The last Frasnian Atrypida (Brachiopoda) in southern Belgium

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Godefroid, J. & Helsen, S. 1998. The last Frasnian Atrypida (Brachiopoda) in southern Belgium. — Acta Palaeontologica Polonica 43, 2, 241–272.

The last representatives of the order Atrypida on the southern flank of the Dinant Synclinorium (Vaulx-Nismes area) in Belgium belong to *Costatrypa, Spinatrypa, Spinatrypina (Spinatrypina (Spinatrypina (Exatrypa), Iowatrypa, ?Waiotrypa, Desquamatia (Desquamatia)* and *Desquamatia (?Seratrypa).* Among the thirteen described taxa, five are new: *Spinatrypa tumuli* sp. n., *Iowatrypa circuitionis* sp. n., *?Waiotrypa pluvia* sp. n., *Desquamatia (Desquamatia) quieta* sp. n. and *Desquamatia (?Seratrypa) derelicta* sp. n. Supposed lissatrypid '*Glassia drevermanni*' Maillieux, 1936 from the late Frasnian Matagne shales is assigned to the Rhynchonellida. On the southern flank of the Dinant Synclinorium and in the Philippeville Massif, the Atrypida become extinct in the *Palmatolepis rhenana* Zone, significantly below the Frasnian-Famennian (F-F) boundary. Their extinction coincides with the first appearance of the green and black shales of the late Frasnian Matagne Formation, recording a transgressive-hypoxic event. Based on conodont data, this event takes place earlier on the southern flank of the Dinant Synclinorium than in the Philippeville Massif.

Key words: Brachiopoda, Atrypida, taxonomy, biostratigraphy, mass extinction, Kellwasser Crisis, Frasnian, Devonian, Belgium.

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Introduction

Atrypid brachiopods (order Atrypida) become extinct near the Frasnian-Famennian (F-F) boundary (e.g., Copper 1966, 1986b), which corresponds to one of the five major Phanaerozoic extinctions. This paper discusses the last Frasnian Atrypida from outcrops at Vaulx, Boussu-en-Fagne, Frasnes and Nismes (southern flank of the Dinant Synclino-rium) (Fig. 1; see Appendix 1). Sampled lithostratigraphical units are the Grand Breux, Neuville and Matagne Formations (see Fig. 2). Although some outcrops do not expose complete stratigraphical successions, they demonstrate distal shelf facies and faunal



Fig. 1. Sketch map showing location of the studied sections in the Ardennes. Vertical hatching – Middle Devonian and Frasnian Formations. Sketch map shown by rectangle in the general map of Belgium (lower right corner).

variations occurring during this interval. Stratigraphical distribution of these brachiopods in the northerly Philippeville Massif (Fig. 1) is compared. Palaeogeographically, the Philippeville area was located closer to shore on the Laurussian shelf than the southern flank of the Dinant Synclinorium. This work continues revision of the Frasnian atrypid brachiopods from Belgium (see Godefroid 1970, 1994, 1998; Godefroid & Jacobs 1986).

The material described in this paper is housed at the Royal Institute for Natural Sciences of Belgium (abbreviated IRScNB).

Stratigraphic setting

Lithostratigraphy. — Although the conclusions of the Belgian Commission on Devonian Stratigraphy concerning the lithostratigraphical units on the southern flank of the Dinant Synclinorium are not yet published, formations and members (Figs 2 and 19) have already been described in various papers.

At the base of the Frasnian, the Nismes Formation and its three members have been defined by Bultynck *et al.* (1983: pp. 5–7) (see also Bultynck in Bultynck *et al.* 1983:

Fig. 2. Location sketches of atrypid sites and distribution of the atrypid brachiopods in the sections: Vaulx (V) (**A**, **E**), Boussu-en-Fagne (BF) and Frasnes (Fr 1: nameless quarry; Fr 2: Philippeville-Couvin road) (**B**, **F**, **G**), Nismes railway section (Ni) (**C**, **H**) and Neuville railway section (Ne) (**D**, **I**). Only the upper part of the Lion Member is represented at Boussu-en-Fagne in Fig. 2F.



pp. 14–32; Godefroid & Jacobs 1986: pp. 68–80; Sartenaer in Bultynck *et al.* 1987: p. 253). The Moulin Lienaux and Grands Breux Formations have been described by Coen-Aubert (1994: pp. 21–29, tab. 1). Tsien (1972: p. 16, fig. 2, tab. 1, 2; 1974: pp. 4, 27–29, 31, fig. 1) denominated and shortly described the Neuville and Matagne Formations, as well as the Chalon, Arche, Ermitage, Lion and Boussu-en-Fagne Members. In this paper, only the Grands Breux, Neuville and Matagne Formations are concerned and briefly discussed hereafter (see details in Appendix 1).

In the Grands Breux Formation, three members are recognized. The Bieumont Member consists of fine, argillaceous, locally nodular, grey limestones with shaly intercalations in the upper part. Atrypid brachiopods from this member are not studied in the present paper. Well exposed in the railway cut at Frasnes, the Boussu-en-Fagne Member is typically shaly, with intercalations of thin limestone beds. Facies and thickness variations within the member are related to the development of reef lenticles of the Lion Member. In the surroundings of reefs, where faunas are more abundant and diversified, the thickness of the Boussu-en-Fagne Member is relatively reduced and, although the number of limestone beds and lenses increases, shales remain the main component. In the Frasnes area, the thickness of the member varies from about 80 m in the absence of reef lenticles (Coen-Aubert 1994: pp. 22–23) to 15–16 m in the cemetery quarry at Boussu-en-Fagne, where the member is reduced to shales with limestone beds and lenses overlying a reef lenticle of the Lion Member.

The Neuville Formation has been defined in the Philippeville Massif by Tsien (1974: p. 31) and subsequently revised by Boulvain, Coen & Coen-Aubert (pp. 20–26 in Boulvain *et al.* 1993). On the southern flank of the Dinant Synclinorium, the Neuville Formation is made up by nodular limestones with thin shaly intercalations and by an alternation of nodular limestones and shales with occasional limestone lenses and nodules. In places, these limestones may be reddish. In addition, small reef lenticles of grey or reddish limestone may occur. In the Frasnes area, the Neuville Formation is about 35 m thick (Coen-Aubert 1994: fig. 3).

The Matagne Formation comprises fine, dark, greenish, brownish or blackish shales. Dark grey, argillaceous and nodular limestones, some of them with abundant goniatites, are interbedded in the basal part of these shales. In the studied area, greenish and brownish shales occur at the base of the formation. They are about 7 m thick at Vaulx, 3 m at Frasnes and 3 m at Nismes. The thickness of the Matagne Formation exceeds 42 m.

Conodont biostratigraphy. — The lithologic succession with atrypid brachiopod faunas is assigned to the *Palmatolepis hassi*, *Palmatolepis jamieae* and *Palmatolepis rhenana* conodont zones (Bultynck 1993: fig. 5). When available, more precise conodont data accompany the descriptions of the outcrops. Late Frasnian conodont biostratigraphy and biofacies in southern Belgium and their importance to event stratigraphy have been studied by Bultynck, Helsen & Haydukiewicz (1998).

Systematic palaeontology

All type specimens, as well as the figured and measured specimens, are stored at the Royal Institute for Natural Sciences of Belgium in Brussels, where they are registered under the numbers a10588–a10625. The material described below includes ca. 800

generally well preserved shells and isolated valves. These specimens have been collected bed by bed by the authors or are part of old collections of the Royal Institute for Natural Sciences of Belgium.

Abbreviations: L – length of the pedicle valve, W – width of the shell, T – thickness of the shell, Tb – thickness of the brachial valve, Tp – thickness of the pedicle valve, Nr – total number of ribs, R-10 – number of ribs per 10 mm near anterior shell margin (adult shells), G – distance in mm between the free edge of two succeeding growth lamellae. Measurements and ratios put between brackets are less frequent.

Family Atrypidae Gill, 1871 Subfamily Atrypinae Gill, 1871 Genus *Costatrypa* Copper, 1973 *Costatrypa variabilis* (Godefroid, 1970) Fig. 3.

