations in Euramerica. *Bulletin of the Geological Society of America* 96: 567-587.
- JOHNSON J. G. & TALENT J. A. 1967. — Cortezorthinae, a new subfamily of Siluro-Devonian dalmanellid brachiopods. *Palaeontology* 10: 142-170.
- KAISIN F., MAILLIEUX E. & ASSELBERGHS E. 1922. — Traversée centrale de la Belgique par la vallée de la Meuse et ses affluents de la rive gauche. *Congrès géologique international*. Livret-guide pour la XIII<sup>ème</sup> session. Excursion A2: 90 p.
- KAESLER R. L. (ed.) 2000a. — *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 2. Geological Society of America, Lawrence: 1-423.
- KAESLER R. L. (ed.) 2000b. — *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 3. Geological Society of America, Lawrence: 424-920.
- KAESLER R. L. (ed.) 2002. — *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 4. Geological Society of America, Lawrence: 921-1688.
- KAESLER R. L. (ed.) 2006. — *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 5. Geological Society of America, Lawrence: 1689-2320.
- KAYSER E. 1883. — Devonische Versteinerungen aus dem südwestlichen China, in RICHTHOFEN F. (ed.), *China, Ergebnisse eigener Reisen und darauf gegründeter Studien*, vol. 4. Reimer, Berlin, 75-105.
- KELUS W. 1939. — Devonische Brachiopoden und Korallen der Umgebung von Pelcza in Volhynien. *Biuletyn Państwowy Instytut Geologiczny* 8: 1-51.
- KING W. 1850. — A Monograph of the Permian Fossils of England. *Palaeontographical Society Monograph* 3: 1-258.
- KLÄHN H. 1912. — Die Brachiopoden der Frasn-Stufe bei Aachen. *Jahrbuch der Königlich Preussischen Geologischen Landanstalt* 33: 1-39.
- LAFUSTE J. & TOURNEUR F. 1888. — *Dendropora* Michelin, 1846, et le nouveau genre dendroporimorphe *Sencliaepora* du Givétien et du Frasnien de la Belgique et du Boulonnais (France). *Bulletin du Muséum national d'Histoire naturelle*, 4<sup>e</sup> série, section C, 10 (4): 307-341.
- LALOUX M., DEJONGHE L., GHYSEL P. & HANCE L. 1996. — *Carte géologique de Wallonie à 1/25.000. Fléron-Verviers 42/7-8* (+ notice explicative). Ministère de la Région wallonne, Namur.
- LAZAREV S. S. 1987. — [Origin and systematic position of the main groups of Productida (brachiopods)]. *Paleontologicheskii Zhurnal* (4): 41-52 (in Russian).
- LAZAREV S. S. 1989. — [Systematics of Devonian brachiopods of suborder Strophalosiida]. *Paleontologicheskii Zhurnal* 1989 (2): 27-39 (in Russian).
- LE MAÎTRE D. 1961. — Spiriféridé nouveau du Frasnien ardennais: *Gürichella trelonensis* sp. nov. *Annales de la Société géologique du Nord* 81: 115-120.
- LIASHENKO A. I. 1958. — [Brachiopods of the Lower Frasnian Deposits of the Central Part of the Russian Platform]. Vsesoiuznyi Nauchno-Issledovatel'skii Geologo-Razvedochnyi Neftianoi Institut (VNIGNI), Trudy 9: 105-156 (in Russian).
- LIASHENKO A. I. 1959. — [Atlas of Brachiopods and Stratigraphy of the Devonian Deposits of the Central Region of the Russian Platform]. Vsesoiuznyi Nauchno-Issledovatel'skii Geologo-Razvedochnyi Neftianoi Institut (VNIGNI). Gostoptekhizdat, Moscow, 267 p. (in Russian).

