Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 131(1): 213-239. **March 2025**
DOI: https://doi.org/10.54103/2039-4942/26428

ORDOVICIAN (DARRIWILIAN–KATIAN) BRACHIOPODS FROM THE SOUTHEASTERN MARGIN OF AVALONIA (CONDROZ INLIER, BELGIUM)

YVES CANDELA[1], DAVID A.T. HARPER[2] & BERNARD MOTTEQUIN[3]

[1*]Department of Natural Sciences, National Museums Collection Centre, 242 West Granton Road, Edinburgh EH5 1JA, United Kingdom.
E-mail: y.candela@nms.ac.uk
[2]Department of Earth Sciences, Durham University, Durham DH1 3LE, United Kingdom.
[3]D.O. Terre et Histoire de la Vie, Institut royal des Sciences naturelles de Belgique, rue Vautier 29, B-1000 Brussels, Belgium.
*Corresponding author.

Associate Editor: Lucia Angiolini.

To cite this article: Candela Y., Harper D.A.T. & Mottequin B. (2025) - Ordovician (Darriwilian–Katian) brachiopods from the southeastern margin of Avalonia (Condroz Inlier, Belgium). *Rivista Italiana di Paleontologia e Stratigrafia,* 131(1): 213-239.

Keywords: Brachiopoda; taxonomy; Ordovician; Avalonia; Belgium; palaeobiogeography.

Abstract. A low-diversity, relatively well-preserved brachiopod fauna is documented in detail for the first time from the Sandbian–Katian (Upper Ordovician) siliciclastic rocks of the Oxhe Inlier (Belgium), i.e. a small Caledonian inlier included in the Condroz Inlier, whereas some preliminary data are also presented for the Darriwilian–Sandbian (Middle–Upper Ordovician) brachiopods of the central part of the Condroz Inlier (Huy and Vitrival-Bruyère formations), Belgium. The brachiopods from the Oxhe Inlier (Oxhe Formation) were collected from several localities in the Oxhe Inlier where they are associated with trilobites, ostracods, molluscs, echinoderms and machaeridians. The Oxhe Formation yielded one lingulate, one craniate, two strophomenates and three rhynchonellates, while the Huy Formation yielded two lingulates to which are added one strophomenate and two rhynchonellates from the Vitrival-Bruyère Formation (Sart-Bernard Member). These taxa are assigned with variable degrees of confidence to existing taxa or described under open nomenclature. An age range of Darriwilian to Katian is confirmed. Multivariate numerical analyses (Nonmetric Multidimensional Scaling together with Network Analysis) indicate close comparison with other Avalonian faunas. Moreover, the combination of taxa suggests habitats in deeper-water environments around the Avalonian continent.

Introduction

Ordovician rocks are known from six regions in Belgium, each characterized by their own distinctive, essentially siliciclastic succession (from north to south): the Brabant Massif, the Condroz Inlier, and the Stavelot–Venn, Serpont, Rocroi and Givonne massifs (Fig. 1). These sediments were deposited on the southeastern margin of the Avalonian microcontinent that moved from high to low latitudes during the Ordovician, from the Tremadocian to Katian (e.g. Cocks & Torsvik 2002, 2021; Verniers et al. 2002) indicated by the faunal and sedimentological changes manifest during this time span, notably in Belgium (e.g. Owens & Servais 2007).

To date, only the Brabant and the Stavelot–Venn massifs and the Condroz Inlier have yielded Ordovician linguliformean and/or rhynchonelli-