Atryparia? variabilis n. sp.; Godefroid 1970: pp. 98-104, pl. 5: 3; text-figs 6-10.

Description and remarks. — See Godefroid (1970).

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Vaulx, Boussu-en-Fagne, Frasnes and Nismes; ?Moulin Lienaux (Godefroid 1998), Grands Breux, Neuville Formations and basal part of the Matagne Formation (rare specimens at Frasnes), Late Devonian, middle–late Frasnian (?*Palmatolepis punctata*, *P. hassi–P. rhenana* Zones).



Fig. 3. Costatrypa variabilis (Godefroid, 1970), Frasnes, nameless quarry (Fr 1), Boussu-en-Fagne Member. A–E. IRScNB a10588 in ventral, dorsal, lateral, posterior and anterior views. All \times 1.5.

Subfamily Spinatrypinae Copper, 1978 Genus Spinatrypa Stainbrook, 1951 Spinatrypa tumuli sp. n. Figs 4A–F, 5A. Holotype: IRScNB a10593; complete shell illustrated in Fig. 4A–D. Type locality: Boussu-en-Fagne, cemetery quarry (Fig. 2F), southern flank of the Dinant Synclinorium, Ardenne, Belgium.



Fig. 4. A–F. Spinatrypa tumuli sp. n., Boussu-en-Fagne, cemetery quarry, Neuville Formation, reef level. A–D. Holotype IRScNB a10593 in ventral, dorsal, posterior and anterior views. E, F. IRScNB a10594 in ventral and dorsal views. G–K. Spinatrypina (Exatrypa) sp., Boussu-en-Fagne, cemetery quarry, Neuville Formation, reef level, IRScNB a10596 in ventral, dorsal, lateral, posterior and anterior views. L–P. Spinatrypina (*Spinatrypina*) cf. comitata Copper, 1967, Boussu-en Fagne, cemetery quarry, Neuville Formation, reef level, IRScNB a10595 in ventral, dorsal, lateral, posterior and anterior views. Q–R. Spinatrypina (*Exatrypa*) sp., Boussu-en-Fagne, cemetery quarry, Boussu-en-Fagne Member, IRScNB a10597 in ventral and dorsal views. A–P, × 1.5, Q–R, × 2.

Type horizon: Neuville Formation, Frasnian (Early Palmatolepis rhenana Zone).

Derivation of the name: From Latin *tumulus* – tomb, monument over grave; allusion to the cemetery of Boussu-en-Fagne close to the type locality.

Material. — 187 specimens of different size.



Fig. 5. Instraspecific variability of *Spinatrypa tumuli* sp. n. (A) and *Iowatrypa circuitionis* sp. n. (B). Scatter diagrams plotting W/L, T/W, Tp/Tb, and frequency diagrams. Dots with vertical dash represent 2 specimens. N – number of specimens.

Diagnosis. — A rather small, generally slightly dorsibiconvex *Spinatrypa* that differs from other species belonging to the genus by the lack of sulcus and fold, its rectimarginate or very weakly uniplicate anterior commissure and the size of its ribs (R-10 = 6-8).

Description. — Shell generally slightly dorsibiconvex, rarely equibiconvex or slightly ventribiconvex, longer than wide and with a roughly elliptical outline, as long as wide or slightly wider than long (Fig. 5A). In ventral view, lateral and anterior margins well rounded and shoulder lines clearly concave or indented. Hinge line shorter than the width. Anterior commissure generally rectimarginate or very weakly uniplicate.

Pedicle valve 3–4 times wider than thick in most specimens, rarely down to 2.7 or up to 5 times; in posterior view, strongly and irregularly convex or, in some specimens, rounded subtriangular; maximum thickness located near the mid-length (lateral profile of the valve more or less regularly curved) or a little posteriorly to it (in lateral view, curvature of valve a little more accentuated posteriorly than anteriorly). Tongue weakly developed on some specimens as a very low, dorsally directed deflection of the commissure; width of tongue corresponding to 55–65% of shell width. Interarea clearly visible, triangular, with subrounded lateral boundaries, orthocline and slightly concave. Beak pointed. Foramen submesothyridid. Deltidial plates partly joined.

Brachial valve 3-4 times wider than thick, rarely down to 2.3 or up to 5.4, rather regularly arched in posterior view.

Ornamentation undulose; R-10 generally 7, more rarely 6 or 8. Spines not observed. **Remarks.** — By its slight dorsibiconvexity, *S. tumuli* is close to species assigned to the subgenus *S.* (*Isospinatrypa*). It is distinguishable from *S. (I.) semiorbis* (Barrande, 1847) and *S. (I.) semiorbis latecostata* (Havlíček, 1956), the nearest species and subspecies, by its finer ribs only. Among Frasnian species, S. sp. A (*sensu* Ma 1998) belongs also to the *Isospinatrypa*-type spinatrypinids, but S. *tumuli* sp. n. is marked by roughly elliptical outline, less globose and rectimarginate shell.

S. (Plicspinatrypa) plicata (Rzhonsnitskaya, 1964) is a small species like S. tumuli sp. n., but the Belgian species displays subdivided ribs which are finer than those of the Russian species (see Rzhonsnitskaya et al. 1998). Like S. tumuli sp. n., also S. planosulcata (Webster, 1921) and S. thomsoni Day, 1998 are nearly biconvex to somewhat dorsibiconvex, but this species is smaller and finer-ribbed, and without sulcus and fold.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne; Neuville Formation (bioherm level 'F2j'), Late Devonian, late Frasnian (Early *Palmatolepis rhenana* Zone).

Genus Spinatrypina Rzhonsnitskaya, 1964 Spinatrypina (Spinatrypina) Rzhonsnitskaya, 1964 Spinatrypina (?Spinatrypina) cf. comitata Copper, 1967 Fig. 4L-P. Material. — Five complete, partly exfoliated shells.

Remarks. — The medium size of the shells (W = 17.7-20.8 mm; L = 16.2-19.0 mm), their more or less equibiconvex profile, their small orthocline to weakly apsacline interarea and the size of the ribs (R-10 = 9-11) bring the Belgian specimens nearer to S. (?S.) comitata Copper, 1967 (1967a: pp. 129-130, pl. 22: 4, 5). As this species is longer than wide or equidimensional (on the basis of the dimensions given in Copper's text-fig. 12, some shells and among them the holotype figured in pl. 22: 5a-d are wider than long) and biconvex-ventribiconvex, the Belgian specimens, which are wider than long (W/L = 1.05-1.1), are only tentatively assigned to S. (?S.) comitata.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne; Neuville Formation (bioherm level 'F2j'), Late Devonian, late Frasnian (Early *P. rhenana* Zone).

Spinatrypina (Exatrypa) Copper, 1967 *Spinatrypina (Exatrypa)* sp. B. Fig. 4G–K.

Material. — Eleven shells.

Description. — Medium sized (maximum W = 23 mm; maximum L = 17.5 mm), wider than long (W/L = 1.1–1.3), dorsibiconvex (Tb/Tp = 1.3–1.6) shell. In ventral view outline roughly elliptical, interrupted by concave shoulder lines and by the sulcus (median part of the anterior margin excavated by the sulcus). Hinge line corresponding to 78–84% of shell width. Anterior commissure markedly uniplicate.

Pedicle valve flat, 4.6 to 5.4 times wider than thick. In posterior view, upper surface of valve more or less regularly curved or rounded triangular; posterolaterally flattened. Maximum thickness slightly posterior to mid-length. Interarea apsacline to nearly orthocline, triangular, sharp-edged, slightly incurved. Sulcus generally marked in adult specimens, starting at mid-length or slightly anteriorly and corresponding to 50–60% of shell width; on some shells, sulcus less prominent, shallower and shorter. Tongue rounded, generally well developed and with a maximum width/height ratio of 2.5. Foramen submesothyridid. Deltidial plates partly joined.

Brachial valve 3.3–3.6 times wider than thick. In posterior view, upper surface of valve widely and regularly arched in its median part and flat or slightly concave in its lateral parts. Posterolateral regions, close to cardinal extremities, moderately concave. Fold poorly defined.