- LIASHENKO A. I. 1973. — [Brachiopods and Stratigraphy of Lower Frasnian Deposits of the South Timan and Volga-Ural Oil-Gas Bearing Province]. Vsesoiuznyi Nauchno-Issledovatel'skii Geologo-Razvedochnyi Neftianoi Institut (VNIGNI), Trudy 134: 1-279 (in Russian).
- LUDVIGSEN R. & PERRY D. G. 1975. — The brachiopod *Warrenella* in the Lower and Middle Devonian formations of northwestern Canada. *Bulletin of the Geological Survey of Canada* 235: 59-106.
- MA X.-P., BECKER R. T., LI H. & SUN Y.-Y. 2006. — Early and Middle Frasnian brachiopod faunas and turnover on the South China shelf. *Acta Palaeontologica Polonica* 51: 789-812.
- MA X.-P., SUN Y.-L., HAO W.-C. & LIAO W.-H. 2002. — Rugose corals and brachiopods across the Frasnian-Famennian boundary in central Hunan, South China. *Acta Palaeontologica Polonica* 47: 373-396.
- MAILLIEUX E. 1909a. — Note sur quelques brachiopodes du Frasnien belge. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie, Procès-verbaux* 23: 9-13.
- MAILLIEUX E. 1909b. — Étude comparative de la répartition des espèces fossiles dans le Frasnien du bord méridional du bassin dinantais et dans les niveaux synchroniques du Boulonnais. Annexe. Notes sur les *Streptorhynchus* de la zone à sp. *Orbelianus* du Frasnien de l'Ardenne. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie, Mémoires* 23: 115-151.
- MAILLIEUX E. 1909c. — Note sur les *Cyrtina* dévoniennes du bord sud du bassin de Dinant. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie, Procès-verbaux* 23: 256-260.
- MAILLIEUX E. 1914. — Nouvelles contribution à l'étude des récifs coralligènes du Frasnien. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie, Procès-verbaux* 28: 82-93.
- MAILLIEUX E. 1922a. — *Terrains, roches et fossiles de la Belgique*. Les Naturalistes belges, Brussels, 164 p.
- MAILLIEUX E. 1922b. — The Geology of Belgium, II: The Palaeozoic formations of the southern part of the Dinant Basin. *Proceedings of the Geologists' Association* 33: 9-19.
- MAILLIEUX E. 1926. — Contribution à l'étude du "Massif" de Philippeville. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 36: 86-112.
- MAILLIEUX E. 1933. — *Terrains, roches et fossiles de la Belgique*. Deuxième édition. Patrimoine du Musée royal d'Histoire naturelle de Belgique, Brussels, 217 p.
- MAILLIEUX E. 1936. — La faune des Schistes de Matagne. *Mémoires du Musée d'Histoire naturelle de Belgique* 77: 1-74.
- 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. 1941a. — Répartition des Spiriferidae et des Spiriferinidae dans le Dévonien de l'Ardenne. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 17 (13): 1-6.
- MAILLIEUX E. 1941b. — Répartition des Brachiopodes dans le Dévonien de l'Ardenne. *Bulletin du Musée royal d'Histoire naturelle de Belgique* 17 (30): 1-14.
- MAILLIEUX E. & DEMANET F. 1929. — L'échelle stratigraphique des terrains primaires de la Belgique. *Bulletin de la Société belge de Géologie* 38: 124-131.
- MARION J. M. & BARCHY L. 1999. — *Carte géologique de Wallonie à 1/25.000. Chimay-Cowin 5717-8* (+ notice explicative). Ministère de la Région wallonne, Namur.
- MARTIN F. 1984. — Acritarches du Frasnien Supérieur et de Famennien Inférieur du bord méridional du Bassin de Dinant (Ardenne belge). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 55 (7): 1-57.
- MARTIN W. 1809. — *Petrefacta derbiensia; or Figures and Description of Petrifications Collected in Derbyshire*. Wigan, London, 28 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.
- MCGHEE G. R. JR. 1996. — *The Late Devonian Mass Extinction*. Columbia University Press, New York, 303 p.
- MCKELLAR R. G. 1970. — The Devonian productoid brachiopod faunas of Queensland. *Geological Survey of Queensland (Palaeontological Paper)* 342: 1-40.
- MERRIAM C. W. 1940. — Devonian stratigraphy and paleontology of the Roberts Mountains Region, Nevada. *Geological Society of America, Special Papers* 25: 1-114.
- MONTY C., VAN LAER P., MAURIN A. F. & BERNET-ROLLANDE M. C. 1988. — The Upper Devonian mud mounds from the south western Dinant Synclinorium, in HERBOSCH A. (ed.), *International Association of Sedimentologists, 9th European Regional Meeting, Excursion Guidebook, Leuven-Belgium*. Ministry of Economic Affairs, Belgian Geological Survey, Brussels: 157-176.
- MOORE R. C. 1952. — Brachiopods, in MOORE R. C., LALICKER C. G. & FISCHER A. G. (eds), *Invertebrate fossils*. McGraw-Hill, New York: 766 p.
- MOTTEQUIN B. 2003. — Two new atrypid brachiopod species from the late Frasnian of Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 73: 69-82.
- MOTTEQUIN B. 2004a. — 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. 2004b. — The genus *Biernatella* Baliński, 1977 (Brachiopoda) from the late Frasnian of Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 74 – supplément: 49-58.