Received: September 23, 2024; accepted: February 24, 2025

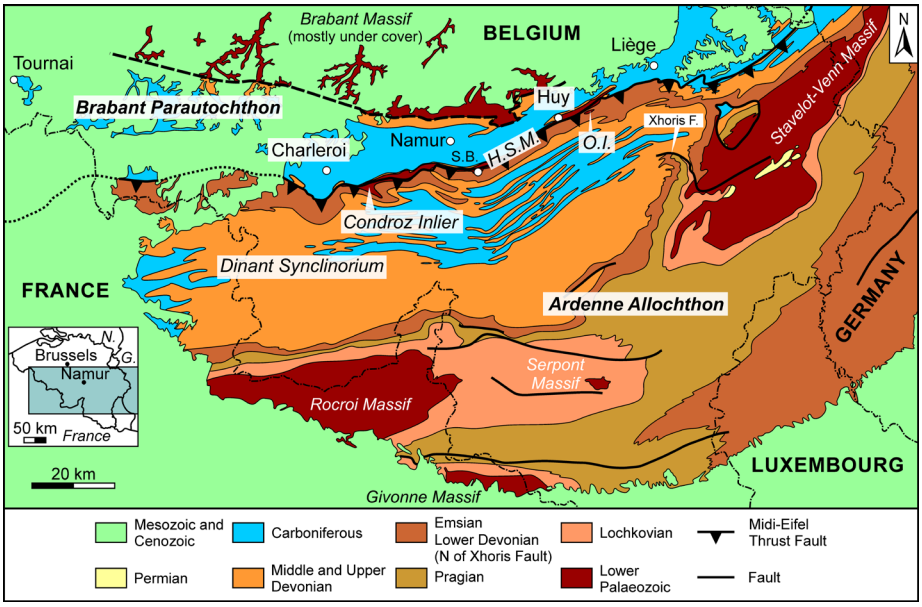

Fig. 1 - Geological map of Belgium with indication of the localities cited in the text (modified from de Béthune (1954) and Mottequin (2021)). Abbreviations: F., fault; H.S.M., Haine – Sambre – Meuse Overturned Thrust sheets (see Belanger et al. 2012); O.I., Oxhe Inlier; S.B., Sart-Bernard. Abbreviations in the insert: G., Germany; N. The Netherlands.

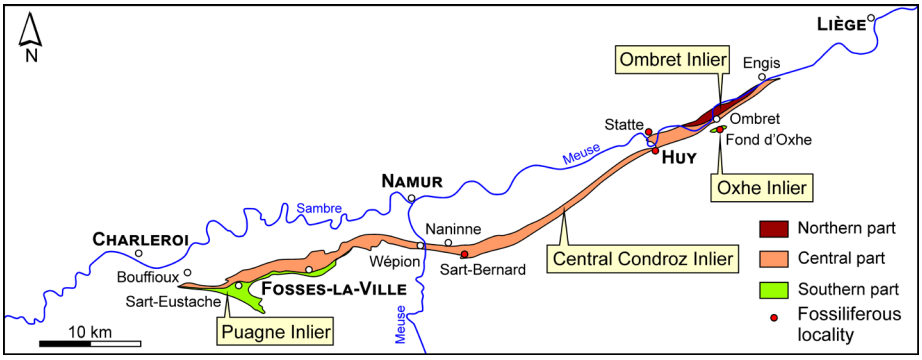

Fig. 2 - Simplified map of the four tectonic zones of the Condroz Inlier (modified from Vanmeirhaeghe (2006); the numerous faults have been removed).

formean brachiopods. Although they have been reported on many occasions in the literature, the number of systematic studies can be counted on the fingers of two hands (Malaise 1873; Maillieux 1939; Sheehan 1987; Candela et al. 2021; Candela & Mottequin 2022, 2023). Therefore, the Ordovician palaeogeographic evolution of Avalonia, requires further detailed study of the long-ignored Belgian brachiopod faunas and, in this case, those from the Darriwilian–Katian interval of the Condroz Inlier, which are almost exclusively known only from faunal lists (Dewalque 1894; Destinez 1896; Forir 1899; Maillieux 1939).

Besides a discussion of the few brachiopods available from the Darriwilian (Huy Formation) and from the Katian (Sart-Bernard Member of the Vitrival-Bruyère Formation) in the central part of the Condroz Inlier, this paper aims especially at providing the first systematic study of the upper Sandbian–lower Katian linguliformean and rhynchonelliformean brachiopods of the Oxhe Formation (Oxhe Inlier), which have been known since Dewalque (1894), but that remain undocumented. The restricted macrofauna from this lithostratigraphic unit is also briefly investigated.