Ornamentation tubular-imbricate. Ribs bifurcating on both valve (intercalations not observed); R-10 = 7-8. G = 2–3 mm; on some well preserved areas, growth lamellae covered by fine concentric striation, particularly visible in rib troughs.

Remarks. — By their outline, their generally well marked sulcus, the number of ribs, these specimens are distinguishable from other *S.* (*Exatrypa*). However, as they are rather rare and poorly preserved, they are identified as *S.* (*E.*) sp.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne; Neuville Formation (bioherm level 'F2j'), Late Devonian, late Frasnian (Early *P. rhenana* Zone).

Spinatrypina (?Exatrypa) sp.

Fig. 4Q–R.

Material. — Twenty eight complete shells.

Remarks. — Most shells are from the shales of the Boussu-en-Fagne Member and the Neuville Formation between the two reefal levels exposed in the cemetery quarry at Boussu-en-Fagne. They are small sized (maximum W = 11.2 mm; maximum L = 11.5 mm), generally longer than wide (W/L = 0.96–0.99), rarely as wide as long, ventribiconvex (Tp/Tb = 1.1–1.8) or, more rarely, nearly equibiconvex. The ventribiconvexity, the well developed apsacline-orthocline interarea (considering the small size of the shells), the ribs (Nr = 18–25) with scarce bifurcations and intercalations, are characters of young individuals. These specimens are very similar to the shell figured by Copper (1967a: pl. 22: 4 a–d) and consequently could be considered as immature specimens of *S.* (*?S.*) *comitata.* However, the absence in the same levels of larger specimens of the same taxon may indicate that all these small specimens belong to a dwarf species. Because of this ambiguity we identify them only as *Spinatrypina* (*?Exatrypa*) sp.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne and Nismes; Grands Breux Formation (upper part of the shaly Boussu-en-Fagne Member), Neuville Formation (shales only), Late Devonian, middle-late Frasnian (?*P. hassi, P. jamieae* – Early *P. rhenana* Zones).

Subfamily Invertininae Copper & Chen, 1995

Genus Iowatrypa Copper, 1973

Iowatrypa rotundicollis Godefroid, 1994

Iowatrypa rotundicollis sp. n.; Godefroid 1994: pp. 86-92, pl. 1: 1-11; text-figs 2-5.

Description and remarks. — See Godefroid (1994).

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne; Neuville Formation (bioherm level 'F2j'), Late Devonian, late Frasnian (Early *P. rhenana* Zone).

Iowatrypa circuitionis sp. n.

Figs 5B, 6A-P, 7.

Holotype: IRScNB a10598; complete shell, illustrated in Fig. 6A-E.

Type locality: Frasnes, road Philippeville-Couvin (Fr 2) (Fig. 2B, G), southern flank of the Dinant Synclinorium, Ardenne, Belgium.

Type horizon: Neuville Formation, late Frasnian (Early *P. rhenana* Zone). The holotype has been collected at the type locality between 32 m and 37 m (Fig. 2G; see also Sartenaer 1974: pp. 7–8).

Derivation of the name: From Latin *circuitio* – turning, deviation; allusion to the location of the type locality along the by-pass road of Frasnes (road Philippeville–Couvin).

Material. --- Seventy five specimens.

Diagnosis. — A small sized, very finely ribbed species of *Iowatrypa* with a subquadratic or subrounded outline; fold and sulcus absent or weakly developed. Differs from *I. owenensis* (Webster, 1921) *sensu* Day (1998) in having a more equidimensional outline and lacking exposed interarea and minute deltidial plates. From *I. rotundicollis*, it is distinguishable by a nearly equidimensional, subquadratic or subrounded shell outline, as well as by a finer and more regular ornamentation (the ribs of *I. rotundicollis* are generally coarser in the posterior part of the shell than in the anterior).

Description. — Shell rather small, more or less equidimensional, ventribiconvex or more rarely nearly planoconvex (Fig. 5B). Hinge line corresponding to 74–92% of shell width. In ventral view, outline roughly quadratic or more rounded with anterior and lateral margins corresponding to a little more than half an ellipse; in some, better(?) preserved shells, cardinal extremities very shortly mucronate. Shoulder lines markedly concave or indented. Anterior commissure rectimarginate or slightly uniplicate.

Pedicle valve strongly arched, with a width/thickness ratio varying from 2.0 to 3.9; in posterior view more or less regularly convex; in lateral view, more curved posteriorly than anteriorly.



Fig. 6. A–J. *lowatrypa circuitionis* sp. n., Frasnes, Philippeville-Couvin road section (Fr 2), 32–37 m, Neuville Formation. A–E. Holotype IRScNB a10598 in ventral, dorsal, lateral, posterior and anterior views. F–J. IRScNB a10599 in ventral, dorsal, lateral, posterior and anterior views. K–P. *lowatrypa circuitionis* sp. n., Boussu-en-Fagne, cemetery quarry, bed 40, Neuville Formation. K–M. IRScNB a10601 in ventral, dorsal and posterior views. N–P. IRScNB a10602 in ventral, dorsal and posterior views. Q–U. *lowatrypa* cf. *circuitionis* sp. n., IRScNB a10605 in ventral, dorsal, lateral, posterior and anterior views, Frasnes, road Philippeville-Couvin (Fr 2), 22–32 m, Neuville Formation. All \times 2.

Posterolateral regions with upper surface slightly concave. Sulcus absent or weakly developed near anterior margin; when present, sulcus corresponding to a flattening rather than a depression of the upper valve surface. In some specimens, median part of anterior commissure undulated by very weak deflection directed dorsally, but not a tongue. Umbo strongly inflated; no visible interarea; beak incurved, in contact with dorsal umbo and pierced by post-apical foramen.

Thickest brachial values 3 times wider than thick, in nearly plano-convex specimens, up to 9 times. Value more or less regularly arched or with a variably flat or even slightly concave peripheral region located in commissural plane (post mortem deformation?); in some specimens, brachial value flat. Fold absent or present close the anterior margin and then very low, flat topped and unsharply delimited.

Imbricate ornamentation poorly preserved. Ribs very fine [R-10 = 24-26(28)], bifurcating on pedicle valve, bifurcating and intercalating on brachial valve. On some specimens, free edge of growth lamellae very slightly upturned; G not exceeding 1 mm; growth lamellae more crowded near anterior and lateral margins.



Fig. 7. *Iowatrypa circuitionis* sp. n., IRScNB a10603, Frasnes, road Philippeville-Couvin (Fr 2), 32–37 m, Neuville Formation. Transverse serial sections. Numbers refer to distances in mm from the top of the ventral umbo. Scale bar 1 mm.

Internal characters of pedicle and brachial valves (Fig. 7) corresponding to those of *Iowatrypa* rotundicollis, described by Godefroid (1994: pp. 90–91) and of *I. owenensis*, illustrated by Copper & Chen (1995: fig. 3). However, it is worth noting here that all our specimens have a strongly

incurved pedicle beak in contact with the dorsal umbo and do not display the interarea and minute deltidial plates of *I. owenensis* as figured by Copper & Chen (1995: fig. 4).

Remarks. — From Anatrypa timanica Markovskii, 1955 in Mikriukov (1955) and Anatrypa timanica var. markovskii Lyashenko, 1959, a species and a variety assigned by Copper (1973: p. 495) to Iowatrypa, I. circuitionis is distinguished by its more or less equidimensional outline and its more accentuated ventribiconvexity. Moreover, the brachial valve of the Russian species and variety displays a median depression, a characteristic absent in the Belgian species. Atrypa [= Iowatrypa] deflecta Warren, 1928 (in Warren & Stelck 1956: pl. 16: 7–10) is clearly less ventribiconvex and displays a different outline and a less inflated ventral umbo. I. circuitionis sp. n. differs from the small and finely ribbed Russian species I. keranica Yudina 1997, in its slightly transverse, better rounded outline and its more strongly and regularly curved (in posterior and anterior views) pedicle valve (see also Rzhonsnitskaya et al. 1998).