- MOTTEQUIN B. 2005a. — Revision of the brachiopod *Cytina rigauxi* Maillieux, 1909 and description of a new ambocoeliid genus (*Dionacoelia* n. gen.) from the Frasnian of southern Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 75: 53-66.
- MOTTEQUIN B. 2005b. — *Les Brachiopodes de la transition Frasnien/Famennien dans le Bassin de Namur-Dinant (Belgique). Systématique-Paléoécologie-Biostratigraphie-Extinctions*. Ph.D. thesis, University of Liège, Liège, Belgium, 427 p.
- MOTTEQUIN B. 2008. — Late middle Frasnian to early Famennian (Late Devonian) strophomenid, orthotetid and athyridid brachiopods from southern Belgium. *Journal of Paleontology* 82: 1052-1073.
- MUIR-WOOD H. & COOPER G. A. 1960. — Morphology, classification and life habits of the Productoidea (Brachiopoda). *The 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-Bouloonnais. *Bulletin de la Société géologique de France* 11: 250-256.
- NALIVKIN D. V. 1930. — [The Semiluk and Voroneje Beds of the Upper Devonian Voroneje Region]. *Glavnoe Geologo-Razvedochnoe Upravleniye, Izvestiya* 49 (10): 53-93 (in Russian).
- NALIVKIN D. V. 1937. — [Brachiopoda of the Upper and Middle Devonian and Lower Carboniferous of Northeastern Kazakhstan]. Tsentral'nyi Nauchno-Issledovatel'skii Geologo-Razvedochnyi Institut (TSN-IGRI), Trudy 99: 1-200 (in Russian).
- NALIVKIN D. V. 1947. — [Brachiopoda], in NALIVKIN D. V. & VERBER V. N. (eds), [Atlas of Fossil Index Faunas of the USSR – Devonian System]. Vsesoiuznyi Nauchno-Issledovatel'skii Geologicheskii Institut (VSEGEI), Leningrad: 1-245 (in Russian).
- OEHLERT D. P. 1887a. — Appendice: Brachiopodes; notions sur l'anatomie et la physiologie des brachiopodes, in FISCHER P. H. (ed.), *Manuel de Conchyliologie et de Paléontologie conchyliologique, ou Histoire naturelle des mollusques vivants et fossiles*, partie 11. F. Savy, Paris: 1189-1334.
- OEHLERT D. P. 1887b. — Étude sur quelques fossiles dévoniens de l'Ouest de la France. *Annales des Sciences géologiques* 19: 1-80.
- OLENEVA N. 2006. — [Pyramidal spiriferids (brachiopods) from the Middle and Upper Devonian of the Russian Plate: morphology, systematics, and shell wall structure]. *Paleontologicheskii Zhurnal* (4): 64-72 (in Russian).
- PAECKELMANN W. 1913. — Das Oberdevon des Bergischen Landes. *Abhandlungen der Preussischen Geologischen Landesanstalt* 70: 1-356.
- PAECKELMANN W. 1942. — Beiträge zur Kenntnis devonischer Spiriferen. *Abhandlungen des Reichsamts für Bodenforschung* 197: 1-188.
- PAULUS B. 1957. — *Rhynchospirifer* n. gen. im Rheinischen Devon. *Senckenbergiana lethaea* 38: 49-72.
- PEDDER A. E. H. 1959. — *Monelasma bestii*, a new Schizophoriid Brachiopod from the Upper Devonian of Canada. *Geological Magazine* 96: 470-472.
- PHILLIPS J. 1836. — *Illustrations of the Geology of Yorkshire; or a Description of the Strata and Organic Remains: Accompanied by a Geological Map, Sections and Diagrams and Figures of the Fossils, part II, The Mountain Limestone District*. John Murray, London, 253 p.
- PHILLIPS J. 1841. — *Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon, and West Somerset*. Longman & Co., London, 231 p.
- PITRAT C. W. 1965. — Suborder Spiriferidina, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda*, part 2. Geological Society of America, Lawrence: H667-H728.
- POCOCK Y. P. 1966. — Devonian schizophoriid brachiopods from Western Europe. *Palaeontology* 9: 381-412.
- POTY E. & CHEVALIER E. 2007. — Late Frasnian phillipsastroid biostromes in Belgium, in ALVARO J. J., ARETZ M., BOULVAIN F., MUNNECKE A., VACHARD D. & VENIN E. (eds), Palaeozoic reefs and bioaccumulations: climatic and evolutionary controls. *Geological Society Special Publication* 275: 143-161.
- RACHEBOEUF P. R. 1984. — Productidina (Brachiopodes) dévoniens du synclinorium médian armoricain, France. *Bulletin de la Société géologique et minéralogique de Bretagne*, (C) 15 (2): 149-167 (dated 1983, published 1984).
- RACHEBOEUF P. R. 1988. — Brachiopodes Chonetacea du Dévonien de Ferques (Bouloonnais-France), in BRICE D. (ed.), Le Dévonien de Ferques. Bas-Bouloonnais (N. France). Paléontologie – Sédimentologie – Stratigraphie – Tectonique. *Biostratigraphie du Paléozoïque* 7: 397-401.
- RACHEBOEUF P. R. 2000. — Suborder Chonetidina, in KAESLER R. L. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised). Geological Society of America, Lawrence, part 2: 362-423.
- RACKI G. 1992. — Brachiopod assemblages in the Devonian Kowala Formation of the Holly Cross Mountains. *Acta Palaeontologica Polonica* 37: 297-357.
- RACKI G. 2005. — Toward understanding Late Devonian global events: few answers, many questions, in OVER D. J., MORROW J. R. & WIGNALL P. B. (eds), Understanding