Geological setting and fauna

The Condroz Inlier (central part)

The Condroz Inlier is a band of Ordovician–Silurian sedimentary rocks orientated WSW–ENE, c. 65 km long, 0.5–4 km wide, cropping out between Bouffioulx and Engis (Owens & Servais 2007) (Fig. 2). It is developed along the Midi Overthrust Fault that marks the boundary between the Ardenne Allochthon to the south and the Haine-Sambre-Meuse Overturned Thrust sheets to the north (Belanger et al. 2012). The Central Condroz Inlier corresponds to the main part of the inlier and is bordered by three minor ones (Verniers et al. 2002) (Fig. 2). The Oxhe Inlier is one of them, located between Huy and Liège, south of Ombret village (Figs 2, 3). The Ordovician lithostratigraphy of the Condroz In-

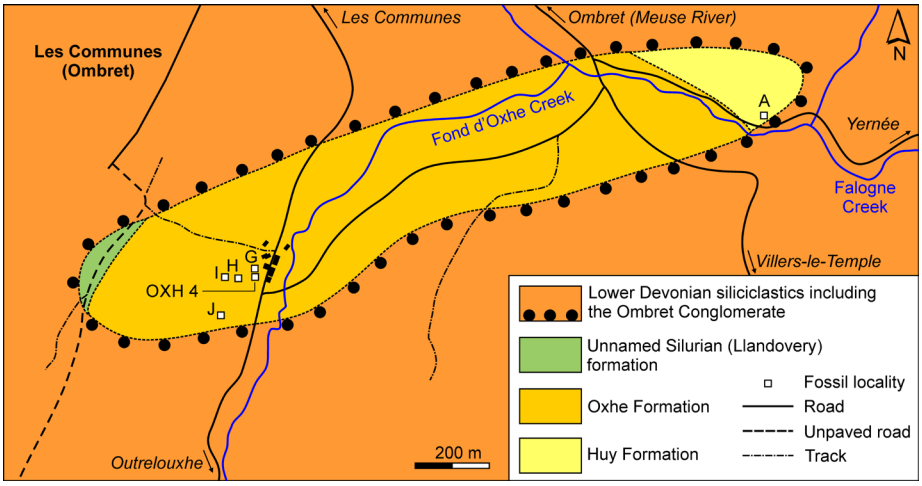

Fig. 3 - Simplified geological map of the Fond d'Oxhe area, locating the Ordovico-Silurian rocks of the Oxhe Inlier (adapted from Dean 1991) with indication of the fossiliferous localities cited in the text.

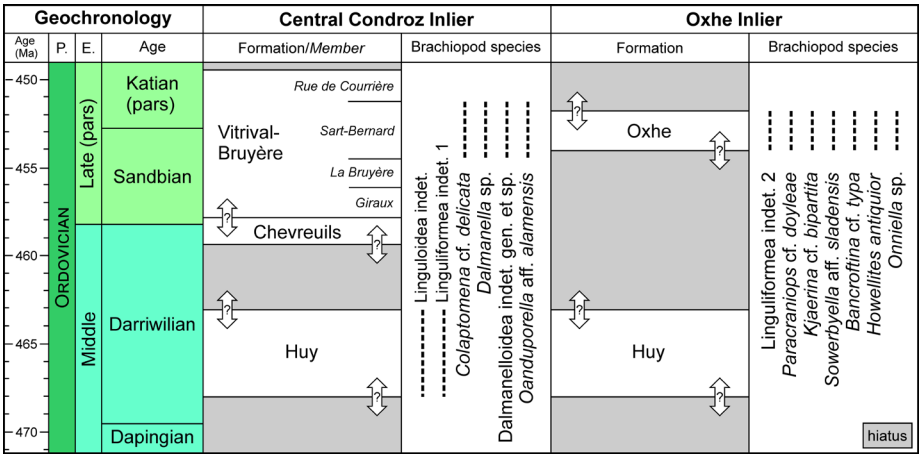

Fig. 4 - Geochronology and lithostratigraphy of the Central Condroz and Oxhe inliers (see Figs. 1–2) with the distribution of the brachiopods recognized within the Huy, Oxhe and Vitrival-Bruyère (adapted from Vanmeirhaeghe (2006), Mortier et al. (2024), Herbosch et al. in Lefebvre et al. (2023) and Mortier et al. (2024)). The double arrows indicate boundaries between formations of uncertain age. Abbreviations: E., Epoch; P., Period.