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Vaulx, Boussu-en-Fagne, Frasnes (Fr 2) and Nismes; Neuville Formation, Late Devonian, late Frasnian (Early *P. rhenana* Zone).

Iowatrypa cf. circuitionis sp. n.

Fig. 6Q-U.

Remarks. — Six shells from the Neuville Formation at Vaulx and Frasnes (Fr 2) display the same fine ribs and the strong ventribiconvexity as *I. circuitionis*, but differ by their wider than long outline and consequently their longer hinge line, in their more developed posterolateral regions with concave upper surface and their weakly marked sulcus near the anterior margin.

Waiotrypa Baliński, 1997

?Waiotrypa pluvia sp. n.

Figs 5C, 8-9.

Holotype: IRScNB a10606, complete shell, illustrated in Fig. 8A-E.

Type locality: Frasnes, road Philippeville-Couvin (Fr 2) (Fig. 2B, G), southern flank of the Dinant Synclinorium, Ardenne, Belgium.

Type horizon: Neuville Formation, late Frasnian (Early *P. rhenana* Zone). The holotype has been collected at the type locality between 32 m and 37 m (Fig. 2G; see also Sartenaer 1974: pp. 7–8).

Derivation of the name: Latin *pluvius* – rainy. Most specimens of this species have been collected in the type locality during a very rainy field day.

Material. — Ninety seven specimens including complete shells and isolated valves.

Diagnosis. — Wider than long, very slightly ventribiconvex species of *?Waiotrypa* which is distinguishable from *W. sulcicarina* Baliński, 1997 by its pedicle valve without low median fold and angular transverse profile and by its brachial valve without sulcus, paired with less important interarea.

Description. — Shell not exceeding 18.2 mm long and 19.6 mm wide, wider than long [W/L = (1.03)1.11-1.16(1.27)], generally slightly ventribiconvex, or equibiconvex (Tp/Tb = 1-1.6; see Fig. 5C). Maximum width seemingly located slightly anterior to hinge line. In ventral view outline of the shell varying from more or less semi-elliptic to rounded subquadratic. Shoulder lines clearly indented. Anterior commissure weakly uniplicate.

Pedicle valve regularly arched [W/Tp = 3.3-4(4.6)] with lateral profile gently convex. Posterolateral parts of valve slightly concave. Most specimens without sulcus but rarely very shallow sulcus. Tongue generally not well developed and corresponding to weak, rounded, poorly defined dorsal deflection; in some rare shells, better marked tongue with half elliptic to rounded trapezoidal outline. Interarea apsacline, reduced, slightly concave. Beak moderately incurved, not concealing median part of interarea. Foramen submesothyridid(?), deltidial plates partly joined.

Brachial valve more or less regularly convex transversally and longitudinally, 3.5–4.9 times wider than thick. Fold absent or weakly developed close to anterior commissure of shells with better developed tongue. Valve weakly concave near cardinal extremities.



Fig. 8. ?Waiotrypa pluvia sp. n. A–E. Holotype IRScNB a10606 in ventral, dorsal, lateral, posterior and anterior views, Frasnes, Philippeville-Couvin road section (Fr 2), 32–37 m, Neuville Formation. F–J. IRScNB a10607 in ventral, dorsal, lateral, posterior and anterior views, Vaulx, 70–74 m, Neuville Formation. K–M. IRScNB a10609 in ventral, dorsal and posterior views, Nismes, bed 79, Neuville Formation. All × 2.

Ornamentation tubular imbricate. Ribs with bifurcations and intercalations; R-10 = 18-20. On some specimens, ribs somewhat coarser posteriorly than anteriorly. Growth lamellae closely spaced: G below 0.5 mm, rarely slightly higher.

In pedicle valve, well developed pedicle collar and bilobed teeth with thick supports without cavities. Notch on interior side of dental supports for insertion of crura as pointed out by Copper & Chen (1995: pp. 255, 256) in *Invertina sinensis* (Kayser, 1883) and *Iowatrypa owenensis*. Zone for muscle attachment slightly raised (Fig. 9). Raised muscle platform with a narrow notothyrial pit in posterior part of brachial valve, progressively sloping downward in anterior direction. Well developed comb-like cardinal process present on the posterior part of the muscle platform and spreading over posterior part of inner socket ridges. Crural bases suberect. Feathered crura oriented laterally (Fig. 9). Jugal processes and spiralium not observed.

Remarks. — The species cannot be assigned without doubt to a known genus of the Invertininae. The ornamentation of *Falsatrypa* Havlíček, 1956 is different. The pedicle collar and the deltidial plates of *Kerpina* Struve, 1961 are of a different type (see Copper 1967b). *Pseudogruenewaldtia* Rzhonsnitskaya, 1964 and *Iowatrypa* Copper, 1963 are more ventribiconvex and have no pedicle collar. In *Invertina* Copper & Chen, 1995, there is no pedicle collar and the ribs are more tubular. Although the species does not display the carinate pedicle valve and the sulcate brachial valve of *Waiotrypa* Baliński, 1997, it is tentatively assigned to this genus on the basis of its transverse, slightly ventribiconvex (lenticular) shell.

The new species is close to the specimens determinated as *Atrypa kadzielniae* or *Anatrypa kadzielniae* (Gürich, 1896) by Nalivkin (1947: p. 103, pl. 23: 11–12; 1951: p. 19, pl. 4: 6,7) and Alekseeva (1962: pp. 144–145, pl. 8: 6). The Belgian specimens have a well developed pedicle



Fig. 9. ?*Waiotrypa pluvia* sp. n., IRScNB a10610, Frasnes, road Philippeville-Couvin (Fr 2), 32–37 m, Neuville Formation. Transverse serial sections. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars 1 mm.

collar which is absent in *A. kadzielniae* (Alekseeva 1962: fig. 67). By the size, outline and ventribiconvexity, *?Waiotrypa pluvia* sp. n. resembles also *Anatrypa timanica* Markovskii in Mikriukov (1955), and especially the variety *A. timanica markovskii* Lyashenko, 1959. It is

distinguishable from the Russian species and variety by the absence of median depression on its dorsal valve.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Vaulx, Frasnes (Fr 2) and Nismes; Neuville Formation, and the basal part of the Matagne Formation (rare specimens at Vaulx), Late Devonian, late Frasnian (Early *P. rhenana* Zone).

Subfamily Variatrypinae Copper, 1978 Genus *Desquamatia* Alekseeva, 1960 Subgenus *Desquamatia* (*Desquamatia*) Alekseeva, 1960 *Desquamatia* (*Desquamatia*) alticoliformis Rzhonsnitskaya, 1975 Figs 10B, 11A–G, 12.

Desquamatia (Desquamatia) alticoliformis sp. nov.; Rzhonsnitskaya, 1975: pp. 131–133, pl. 28: 10–13; fig. 41; Rzhonsnitskaya et al. 1998: pp. 318–320, figs 8–10, 11A–F.

Material. — Ninety eight complete shells.

Description. — Slightly dorsibiconvex or more rarely equibiconvex [Tb/Tp = (0.9)1.0-(1.4)1.7], generally wider than long (Fig. 10B), finely ribbed shell with, except posterior margin, a roughly elliptical outline. Shoulder lines gently concave. Hinge line corresponding to (65)72-80(84)% of shell width. In ventral view, anterior margin not or weakly excavated by sulcus. Anterior commissure uniplicate.

Pedicle valve (3.1)3.3-4.6(5.2) wider than thick; in posterior view, irregularly convex with flattened flanks; in lateral view, convexity more accentuated posteriorly than anteriorly; maximum thickness located slightly posterior to mid-length or, more rarely, at mid-length. In adult specimens, sulcus very shallow and laterally weakly delimited, starting imperceptibly at about anterior third or more anteriorly; width of sulcus corresponding to 63-72(77)% of shell width. Tongue moderately developed, low and widely rounded, not sharply delimited laterally and with distal part not oriented vertically to commissure plane. Interarea well exposed, clearly delimited laterally, curved, apsacline. Beak incurved but not projecting beyond commissural plane. Foramen submesothyrididid. Hollow deltidial plates, partly joined (Fig. 12).