- Late Devonian and Permian-Triassic biotic and climatic events: towards an integrated approach. *Developments in Paleontology and Stratigraphy* 20: 5-36.
- REED F. R. C. 1943. — Notes on certain Upper Devonian brachiopods figured by Whidborne, part 1-2. *Geological Magazine* 80 (2-3): 69-78, 95-106.
- RIGAUX É. 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 É. 1908. — *Le Dévonien de Ferques et ses brachiopodes*. Deligny éditeur, Boulogne-sur-Mer, 33 p.
- ROEMER C. F. 1844. — *Das Rheinische Uebergangsgebirge. Eine paläontologische-geognostische Darstellung*. Verlag der Hahn'schen Hofbuchhandlung, Hanover, 96 p.
- ROEMER F. A. 1843. — *Die Versteinerungen des Harzgebirges*. Hahn, Hannover: 40 p.
- RZHONSNITSKAYA M. A. & MODZALEVSKAYA T. L. 1996. — Evolution of Devonian plicathyridine brachiopods, Northern Eurasia, in COPPER P. & JIN J. (eds), *Brachiopods. Proceedings of the Third International Brachiopod Congress Sudbury, Ontario, Canada, 2-5 September 1995*. A. A. Balkema. Rotterdam: 233-238.
- 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. 1967. — Commentaires sur le genre nominal *Adolfia* Gürich G., 1909 et sur le nom générique *Guerichella* (Brachiopoda, Spiriferacea). *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 75: 380-389.
- 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.
- SARTENAER P. 1989. — Deux genres Rhynchonellides nouveaux d'âge frasnien moyen et supérieur, résultant du brisement de *Calvinaria* Stainbrook, 1945. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 59: 61-77.
- SARTENAER P. & HARTUNG W. 1992. — Die Biozonierung der Oberen Frasnies-Stufe (Frasnes-Knollenkalke und Frasnies-Schiefer) am Nord-Afball des Hohen Venns mit Hilfe von Rhynchonelliden. *Senckenbergiana lethaea* 72: 49-60.
- SARYTCHEVA T. G. & SOKOLSKAYA A. N. 1959. — [On the classification of pseudopunctate brachiopods]. *Akademia Nauk SSSR, Doklady*, Moscow, 125 (1): 181-184 (in Russian).
- SCHINDLER E. 1993. — Event-stratigraphic markers within the Kellwasser Crisis near the Frasnian/Famennian boundary (Upper Devonian) in Germany. *Palaeogeography, Palaeoclimatology, Palaeoecology* 104: 115-125.
- SCHNUR J. 1851. — *Die Brachiopoden aus dem Uebergangsgebirge der Eifel*. Programm vereinigten höhern Bürger- und Provinzial-Gewerbeschule zu Trier für das Schuljahr 1851, Lintz, Trier, 16 p.
- SCHNUR J. 1853. — Zusammenstellung und Beschreibung sämtlicher im Uebergangsgebirge der Eifel vorkommenden Brachiopoden nebst Abbildungen derselben. *Palaeontographica* 3: 169-247.
- SCHUCHERT C. 1913. — *Class Brachiopoda. The Lower Devonian Deposits of Maryland*. Maryland Geological Survey, Baltimore: 290-449.
- SCHUCHERT C. 1929. — Classification of brachiopod genera, fossil and recent, in SCHUCHERT C. & LEVENE C. M., *Animalia*, pars 42, in POMPECKJ J. F. (ed.), *Fossilium Catalogus*, vol. 1. W. Junk, Berlin: 10-25.
- SCHUCHERT C. & COOPER G. A. 1931. — Synopsis of the brachiopod genera of the suborders Orthoidea and Pentamerioidea, with notes on the Telotremata. *American Journal of Science* (series 5) 22: 241-251.
- SCHUCHERT C. & COOPER G. A. 1932. — Brachiopod genera of the suborders Orthoidea and Pentamerioidea. *Memoirs of the Peabody Museum of Natural History* 4 (1): 1-270.
- SCHUCHERT C. & LEVENE C. M. 1929. — Brachiopoda (generum et genotyporum index et bibliographia), in POMPECKJ J. F. (ed.), *Fossilium Catalogus*, vol. 1, *Animalia*, pars 42. W. Junk, Berlin, 140 p.
- SCUPIN H. 1900. — Die Spiriferen Deutschlands. *Palaeontologische Abhandlungen* (new series 4) 8 (3): 207-344.
- SEPKOSKI J. J. JR 1986. — Phanerozoic overview of mass extinctions, in RAUP D. M. & JABLONSKI D. (eds), *Pattern and Processes in the History of Life*. Springer-Verlag, Berlin: 277-295.
- SOLLE G. 1936. — Revision der Fauna des Koblenz-Quarzits an Rhein und Mosel. *Senckenbergiana* 18 (3-4): 154-215.
- SOWERBY J. DE C. 1840. — On the physical structure and older stratified deposits of Devonshire, in SEDGWICK A. & MURCHISON R. I. (eds), *Geological Society of London, Transactions* (2nd series) 5: 633-703.
- SOWERBY J. DE C. 1840-1846. — *The Mineral Conchology of Great Britain*, vol. 7. Published by the author, London, 80 p.
- STAINBROOK M. A. 1943. — Strophomenacea of the Cedar Valley Limestone of Iowa. *Journal of Paleontology* 17: 39-59.
- 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.
- STEHLI F. G. 1954. — Lower Leonardian Brachiopoda of the Sierra Diablo. *Bulletin of the American Museum of Natural History* 105: 257-358.
- 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. 1964. — Beiträge zur Kenntnis devonischer Brachiopoden, 8) über einige homöomorphe Brachiopoden-Arten (Meristellidae). *Senckenbergiana lethaea* 45: 507-521.