lier was summarized by Verniers et al. (2002) and modified by Vanmeirhaeghe (2006, 2007a, b) (see also Owens & Servais 2007 and Herbosch et al. in Lefebvre et al. 2023). Correlations with contemporaneous siliciclastic successions of the Brabant and Stavelot–Venn massifs were proposed by Verniers et al. (2002) and Herbosch & Verniers (2014).

In the Central Condroz Inlier, the material investigated here is from two lithostratigraphic units, namely the Huy and Vitrival-Bruyère (Sart-Bernard Member) formations (Fig. 4). The Huy Formation consists of dark grey or black, micaceous shales with intercalations of grey siltstones and few sandstones (Vanmeirhaeghe 2007a). Graptolites revised by Servais & Maletz (1992) belongs to the lower *Didymograptus artus* Zone (middle Darriwilian; lower Llanvirn and lower Abereiddian of the British series and stages; see Fortey et al. 1995, 2000). The Sart-Bernard Member of the Vitrival-Bruyère Formation consists of grey micaceous siltstones including some beds of micaceous sandstone of similar colour (Vanmeirhaeghe 2007a). On the basis of their studies on graptolites, trilobites and chitinozoans, Servais & Maletz (1992), Owens & Servais (2007) and Vanmeirhaeghe (2007a, b) proposed a late Darriwilian (late Llanvirn) to early Katian (Cheneyan) age for this member, noting that a Sandbian–early Katian age is the most probable (middle Caradoc age).

Localities in the Condroz Inlier

Huy-Statte. As noted by Servais & Maletz (1992: fig. 3), the sections of the Huy Formation, which are located between the train stations of Statte (to the NW) and Huy (formerly Huy-Nord) (to the ENE) and separated by a tunnel, yielded a considerable number of graptolites (Malaise 1873, 1887a, b, 1888a, b, c, 1890; Cluysenaar & Lecrenier 1887; Lecrenier 1887), but they are no longer accessible due to changes in the position of the latter station and the route of the Namur–Liège railway line. Today, the Huy Formation is very poorly exposed on both sides of the railway tunnel. Linguliformeans were reported from these sections by Cluysenaar &

Lecrenier (1887), Malaise (1900a, 1901a,b) and Servais & Maletz (1992) but none of these specimens have been traced in the palaeontological collections of Liège University and the Royal Belgian Institute of Natural Sciences (RBINS).

Sart-Bernard (Naninne 1 in the archives of the RBINS). This section displays the dark shales of the Huy Formation and is located along the northern flank of the trench of the Namur–Luxembourg railway line, about ten meters NNW of the kilometer post 72.4, in proximity of the Sart-Bernard halt (Maillieux 1939, Servais & Maletz 1992: fig. 4). The graptolites and trilobites from this overgrown exposure were reviewed by Servais & Maletz (1992) and Owens & Servais (2007), respectively. Based on the graptolites, the former authors placed this outcrop in the *Didymograptus artus* Biozone. Brachiopods are scarce, only one linguliformean was available for study.

Sart-Bernard (Naninne 2a in the archives of the RBINS). This outcrop is situated to the ESE of the Sart-Bernard railway stop, also along the aforementioned railway line (Servais & Maletz 1992: fig. 4) but was not precisely located by Maillieux (1939). Servais & Maletz (1992), Vanmeirhaeghe (2006, 2007a) and Owens & Servais (2007) discussed in detail the graptolites, chitinozoans and trilobites, respectively. It belongs to the Sart-Bernard Member of the Vitrival-Bruyère Formation. Maillieux (1939) illustrated an orthide identified as *Pionodema redux* (Barrande) from this locality, but the specimen has not been traced in the palaeontological collections of the Royal Belgian Institute of Natural Sciences. Restricted rhynchonelliformean material (associated with bryozoans), collected by E. Poty, was studied herein.