Brachial valve 2.7–4(4.6) times wider than thick, in posterior view rather irregularly arched, with a convex median part and flattened flanks; in lateral profile, more arched posteriorly than anteriorly. Upper surface of valve weakly concave near cardinal extremities. Fold absent.

Ribs very fine, bifurcating on the pedicle valve, bifurcating and intercalating on brachial valve. In the centre, 22-24 ribs on 10 mm at 10 mm (unrolled length) from the beak, 20-22 ribs between 10 mm and 15 mm from the beak; 19-20 ribs more anteriorly. Growth lamellae not deflected, more or less regularly spaced: G = 1.5-2.0 mm. Frills present peripherally (see Fig. 12).

Pedicle valve with wide apical central cavity and less developed lateral cavities. No pedicle collar or pedicle layer observed. Teeth bilobed and supported by short and relatively thick dental plates (Fig. 12). Small notothyrial cavity with lamellar cardinal process, dental sockets with submedian ridge, crural bases bulbous posteriorly, anteriorly elongated and oriented ventrolaterally; crura feathered, oriented laterally, jugal processes disjunct, jugal plates hook-like, spiralia dorsomedial with 10–11 whorls.

Remarks. — Rzhonsnitskaya *et al.* (1998) assign the species *alticoliformis* to *Variatrypa* Copper, 1965. The Belgian specimens determinated as *alticoliformis* display the general shape, size and fine ribs of the Russian specimens. They have, however, more numerous growth lamellae and for this reason the species is considered as belonging to *Desquamatia (Desquamatia)*.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne and Frasnes (Fr 1); Grands Breux Formation (Boussu-en-Fagne Member) and Neuville Formation, Late Devonian, middle to late Frasnian (?*P. hassi, P. jamieae*, Early *P. rhenana* Zones). The first occurrence of the species is not yet known precisely.

Desquamatia (Desquamatia) quieta sp. n. Figs 11H–P, 13A, 14.



Fig. 10. Instraspecific variability of *?Waiotrypa pluvia* sp. n. (A) and *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975 (B). Scatter diagrams plotting W/L, T/W, Tp/Tb, and frequency diagrams. Dots in Fig. 11B: specimens from the reef (bioherm) level within the Neuville Formation; circles: specimens from the shales of the Boussu-en-Fagne Member. Dots with vertical dash represent two specimens. N – number of specimens.

Holotype: IRScNB a10614, complete shell, illustrated in Fig. 11H-L.

Type locality: Boussu-en-Fagne, cemetery quarry (Fig. 2B, F), southern flank of the Dinant Synclinorium, Ardenne, Belgium.

Type horizon: Grands Breux Formation (Boussu-en-Fagne Member), Frasnian (P. jamieae Zone).

Derivation of the name: From Latin *quietus* – peaceful; allusion to the peacefulness of the locus typicus, an abandoned quarry.

Material. — Fifty four specimens.

Diagnosis. — A species of *Desquamatia (Desquamatia)* wider than long, generally dorsibiconvex, with a subelliptic outline and very weak sulcus and fold. The species differs from the type species, *Atrypa (Desquamatia) khavae* Alekseeva, 1960, by its wider than long outline, generally more accentuated dorsibiconvexity and reduced interarea.

Description. — Shell dorsibiconvex or, more rarely, nearly equibiconvex [Tb/Tp = 1-1.8(2.1)] and wider than long (Fig. 13A). In ventral view, anterior and lateral margins outlining little more than half ellipse (anterior margin well rounded or only slightly excavated by very shallow sulcus); posterior margin with concave to weakly indented shoulder lines. Hinge line corresponding to (63)67–82% of shell width. Anterior commissure uniplicate.

Pedicle valve relatively low [W/Tp = (3.9)4.5-5.3(6)] and irregularly convex. In posterior view, central part convex, lateral parts approximately plane, forming low angle with commissural

Fig. 11. A–G. Desquamatia (Desquamatia) alticoliformis Rzhonsnitskaya, 1975, Boussu-en-Fagne, cemetery quarry. A–D. IRScNB a10611 in ventral, dorsal, lateral and anterior views, Boussu-en-Fagne Member. E–G. IRScNB a10612 in ventral, dorsal and posterior views, Neuville Formation, reef level. H–P. Desquamatia (Desquamatia) quieta sp. n., Boussu-en-Fagne, cemetery quarry, Boussu-en-Fagne Member.



H–L. Holotype IRScNB a10614 in ventral, dorsal, lateral, posterior and anterior views. M–P. IRScNB a10615 in ventral, dorsal, posterior and anterior views. Q–S. Atrypida indet., Nismes, railway section, beds 77 and 79, Neuville Formation. Q, R. IRScNB a10620 in ventral and dorsal views. S. IRScNB a10621 in dorsal view. A–P, \times 1.5; Q–S, \times 2.



Fig. 12. *Desquamatia (Desquamatia) alticoliformis* Rzhonsnitskaya, 1975, IRScNB a10613, Boussu-en-Fagne, cemetery quarry, Boussu-en-Fagne Member. Transverse serial sections. Numbers refer to distances in mm from the top of ventral umbo. In the drawings 3.2, 5.1, 5.2, and 5.3 only the jugal process and jugal plates are figured. Scale bars 1 mm.

plane. Maximum thickness located posteriorly to mid-length (in most specimens), rarely situated at about mid-length. Upper surface of posterolateral parts of valve weakly concave near cardinal extremities. Sulcus absent or very shallow, and poorly delimited close to anterior commissure; on



Fig. 13. Instraspecific variability of *Desquamatia (Desquamatia) quieta* sp. n. (A) and *Desquamatia (?Seratrypa) derelicta* sp. n. (B). Scatter diagrams plotting W/L, Tp/Tb, and frequency diagrams. Circles with vertical dash represent two specimens. N – number of specimens.

some shells, sulcus flattened. Tongue present, but variably developed, from low and corresponding to weak undulation of anterior commissure, to high and with half-elliptical outline; distal part of highest tongues oriented more or less perpendicular to commissural plane; tongue with width corresponding to (60)67–77% of shell width and, when well developed, with variable width/height ratio up to 1.8. Interarea reduced, apsacline at base, incurved; interarea of the largest specimens concealed by strongly curved beak. Foramen (?)submesothyridid; small deltidial plates.

Brachial valve, highly variable in thickness, 2.3 to 5.3 times wider than thick, transversely rather regularly arched. Maximum thickness located anterior to mid-length. Valve concave near cardinal extremities. Fold absent or only very weak, with imprecise boundaries; maximum length of fold not exceeding 1/3 of valve length.

Ribs tubular, interrupted by slightly deflected and more or less regularly spaced growth lamellae; ornamentation intermediate between tubular-imbricate and tubular lamellar. Number of ribs increasing mainly by bifurcations on both valves; intercalations much less frequent and only occurring on brachial valve; R-10 = 13-15. G varying from 2 mm to 3 mm; close to commissure, growth lamellae more closely spaced. No frills observed.

In brachial valve (Fig. 14), small cardinal process, dental sockets with submedian ridge. Crural bases oriented ventrally or ventromedially; feathered crura directed laterally; jugal processes disjunct with hook-like jugal plates; spiralium with 11–12 whorls.

Remarks. — The new species is marked off from *D*. (*D*.) *zonataeformis* (Alekseeva, 1962) by its more transverse outline and reduced interarea. *Desquamatia* (*Desquamatia*) *quieta* sp. n. is slightly more transverse than *D*. (*D*.) *alticoliformis* and its ribs are coarser. It is distinguishable from *D*. (*D*.) *schroeteri* Copper, 1967 by its more transverse (more elliptical) outline and by its coarser ribs.