- STRUVE W. 1965. — Beiträge zur Kenntnis devonischer Brachiopoden, 11: *Schizophoria striatula* und *Schizophoria excisa* in ihrer ursprünglichen Bedeutung. *Senckenbergiana lethaea* 46: 193-215.
- STRUVE W. 1970. — “Curvate Spiriferen” der Gattung *Rhenothyris* und einige andere Reticulariidae aus dem Rheinischen Devon. *Senckenbergiana lethaea* 51: 449-577.
- STRUVE W. 1992. — Neues zur Stratigraphie und Fauna des rhenotypen Mittel-Devon. *Senckenbergiana lethaea* 71: 503-623.
- SUËSS E. 1851. — Ueber ein neues Brachiopoden-Geschlecht *Merista*. *Jahrbuch der Kaiserlich-Königlichen Geologischen Reichsanstalt* 2 (4): 150.
- THOREZ J., DRESEN R. & STREEL M. 2006. — Famennian, in DEJONGHE L. (ed.), Current status of chronostratigraphic units named from Belgium and adjacent areas. *Geologica Belgica* 9: 27-45.
- TIEN C. C. 1938. — Devonian Brachiopoda of Hunan. *Palaeontologia Sinica*, new series B, 4: 1-192.
- TONNARD V. 1956. — Sur l'apparente hétérogénéité de *Spirifer* (*Cyrtospirifer*) *Verneuili* du gîte de Barvaux. *Bulletin de l'Institut agronomique et de la Station de Recherches de Gembloux* 24: 351-359.
- TORLEY K. 1934. — Die Brachiopoden des Massenkalkes der Oberen Givet-Stufe von Bilveringsen bei Iserlohn. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* 43 (3): 67-148.
- VANDERCAMMEN A. 1955. — Quelques Spiriferidae nouveaux du Dévonien de la Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 31 (90): 1-4.
- VANDERCAMMEN A. 1956. — Révision des Ambocoeliinae du Dévonien de la Belgique. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 32 (43): 1-51.
- VANDERCAMMEN A. 1957a. — Révision de *Spirifer euryglossus* Schnur, 1851 = *Minatothyris* nov. gen. *euryglossa* (Schnur) (Brachiopoda, Dévonien supérieur). *Senckenbergiana lethaea* 38: 177-193.
- VANDERCAMMEN A. 1957b. — Révision des Reticulariinae du Dévonien de La Belgique. 1. — Genre *Minatothyris* A. Vandercammen, 1957. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 33 (14): 1-19.
- VANDERCAMMEN A. 1957c. — Révision des Reticulariinae du Dévonien de la Belgique. 2: Genre *Plectospirifer* A. Grabau, 1931. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 33 (24): 1-23.
- VANDERCAMMEN A. 1957d. — Révision du genre *Gürichella* W. Paeckelmann, 1913. *Mémoires de l'Institut royal des Sciences naturelles de Belgique* 138: 1-50.
- VANDERCAMMEN A. 1959. — Contribution à la révision de quelques Spiriferidae de la collection E. de Verneuill. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 35 (4): 1-38.
- VANDERCAMMEN A. 1966. — Observations nouvelles sur les Gürichellinae W. Paeckelmann. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie* 74: 265-285.
- VANDERCAMMEN A. 1967. — Révision de quelques Spiriferida conservés à l'Université de Bonn. *Bulletin de l'Institut royal des Sciences naturelles de Belgique* 43 (14): 1-10.
- VEEVERS J. J. 1959a. — The type species of *Productella*, *Emanuella*, *Crurithyris* and *Ambocoelia* (Brachiopoda). *Journal of Paleontology* 33: 902-908.
- VEEVERS J. J. 1959b. — Devonian Brachiopods from the Fitzroy Basin, Western Australia. *Bureau of Mineral Resources, Geology and Geophysics Bulletin* 45: 1-220.
- VERNEUIL E. DE 1845. — Paléontologie, mollusques, brachiopodes, in MURCHISON R. I., VERNEUIL E. DE & KEYSERLING A. DE (eds), *Géologie de la Russie d'Europe et des Montagnes de l'Oural*, volume 2 (3): *Paléontologie*. John Murray, London; Bertrand, Paris: 17-395.
- VERNEUIL E. DE 1850. — Notes sur les fossiles du district de Sabero (Léon). *Bulletin de la Société géologique de France* 7: 155-186.
- VON BUCH L. 1834. — Über Terebrateln, mit einem Versuch, sie zu classificiren und zu beschreiben. *Physikalische Abhandlungen Königliche Akademie für Wissenschaften aus den Jahre 1833*: 1-124.
- VON BUCH L. 1838. — Ueber *Delthyris* oder *Spirifer* und *Orthis*. *Physikalische Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, Aus den Jahre 1836: 1-79.
- VON SCHLOTHEIM E. F. 1813. — *Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. Taschenbuch für die gesammte Mineralogie mit Hinsicht auf die neuesten Entdeckungen*, vol. 7, no. 1. Hermann, Frankfurt am Main: 3-134.
- WAAGEN W. 1883. — Salt Range fossils, vol. 1, part 4. *Productus* Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica* (series 13), 2: 391-546.
- WAAGEN W. 1884. — Salt Range fossils, vol. 1, part 4. *Productus* Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica* (series 13), 3-4: 547-728.
- WHIDBORNE G. F. 1893. — A monograph of the Devonian fauna of the south of England. *Palaeontographical Society* 1: 1-344.
- WILLIAMS A. & HARPER D. A. T. 2000. — Order Orthida, in KAESLER, R. L. (ed), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda* (revised), part 3. Geological Society of America, Lawrence: 714-782.
- WILLIAMS H. S. 1908. — The dalmanellas of the Chemung