Sart-Bernard 72270a. As for Naninne 1, this section showing the Huy Formation is located W of the eponymous halt (Servais & Maletz 1992: fig. 4). Few linguliformeans, which were investigated in this paper, were collected by Servais & Maletz (1992), who reported the presence of graptolites and trilobites.

The Oxhe Inlier

The Oxhe Inlier (Figs 2, 3) poorly exposes Ordovician and Silurian siliciclastics and is bordered by conglomerates (Ombret Conglomerate) of the basalmost part of the Fooz Formation of Early Devonian age (Lochkovian, Gedinnian of the traditional subdivision) (Michot 1934, 1969; Dean 1991; Mottequin et al. 2021; Denayer & Mottequin 2024). Three lithostratigraphic units are recognized: the Huy and Oxhe formations and an unnamed Silurian unit. The Huy Formation is poorly exposed at its eastern extremity (Dean's (1991) locality A, Fig. 3) where it corresponds to dark grey micaceous mudstones, often soft and finely laminated yielding notably trilobites, linguliformean brachiopods and graptolites (Malaise 1900a, 1901a; Dean 1991; Owens & Servais 2007; Servais & Maletz 1992). The last group of fossils indicate an early Llanvirn *Didymograptus artus* graptolite Biozone age for the Huy Formation in the Oxhe Inlier (Owens & Servais 2007). The specimens of linguliformeans have not been traced. The Oxhe Formation occupies the largest part of the Oxhe inlier. The most common lithologies encountered are micaceous mudstones and siltstones, sometimes cleaved, with thin, lenticular beds of fine-grained sandstone developed in the mudstones and generally thin, lenticular commonly decalcified bands with a shelly fauna (e.g. brachiopods and trilobites) according to Dean (1991) (see also Michot 1954, 1957). Following Dean (1991), all the rock types are blue-grey when fresh but brown or brown-green on weathering. Based on the trilobite fauna (see below), including essentially *Broeggerolithus nicholsoni* (Reed, 1910) (Pl. 1, fig. 8-10) and *Brongniartella minor minor* (Salter, 1852) (Pl. 1, fig. 11-14), Dean (1991) attributed the Oxhe Formation to the Longvillian Substage of the Burrellian Stage of the British Caradoc Series (Sandbian) (see Fortey et al. 1995), thus a late Sandbian to earliest Katian age was suggested by Mortier et al. (2024). An unnamed Silurian lithostratigraphic unit was noted by Michot (1969) at the western extremity of the Oxhe Inlier that corresponds to thin beds of micaceous, fine-grained sandstone with interbedded mudstone and laminated siltstone that yielded acritarchs indicating a Llandovery age, but perhaps excluding the Rhuddanian (Martin in Dean 1991).

Localities in the Oxhe Inlier

Martin (1969, fig. 14) and especially Dean (1991, figs. 2-3) provided information on the most important fossiliferous localities in the Fond d'Oxhe area, where the main outcrops are scattered on

the steep, wooded left bank of the Fond d'Oxhe Creek (Fig. 3), which is a minor tributary of the Meuse River (Fig. 2). Most of the specimens were collected by these two authors, who carried out several field surveys in the 1970s to collect acritarchs and trilobites.

Fossiliferous localities (Fig. 3) registered by a letter (e.g. locality G) follows Dean's (1991) terminology and corresponds to F. Martin's unpublished survey notes housed at the RBINS: localities G (outcrop FM-77-2-4), H (outcrop FM-77-2-3), I (outcrop FM-77-2-2) and J (outcrop FM-77-2-1). The locality OXH-4 in Martin (1969) correspond to her outcrops FM-75-3a and FM-75-3b (Fig. 3). Other specimens included in this study (see below) are from historical collections and unfortunately devoid of precise geographic indication; consequently, they are only referred to the Fond d'Oxhe, without more information. Nevertheless, it is obvious that most of them probably come from the outcrops of the left bank of the Fond d'Oxhe Creek.