Fig. 14. *Desquamatia (Desquamatia) quieta* sp. n., IRScNB a10616, Boussu-en-Fagne, cemetery quarry, Boussu-en-Fagne Member. Transverse serial sections. Numbers refer to distances in mm from the top of the ventral umbo. In the drawings 4.9, 6.1 and 6.3 only the jugal processes and the jugal plates are figured. Scale bars 1 mm.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne and Frasnes (Fr 1); Grands Breux Formation (Boussu-en-Fagne Member) and Neuville Formation (with exception of the enclosed reef mounds), Late Devonian, middle to late Frasnian (*P. jamieae*, Early *P. rhenana* Zones).

Subgenus Desquamatia (Seratrypa) Copper, 1967 Desquamatia (?Seratrypa) derelicta sp. n. Figs 13B, 15, 16.

Holotype: IRScNB a10617, complete shell, illustrated in Fig. 15A-E.

Type locality: Boussu-en-Fagne, cemetery quarry (Fig. 2B, F), southern flank of the Dinant Synclinorium, Ardenne, Belgium.

Type horizon: Neuville Formation, late Frasnian (Early P. rhenana Zone).

Derivation of name: Latin derelictus, abandoned; the type locality is an abandoned quarry.

Material. - About 300 hundred specimens.

Diagnosis. — A species of *Desquamatia* (?*Seratrypa*) characterized by medium sized, more or less equidimensional shell with well rounded anterior and lateral margins; sulcus and fold absent or very weakly developed. It differs from *D*. (?*S.*) *suppinguis* Godefroid & Jacobs, 1986 by its clearly weaker dorsibiconvexity, and from *D*. (*S.*) *frasniensis* Godefroid, 1970 by its smaller size and its outline [*D.* (*S.*) *frasniensis* is generally wider than long]. *D*. (?*S.*) *derelicta* is marked off from *D*. (*S.*) *orbiculata* Godefroid & Jacobs, 1986 by its less circular outline and coarser ribs.

Description. — Dorsibiconvex [Tb/Tp = 1.1-1.7(2.3)], slightly wider than long, as wide as long, rarely longer than wide shell (Fig. 13B). Hinge line corresponding to (64)66–79(85)% of shell width.



Fig. 15. Desquamatia (?Seratrypa) derelicta sp. n., Boussu-en-Fagne, cemetery quarry, Neuville Formation, reef level. A-E. Holotype IRScNB a10617 in ventral, dorsal, lateral, posterior and anterior views. F-J. IRScNB a10618 in ventral, dorsal, lateral, posterior and anterior views. $All \times 1.5$.



Fig. 16. *Desquamatia* (*?Seratrypa*) *derelicta* sp. n., IRScNB a10619, Boussu-en-Fagne, cemetery quarry, reef (bioherm) level within the Neuville Formation. Transverse serial sections. Numbers refer to distances in mm from the top of the ventral umbo. Scale bars 1 mm.

In ventral view, anterior and lateral margins well rounded (anterior margin lacking sulcus), corresponding to a little more than half ellipse or circle; shoulder lines clearly concave to indented. Anterior commissure moderately to very weakly uniplicate. Pedicle valve (3.2)3.4–4.1(4.7) times wider than thick; in posterior view, irregularly arched, broadly convex, and flanks nearly plane; maximum thickness located posterior to mid-length. Sulcus absent or only very weak, shallow and imprecisely delimited. Tongue generally present, but variably developed, from very low to more accentuated (highest tongue 2.1 times wider than thick), nearly semi-elliptic undulation; width of tongue, and of sulcus (when present), corresponding to (50)57–69%(74?) of shell width; tongue distally never oriented vertically to commissural plane. Interarea very reduced, with its median part completely hidden by the strongly incurved beak (pierced by foramen?) in contact with dorsal umbo. Deltidial plates not observed.

Brachial valve more or less regularly curved transversally and longitudinally, (1.8)2–3.2 times wider than thick. Fold absent or barely marked.

Ornamentation (?)subtubular-sublamellar (exfoliated specimens). Ribs bifurcating on pedicle valve, bifurcating and intercalating on brachial valve; 10–12 ribs on 10 mm in median part. G not known; one specimen with long frills.

Posterior pedicle valve thick shelled. Thickened floor of apical cavity with narrow median groove. Pedicle layer present. Bilobed teeth with thick support, lacking cavities (Fig. 16). Brachtal valve thick shelled posteriorly. Cardinal process minute in notothyrial pit. Crural bases suberect. Crura oriented laterally, with inner edge inserted into ventral valve notch. Jugal processes disjunct. Jugal plates not observed. Spiralium with 7–8 whorls. Relatively thick median crest dividing muscle field (Fig. 16).

Remarks. — The shell of *Desquamatia* (?*Seratrypa*) *derelicta* sp. n. is thicker than shell of *D*. (*S.*) *pectinata*, the type species of the subgenus. The median groove in the posterior part of the floor of the pedicle valve and the strongly developed median crest in the brachial valve of *D*. (?*S.*) *derelicta* sp. n. are absent in *D*. (*S.*) *pectinata*. The lateral cavities present in *D*. (*S.*) *pectinata* (see Copper 1967a: fig. 15) are not developed in *D*. (?*S.*) *derelicta*. In addition, *D*. (?*S.*) *derelicta* is smaller than *D*. (*S.*) *pectinata* and its ribs are coarser, at least as compared to the finely ribbed shells of the last species. For these reasons, the species is questionably assigned to the subgenus *Seratrypa*.

Occurrence. — Belgium, Ardenne, southern flank of the Dinant Synclinorium, Boussu-en-Fagne, Nismes (rare specimens); Neuville Formation (reef level), Late Devonian, late Frasnian (Early *P. rhenana* Zone).

Atrypida indet.

Fig. 11Q-S.

Remarks. — Very small sized and rare atrypid brachiopods occur in the upper beds of the Neuville Formation at Frasnes (Fr 2) and Nismes (see Fig. 2G, H). They are distinguished by their size, wider than long outline, very flat shell and fine ribs. Their internal characters are presently unknown. They may possibly belong to a dwarf species.

Systematic position of Glassia drevermanni Maillieux, 1936

Maillieux (1936: p. 25) shortly described small smooth brachiopods (Fig. 17) from the late Frasnian Matagne Formation, as *Glassia drevermanni* nov. nom. Copper (1986a: p. 858) assigned this species tentatively to the lissatrypid genus *Peratos*. Belgian material comes from three localities: Couvin 6158 (51 specimens, from the cemetery quarry at Boussu-en-Fagne where the Matagne Formation is presently no more exposed), Couvin 8706 (to date, the specimens from this locality have not been recovered in the IRScNB collections) and Sautour 7571 (some embedded specimens on seven small shale slabs).

Serial sections in a specimen from Couvin 6158 partly display internal structures: a thick pedicle valve, not distinguishable dental plates and, in the brachial valve, a median septum and crura of a non-atrypid type (Fig. 18). These observations are confirmed by



Fig. 17. Immature shells of *Ryocarhynchus tumidus* (Kayser, 1872), originally described as *Glassia drevermanni* Maillieux, 1936, Boussu-en-Fagne, cemetery quarry, Matagne Formation (no longer exposed). A_1 - A_5 . IRScNB a10622, internal cast in ventral, dorsal, lateral, posterior and anterior views. B_1 - B_5 . IRScNB a10623, shell in ventral, dorsal, lateral, posterior and anterior views. C_1 - C_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 . IRScNB a10624, internal cast in ventral, dorsal, lateral, posterior and anterior views. A_1 - A_5 .

the examination of some internal molds (Fig. 17A₁–A₅, C₁–C₅). On the basis of these characters, we assign the Belgian material of '*Glassia drevermanni*' to rhynchonellid species *Ryocarhynchus tumidus* (Kayser, 1872), as representing immature specimens.

General survey of Frasnian atrypid brachiopods in the Philippeville Massif

A study of the atrypid faunas in the Philippeville Massif is in progress. However, available data are briefly discussed in order to analyse the extinction of atrypid brachiopods in an area with facies different from the southern flank of the Dinant Synclinorium. The Philippeville Massif is situated in the central part of the Dinant Synclinorium (Fig. 1). Frasnian lithostratigraphical units in the Philippeville Massif, described by Boulvain *et al.* (1993), differ from the lithological succession on the southern flank of the synclinorium by the development of the Les Valisettes Formation located between the Neuville and Matagne Formations (Fig. 2D, I).