- Formation, and a closely related new brachiopod genus *Thiemella*. *Proceedings of the United States National Museum* 34: 35-64.
- WRIGHT A. D. 1965. — Superfamily Enteletacea, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology*, part H, *Brachiopoda*. Geological Society of America, Lawrence, part 1: H328-346.
- WULFF R. 1923. — Das Famennien der Aachener Gegend. *Jahrbuch der Preussischen Geologischen Landesanstalt* 43: 1-70.

*Submitted on 21 May 2007;  
accepted on 28 May 2008.*

## APPENDIX 1

Tables 1-4.

TABLE 1. — Measurements of productids (in mm). Abbreviations: **L**, shell length; **T**, shell thickness; **ULv**, ventral valve unrolled length; **W**, shell width.

	<b>IRScNB</b>	<b>W</b>	<b>L</b>	<b>ULv</b>	<b>T</b>
<i>Productella</i> sp.	a12370	28.6	28.3	46	(15.2)
	a12371	24.8	30	54	–
	a12372	25.5	(27.9)	(47)	19.3
? <i>Caucasiproductus</i> sp.	a12373	32.9	(30.7)	(52)	18.9
	a12376	19	17.1	26	7.4
	a12377	26.2	20.5	29	8.2
	a12378	14.7	12.7	19	5.4
	a12379	17.7	13.6	18	6.3
	a12380	15	12.4	17	5.7
	a12381	16.1	12.6	18	6.45
	a12382	26.3	18.1	27	9.2
	a12383	25.7	19.45	29	–
	a12384	24.1	16.9	27	–
	<i>Devonoproductus</i> sp. A	a12386	16.1	14.1	21
a12387		18.2	15.8	24	7.3
a12388		19.1	15.3	23	8
a12389		15.4	11.9	17.5	5.2
a12390		–	14.6	21	6.45
a12391		18	16.7	25	8.5
a12392		15.2	13.6	19	5.1
a12394		(14.3)	13.1	18	6

TABLE 2. — Measurements of orthids (in mm). Abbreviations: **dv**, dorsal valvae; **Ht**, tongue height; **L**, shell length; **T**, shell thickness; **vv**, ventral valve; **W**, shell width; **Whl**, hinge line width; **Ws**, sulcus width.

	<b>IRScNB</b>	<b>W</b>	<b>L</b>	<b>T</b>	<b>Ws</b>	<b>Whl</b>	<b>Ht</b>
?Isorthinae gen. et sp. indet.	a12349	12.7	10.2	2.1	–	10.1	–
	a12350	11.1	9	3.4	–	8.4	–
			(dv)	(dv)			
a12351	12.8	11.1	4.05	–	10.9	–	
		(vv)	(vv)				
? <i>Hypsomyonia</i> sp.	a12358	3.1	2.1	1.4	–	1.9	–
<i>Monelasma</i> cf. <i>deshayesi</i>	a12359	6.1	5.8	3.5	–	4.1	–
	a12360	6	5.6	3	–	4.6	–
<i>Schizophoria</i> cf. <i>simpsoni</i>	a12367	26.2	21.35	16	16.3	15.6	7.25



TABLE 3. — Measurements of athyridids (in mm). Abbreviations: **Ht**, tongue height; **L**, shell length; **T**, shell thickness; **W**, shell width; **Ws**, sulcus width.