The Les Valisettes Formation comprises some 100 m of shales with one intercalation of red and green nodular limestones and shales with nodules (see Appendix 1). Locally, reef lenticles, developing from the underlying Neuville Formation onwards, occur (Coen *et al.* 1977: pp. 328–330; Boulvain *et al.* 1993: pp. 21–22). In this paper, 9 m of black shales included in the top of the Les Valisettes Formation by Boulvain *et al.* (1993: p. 28) are assigned to the Matagne Formation, whose thickness is reduced in the Philippeville Massif.



Fig. 18. *Ryocarhynchus tumidus* (Kayser, 1872) (= *'Glassia drevermanni'* Maillieux, 1936), IRScNB a10625, Boussu-en-Fagne, cemetery quarry, Matagne Formation (no longer exposed). Transverse serial sections. Numbers refer to distances in mm from the top of the ventral umbo. Scale bar 1 mm.

Atrypid brachiopods are numerous in the Neuville and Les Valisettes formations in the new railway cut at Neuville (Fig. 2H, I). The fauna of the Neuville Formation includes *Costatrypa* sp., *?Spinatrypina* sp. and a finely ribbed *Desquamatia* close or similar to *D*. (*D*.) alticoliformis of the southern border. The fauna of the Les Valisettes Formation comes from nodular limestones and shales of the middle part and includes two undescribed species: *Costatrypa* sp. (a species different from *C. variabilis*) and

?Waiotrypa sp. (distinct from *?W. pluvia* sp. n.). The Atrypida disappear at the top of the middle unit, 9 m below the base of the Matagne Formation.

Stratigraphical and ecological summary

Stratigraphical distribution. — On the southern flank of the Dinant Synclinorium, *Spinatrypa tumuli* sp. n., *Spinatrypina* (?*Spinatrypina*) cf. *comitata*, *Spinatrypina* (*Exatrypa*) sp., *Spinatrypina* (?*E.*) sp., *Iowatrypa rotundicollis*, *Iowatrypa circuitionis* sp. n., *Desquamatia* (*Desquamatia*) alticoliformis, *Desquamatia* (*Desquamatia*) quieta sp. n., *D.* (?*Seratrypa*) derelicta sp. n. and Atrypida sp. indet. do not cross the Neuville/Matagne boundary, dated with conodonts as being in the Early *Palmatolepis rhenana* Zone (see Fig. 19). In the studied area, where the exact, total thickness of the Matagne Formation is not known, this boundary is situated at least 45–50 m below the F-F boundary.

In this same area, the most common species, *Costatrypa variabilis*, and *?Waiotrypa pluvia* sp. n. are the last atrypids to become extinct. Rare representatives of the both species are still present in the greenish shales at the base of the late Frasnian Matagne Formation. These last Frasnian atrypids disappear completely with the first occurrence of the blackish shales, a few meters above the Neuville/Matagne boundary (i.e., 3 m in the road Philippeville-Couvin road section at Frasnes, ca. 7 m in the Vaulx section).

In the Philippeville Massif, among the atrypid species occurring in the Neuville section (Fig. 2I), *Costatrypa* sp. and *?Waiotrypa* sp. cross the upper boundary of the Neuville Formation and are abundant in the Les Valisettes Formation. These two species disappear 9 m below the first occurrence of the blackish shales of the Matagne Formation.

Ecological remarks. — Spinatrypa tumuli sp. n., Spinatrypina (?Spinatrypina) cf. comitata, Spinatrypina (Exatrypa) sp., Iowatrypa rotundicollis, and Desquamatia (?Seratrypa) derelicta sp. n., were living exclusively in a bioherm environment. In the cemetery quarry at Boussu-en-Fagne, numerous specimens are present in reef limestones intercalated in the Neuville Formation. Fewer shells of the last species are from the Neuville Formation at Nismes where reef slope facies is developed. To date, these species have not been found in the Neuville Formation when reefs are absent. Desquamatia (Desquamatia) alticoliformis is present in shaly and reefal environments, but gives marked preference to the reefs.

Spinatrypina (?Exatrypa) sp., Iowatrypa circuitionis sp. n., ?Waiotrypa pluvia sp. n., Desquamatia (Desquamatia) quieta sp. n., and Atrypida indet. occur in shales and bedded limestones beds of the Boussu-en-Fagne Member and/or of the Neuville Formation. The most favorable conditions for their development seem to be near reefs. All these species, except D. (D.) quieta sp. n., are small-sized.

Costatrypa variabilis, is particularly abundant in the shales between the top of the Lion Member and the base of the unnamed reef level within the Neuville Formation. In the cemetery quarry (also in the nameless quarry), *Costatrypa* forms lumachelle accumulations of uneven thickness (2.70 m, beds 6 to 10, in the western part of the quarry; 1.80 m, beds 6 to 12, in the eastern part of the quarry) above the basal, coral-rich beds (beds 2–5) topping the biohermal Lion Member. Specimens are preserved as complete shells,



Fig. 19. Distribution of the atrypid taxa in upper part of the Frasnes Group in the Vaulx-Nismes area (southern flank of the Dinant Synclinorium). Conodonts zones are according to Bultynck (1993: fig. 5). Explanations: GIV. – Givetian, FAM. – Famennian, SDS – standard Devonian stages, r – occurrence in reef lenticles, *M. – Mesotaxis, P. – Palmatolepis, Po. – Polygnathus.*

some of them with their frills. In the cemetery quarry at Boussu-en-Fagne, they form a continuous coquina level, although some variations may occur within it: the concentration of shells is slightly greater in the western than in the eastern wall of the cemetery quarry, suggesting weak shell reworking. In inter-reef environments, i.e. in the Frasnes by-pass road and railway sections (the latter not described here), this *Costatrypa* level disappears completely and the genus is only represented by isolated shells.

Atrypid brachiopod extinction on the Ardenne shelf

On the southern flank of the Dinant Synclinorium, the extinction of the atrypid brachiopods evidently coincides with the onset of deposition of the greenish to blackish shales of the Matagne Formation (Fig. 19). This facies change indicates a significant deepening event over the Laurussian shelf, paired with expanding hypoxic-anoxic (Kellwasser-type) conditions (e.g., Johnson *et al.* 1985; Sandberg *et al.* 1992). Apparently, merely two species *Costatrypa variabilis* and *?Waiotrypa pluvia* sp. n., represented by very rare specimens, survived in the very lower part, i.e. in the 3–4 m of green shales above the base of the formation. In the absence of complete sections, the entire



Fig. 20. Stratigraphical range and extinction (thick black arrow) of the atrypid brachiopods in the upper part of the Frasnes Group on the southern border of the Dinant Synclinorium and in the Philippeville Massif, in respect to the first occurrence of guide conodont *Ancyrognathus asymmetricus*.

Matagne Formation has never been studied. However, up to now, none of the isolated outcrops in blackish Matagne Formation have delivered atrypid brachiopods. In the Philippeville-Couvin road section, where conodont data are available, the extinction of the Atrypida occurs below the first occurrence of *Ancyrognathus asymmetricus* Younquist, 1947 (see Appendix 1). In the Nismes section, the last Atrypida were collected in bed 79, which belongs to the Early *P. rhenana* conodont Zone (Helsen & Bultynck 1992: fig. 5). In the Neuville railway section, in the more northerly Philippeville Massif, the extinction of the Atrypida is a few meters below the lower boundary of the Matagne Formation. However, in this area, where the Les Valisettes Formation is developed, the thickness of the Matagne Shales is strongly reduced in comparison to the southern flank of the Dinant Synclinorium, and its lower boundary is located well above the first occurrence of *A. asymmetricus* (Late *P. rhenana* Zone).

As a result, the deepening event, responsible for the oxygen-depleted sedimentation of the Matagne Shales and for the regional extinction of the atrypid brachiopods on the Ardenne shelf, records later in the Philippeville Massif than in the southern flank of the Dinant Synclinorium (Fig. 20). A more precise description of the late Frasnian atrypid faunas of the Philippeville Massif and an analysis of the extinction of the atrypids on the eastern and northern flanks of the Dinant Synclinorium and in the Namur Synclinorium (see Fig. 1) where the Frasnian facies differ is in preparation.

Acknowledgments

Thanks are due to Dr. Paul Sartenaer for making available the atrypid brachiopods collected by him in the outcrop of the road Philippeville-Couvin at Frasnes.

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Appendix 1

Studied sections (see Fig. 2):

Vaulx (Fig. 2A, E). — The outcrop at Vaulx is located on the eastern side of a short blind road. Considering the weathering of the rocks and their poor exposure, measurements and descriptions of the lithostratigraphical units and the fossiliferous beds may include some imprecisions. The following lithostratigraphical units are recognized, from the south-west to north-east.

Grands Breux Formation (0-9 m; observed thickness ca. 4 m) Weathered, greenish and brownish shales of the Boussu-en-Fagne Member with rare limestone nodules and a poor brachiopod fauna (unit 1).

Neuville Formation (9-82 m; thickness ca. 32 m)

- ca. 6 m of nodular, argillaceous and fossiliferous limestone with shaly intercalations (unit 2);
- ca. 4.5 m of fine, weathered, brownish shales with rare limestone nodules (unit 3);
- ca. 1.5 m corresponding to a hiatus (unit 4);
- ca. 20 m of argillaceous, nodular limestone beds and shales with limestone nodules. Fossils include few corals, brachiopods and goniatites in the very lower part (unit 5).

Matagne Formation (from 82 m to the end of the outcrop; observed thickness ca. 35 m)

- ca. 7 m of fine, greenish to brownish shales with some limestone nodules and a quite rich brachiopod fauna (unit 6);
- ca. 4 m corresponding to a hiatus;

- ca. 24 m of fine, dark grey to blackish shales with rare limestone nodules and abundant *Buchiola*. According to the debris on the slopes of the exposure, dark grey limestone beds occur in the basal part. Although goniatites have not been found, these beds may correspond to the goniatite-rich beds observed at the base of the Matagne Formation at Frasnes (Fr 2) and Nismes (see further) (unit 7).

Boussu-en-Fagne, cemetery quarry (Fig. 2B, F). — Described by Lecompte (1960: pp. 70–71, pl. 7: 1) and Coen-Aubert (1992; 1994: p. 28, fig. 6) among others, the most complete section in the cemetery quarry is exposed on the eastern wall of the quarry and along the access-path.

Grands Breux Formation

- Lion Member. Approximately 23 m of massif, locally biodetrital, light-grey limestone with stromatopores and corals are exposed in the quarry (bed 1). They represent the upper part of the reefal unit.
- Boussu-en-Fagne Member (beds 2-33; thickness 15 m). In this section, only the upper part of the member is developed. Minor lithological subdivisions of the shales overlying the Lion Member are recognized from the base to the top:

Beds 2–5. Thin beds of crinoidal limestone and shaly intercalations are followed by shales with limestone lenses and nodules. This basal part is particularly rich in corals.

Beds 6–12. Subnodular, locally crinoidal limestone beds alternate with shales including limestone lenses and nodules. Corals become less important while the atrypid brachiopods, mostly belonging to *Costatrypa variabilis* (Godefroid, 1970) are numerous and, in some beds, extremely abundant. On the western wall of the quarry and the access-path, beds 6 to 10 contain a huge accumulation of shells of this species.

Beds 13–33. Although the lithology is similar to that of the preceding beds, the fauna is not marked by a predominance of a certain group. Corals and brachiopods are of equal importance. Among the brachiopods, however, atrypids remain the most important group.

Neuville Formation (beds 34-43; thickness 13.5 m)

Beds 34-40. The succession starts with an alternation of shales and light grey, argillaceous or crinoidal limestones with reddish colored spots.

Beds 41–43. Fine, massif, grey and locally reddish limestones with corals and brachiopods represent a reef level. *Ancyrognathus triangularis* is reported by Coen-Aubert (1994: p. 28) at the base of the 'petit bioherme de marbre rouge' which corresponds to beds 41–43.

Matagne Formation

According to Maillieux (1936: p. 8; 'gisement fossilifère Pl. Couvin: 6158d'), Matagne shales with *Glassia drevermanni* were exposed north of the cemetery quarry. Unfortunately, at present-day, the outcrop has completely vanished.

Frasnes, small nameless quarry (Fr 1) (Fig. 2B). — The top of the Lion Member, the Boussuen-Fagne Member and the base of the Neuville Formation are exposed in this outcrop (Coen-Aubert 1994: pp. 27–28, figs 2, 5, 6; = outcrop MC-1980-13).

Frasnes, road Philippeville-Couvin or by-pass road of Frasnes (Fr 2) (Fig. 2B, G). — In this outcrop, Sartenaer (1974: pp. 7–8) recognized six lithological units. Providing an overview of the fauna, he also defined more precisely the *Caryorhynchus tumidus* Zone (now *Ryocarhynchus tumidus*).

Grands Breux Formation

- Boussu-en-Fagne Member (unit 1 of Sartenaer; observed thickness 5 m).

N e u ville Formation (units 2 and 3 of Sartenaer; thickness 29 m). The base of the formation corresponds to the base of unit 2 in which thin, purple-red limestone beds occur.

Matagne Formation (unit 4, 5 and 6 of Sartenaer; observed thickness 42 m). The lower boundary of the formation corresponds to the base of the first bed displaying a 'Matagne' aspect (Sartenaer 1974). The Formation is made up by fine, greenish, bluish and blackish shales and starts with 3 m of fine greenish shales. Limestone lenses and nodules are more common in the lower 13–14 m than in the upper 28–29 m. Large cephalopods are present in the limestone lenses between 2.40 m and 3.50 m above the base of the unit. According to Mouravieff (in Sartenaer 1974: pp. 6–7), *Ancyrognathus triangularis* and *A. asymmetricus* occur for the first time, respectively at 2.40 m and 3.60 m above the base of the Formation.

Nismes, railway section (Fig. 2C, H). — This outcrop is described by Helsen & Bultynck (1992) who gave the general inventory of the megafauna and studied of the conodonts.

Neuville, railway section (Fig. 2D, I). — The new railway section at Neuville was described in several papers (Bouckaert *et al.* 1970; Mouravieff 1974: p. 7; Coen & Coen-Aubert 1974: pp. 2–6; Coen 1978: fig. 3 partim, 'Neuville, nouv. tranchée'; Boulvain *et al.* 1993: pp. 27–28). From the south-west to the north-east (from the base to the top), the following units are exposed (distances refer to hectometric posts along the railway):

Philippeville Formation (103/560–103/478; observed thickness ca. 5 m). Massive limestones with numerous stromatoporoids forming the core of a low anticline.

Neuville Formation (103/478–103/440; thickness 16 m). Nodular limestones and rare shaly intercalations with or without limestone nodules. Within this unit, *Ancyrognathus triangularis* is reported (Mouravieff 1974; p. 7).

Les Valisettes Formation (103/440-103/167; thickness ca. 100 m).

- some 50 m of fine shales with, at the base, 4 thin limestone beds, yielding Ancyrognathus asymmetricus (see Mouravieff 1974);
- 34 m of red and green nodular limestones and shales with limestone nodules;
- 9 m of green shales.

Matagne Formation (103/167-103/154; thickness 9 m): Fine, black shales.

North-west of 103/154 and beyond a faulted zone of greenish shales, a locally tectonically sequence between 103/148 and 103/019 is attributed to a part of the Les Valisettes Formation. It is followed by the Matagne Formation (103/019–103/005). The succession exposed between 103/154 and 103/005 is considered herein as a repetition, with some minor lithological variations, of the rocks exposed south-east of 103/154. Alternatively, it is possible that this succession forms a part of a continuous sedimentary succession with the beds exposed south-easterly; in that case, the Les Valisettes Formation includes an intercalation of fine black shales and would be more than 100 m thick.