	<b>IRScNB</b>	<b>W</b>	<b>L</b>	<b>T</b>	<b>Ws</b>	<b>Ht</b>
<i>Athyris cf. purchisoni</i>	a12319	26.9	20.3	15.9	16.5	8.1
<i>Cleiothyridina sp. A</i>	a12320	30.2	25.3	18.9	14.6	11.7
	a12321	30.9	24.8	18.4	13.8	9.9
	a12322	30.2	25.35	16	14.2	10.6
	a12323	31.6	22.7	17.9	15.8	—
	a12324	30.1	28.4	16.05	12.9	7
	a12325	30.8	25.8	16.8	—	—
	a12326	30.3	24.5	15.2	12.85	4.7
	a12327	30.3	24.45	16.4	15.2	6.2
<i>Camarium sp.</i>	a12328	17.9	14.8	10.3	12.3	6.6

TABLE 4. — Measurements of spiriferids and spiriferinids (in mm). Abbreviations: **Hi**, interarea height; **Ht**, tongue height; **L**, shell length; **T**, shell thickness; **W**, shell width; **Whl**, hinge line width; **Ws**, sulcus width.

	<b>IRScNB</b>	<b>W</b>	<b>L</b>	<b>T</b>	<b>Ws</b>	<b>Whl</b>	<b>Hi</b>	<b>Ht</b>
<i>Adolfia biverrucosa</i>	a12284	24.8	17	18	12	22.3	5.9	7.6
	a12285	26.5	17.3	19.1	13.5	—	5.3	9.3
	a12286	21.4	15.5	14.1	10.1	16.4	4.3	—
<i>A. cf. trelonensis</i>	a12289	(40.6)	22.1	18.8	12.2	(40.6)	5.9	6.6
<i>Emanuelia sp.</i>	a12290	9.2	8.5	5.9	—	—	—	—
	a12991	7.6	7.2	5.2	—	1.4	5.1	—
	a12292	8.8	8.6	5.9	—	1.8	6.55	—
	a12293	16.4	13.3	10.5	—	1.75	11.2	—
Rhynchospiriferinae gen. et sp. indet.	a12294	7.9	7.9	5.3	—	5.7	1.1	—
	a12295	6.5	6	3.9	—	4.0	1.4	—
	a12296	8.1	7.6	4.8	—	—	—	—
	a12297	7.5	7.8	4.2	—	5.4	1.3	—
	a12298	6.8	7.1	4.4	—	4.7	1.4	—
<i>Cyrtina douvillei</i>	a12308	12.9	8.8	11.8	12.2	7.5	8.1	5.4
	a12309	14.9	11.5	12.1	13.6	8.5	7.1	4.4
	a12310	14.1	10.2	12.4	12	7.5	7.7	4.9
	a12311	13.2	13.4	9.4	12.5	7.7	8.4	3.6
	a12312	12.9	8.6	13.05	11.9	7.7	8.7	5.2
	a12313	12.6	8.6	11.9	11.1	6.7	7.1	5.6

## APPENDIX 2

## Geological and geographical data of the sampled localities.

Only the formations from where the studied specimens originate are mentioned below (see Mottequin (2005b) for more details concerning the species ranges for each outcrop).

**BM-2001-1.** Engis (La Mallieue), outcrop along the north-western side of the road from Engis to Amay (Poty & Chevalier 2007); Aisemont Formation. Grid references (Belgian Lambert system) (East-North): 221.725; 140.745 (IGN map 41/7-8).

**BM-2001-2.** Hony, railway section, east of the station (Mottequin 2003); Lambermont Formation. Grid references: 245.555-137.350 (IGN map 49/1-2).

**BM-2001-3.** North-western side of the N929 road, between the km 46.1 and km 46.3, north-west of Deulin; Famenne Group. Grid references: 222.940-111.425 (IGN map 57/3-4).

**BM-2001-4.** North-eastern and south-western sides of the road from Dinant to Neufchâteau (N94) between km 15.1 and km 15.2, north of Hérock (IGN map 59/1-2) (Coen *in* Boulvain *et al.* 1999); Barvaux Formation. Grid references: 198.800-97.330 (IGN map 59/1-2).

**BM-2001-5.** North-eastern side of the road from Dinant to Neufchâteau (N94) between km 15.3 and km 15.5, north of Hérock (Martin 1984); Famenne Group. Grid references: 198.920-97.215 (IGN map 59/1-2).

**BM-2002-1.** Lambermont, western access road to the highway Verviers-Prüm (Laloux & Ghysel *in* Boulvain *et al.* 1999); Lambermont Formation. Grid references: 254.335-143.600 (IGN map 42/7-8).

**BM-2002-5.** Biron, along the south-western side of the forest track linking the village to the disused halt of Biron (Coen *in* Boulvain *et al.* 1999); Neuville, Les Valisettes and Barvaux formations. Grid references: 228.915-112.460 (IGN map 55/1-2).

**BM-2002-6.** North-eastern side of the trench dug for the Brussels-Arlon railway, south of Hogue, on both sides of the km 108 (Gosselet 1888); Barvaux Formation and Famenne Group. Grid references: 215.000-103.555 (IGN map 54/7-8).

**BM-2002-7.** Heure, small disused quarry in the north-eastern flank of the N929, west of Heure (Coen 1974); Neuville Formation. Grid references: 215.218-109.450 (IGN map 57/3-4).

**BM-2002-8.** Neuville, south-west of the village, on the eastern side of a trench dug for the Couvin-Charleroi railway (Godefroid & Helsen 1998); Neuville and Les Valisettes formations. Grid references: 159.395-95.275 (IGN map 57/3-4).

**BM-2003-2.** Senzeille railway “reference section”, southwest of the N978 road, south of Senzeille (Martin 1984; Bultynck & Martin 1995); Famenne Group. Grid references: 156.080-94.835 (IGN map 57/3-4).

**BM-2003-3.** Cerfontaine, eastern side of the by-pass road of Cerfontaine at the La Redoute locality (Mottequin 2004a); Les Valisettes Formation. Grid references: 152.300-94.850 (IGN map 57/3-4).

**BM-2003-4.** Cerfontaine, eastern side of the by-pass road of Cerfontaine at the La Redoute locality, beginning 75 m north of BM-2003-3; Les Valisettes and Matagne formations. Grid references: 152.240-95.160 (IGN map 57/3-4).

**BM-2003-5.** Cerfontaine, southern side of the N978 at the La Besace locality; Les Valisettes Formation. Grid references: 153.815-94.700 (IGN map 57/3-4).

**BM-2003-6.** Frasnès, Couvin-Charleroi railway cut (Coen-Aubert 1994); Grands Breux (Boussu-en-Fagne Member) and Neuville formations. Grid references: 159.780-84.425 (IGN map 57/7-8).

**BM-2003-7.** Frasnès, southern access to the disused Lion quarry (Coen-Aubert 1994); Grands Breux (Boussu-en-Fagne Member) and Neuville formations. Grid references: 160.160-84.545 (IGN map 57/7-8).

**BM-2003-8.** Nismes, railway section between Mariembourg and Nismes (Helsen & Bultynck 1992; Godefroid & Helsen 1998) (IGN map 58/5-6); Neuville and Matagne formations. Grid references: 162.600-86.075 (IGN map 58/5-6).

**BM-2003-9.** Vaulx, eastern side of a short blind road to the north of Vaulx (Godefroid & Helsen 1998);

Mottequin 2004b); Neuville Formation. Grid references: 150.050-84.550 (IGN map 57/7-8).

**BM-2003-10.** Boussu-en-Fagne, eastern wall of the disused cemetery quarry and along the access-path (Godefroid & Helsen 1998); Grands Breux (Boussu-en-Fagne Member) and Neuville formations. Grid references: 157.690-84.985 (IGN map 57/7-8).

**BM-2003-11.** North-western side of the road N86 at the southern exit of the Hotton (Tonnard 1956); Grands Breux (Boussu-en-Fagne Member) and Neuville formations. Grid references: 226.480-106.570 (IGN map 55/5-6).

**BM-2003-12.** Railway section, east of disused station of Lompret (Marion & Barchy 1999); Grands Breux (Boussu-en-Fagne Member) and Neuville formations. Grid references: 150.900-84.470 (IGN map 57/7-8).

**BM-2004-1.** Senzeille, northern wall of the disused Beauchâteau quarry (Boulvain 1993); Les Valisettes Formation. Grid references: 158.300-94.300 (IGN map 57/3-4).

**BM-2004-2.** Neuville, Tapoumont quarry south-west of Neuville (Boulvain 1993); Les Valisettes Formation. Grid references: 159.600-94.675 (IGN map 57/3-4).

**BM-2004-4.** Baugnée, along the road from Nandrin to Esneux, north-west of the Tavier stream (Poty & Chevalier 2007); Aisemont Formation. Grid references: 228.565-133.625 (IGN map: 49/1-2).

**BM-2004-5.** Huccorgne, south-western side of a road parallel to the highway E42 (Boulvain 1993); Aisemont Formation. Grid references: 207.250-139.850 (IGN map 41/5-6).

**Couvin 6158p.** See BM-2003-10.

**JG-1995-4.** See BM-2003-10.

**JG-1995-5.** See BM-2003-8.

**JG-1996-1.** See BM-2003-9.

**JG-1996-3.** See BM-2002-8.

**Durbuy 5337.** Biron, Liège-Jemelle railway section between the km 43 and 44 (Coen *in* Boulvain *et al.* 1999); Barvaux Formation. Grid references: 228.630-112.900 (IGN map 55/1-2).

**Olloy 575.** See BM-2003-8.

**Senzeille 6839b.** Senzeille, old railway section west of the tunnel (Sartenaer 1960). See also locality BM-2003-2.

**Senzeille 6840.** See BM-2004-1.

**Senzeille 6854.** Neuville, 660 m south of the village along the way of the marble quarries; Les Valisettes Formation. Grid references: not precisely located (IGN map 57/3-4).