Fauna of the Oxhe Formation

Brachiopods. Forir (1899) compiled the lists of brachiopods from the Oxhe Formation provided by Dewalque (1894), Destinez (1896) and Malaise (1894a, 1899); they would be later discussed by Malaise (1900a, 1901a). Only the four following brachiopod species were mentioned, but not illustrated: *Leptaena sericea* Sowerby, *Orthis budleighensis* Davidson (= *O.* aff. *redux* Barrande sensu Malaise 1894a, 1899, 1900a), *O. testudinaria* Dalman and *Chonetes tenuissimestriata* M'Coy. Maillieux (1926, 1933) only cited *Dalmanella redux* whereas Dean (1991) reported the genera *Sowerbyella* and *Dalmanella*. The original and revised identifications are given in Table 1.

Echinoderms. Dean (1991) noted the presence of pelmatozoan echinoderm fragments that have been identified by B. Lefebvre (pers. com., June 2022) as pentameric stems of crinoids (Pl. 1, fig. 1), but they remain impossible to determine further due to the absence of calices and/or arms.

Machaeridians. Some poorly-preserved external moulds of isolated plates (Pl. 1, fig. 2) were identified as *Lepidocoleus* by Dean (1991). The ventro-dorsal curve of the plate, convex then concave (here shown as mould material, therefore the opposite curve) indicates that Dean's (1991) identification is plausible, albeit the plate being broken along the accreting and non-accreting margins.

Former identifications	This work
Leptaena sericea	*Sowerbyella* aff. *sladensis*
Orthis budleighensis (=*O.* aff. *redux*)	*Bancroftina* cf. *typa*
O. testudinaria	*Howellites antiquior*
Chonetes tenuissimestriata	*Sowerbyella* aff. *sladensis*

Tab. 1 - Former (Dewalque 1894; Destinez 1896; Malaise 1894a; 1899; Forir 1899) and new identifications of the rhynchonelliformean brachiopod species recognised in the Oxhe Formation (Oxhe Inlier, Belgium).

Molluscs. The Oxhe Formation yielded a few bivalves (Pl. 1, figs. 3-4) and gastropods and some shells of orthoconic cephalopods (*Orthoceras* in former faunal lists; Pl. 1, figs. 6-7), (e.g. Dewalque 1894; Forir 1899; Malaise 1901a; Maillieux 1926). Dean (1991) reported two distorted specimens doubtfully assigned to the bellerophontid genus *Sinuites* (Pl. 1, fig. 5).

Ostracods. Ostracods were reported from the Oxhe Formation notably by Dewalque (1894), Malaise (1894a,b, 1899, 1900a), Forir (1899), and Dean (1991). Jones (in Dewalque, 1894) assigned them to the genus *Beyrichia* and Schallreuter et al. (2000) described the predominant species as a representative of the ctenonotellid genus *Harperopsis* (*H. ohensis*), which is also known from Wales and Northern England (Jones & Siveter 1983; Siveter 2009). Furthermore, Schallreuter et al. (2000) also recognized one or two 'smooth' undescribed forms that are rare. Internal moulds of dissociated valves of the palaeocope *Harperopsis*, which is inferred to be benthic (Siveter 1984), is locally abundant. A specimen (single valve?) is also known from the interior (apical end) of an orthoconic cephalopod shell (Pl. 1, fig. 7), but it cannot be confirmed that ostracods colonized the post-mortem mollusc shell.

Trilobites. Before the first systematic study by Dean (1991), these were cited by Dewalque (1894), Malaise (1894a, 1899, 1900a,b, 1901a,b, 1911), Forir (1899), and Lohest & Forir (1900). The most common species *Broeggerolithus nicholsoni* (Reed, 1910) and *Brongniartella minor minor* are re-illustrated here (Pl. 1, figs. 8-10 and Pl. 1, figs 11-14, respectively). According to Owens & Servais (2007), the trilobite fauna from the Oxhe Formation is characteristic of the eastern part of Avalonia as it also occurs in northern England, North Wales, south Shropshire, and southeastern Ireland, but it displays some links with Baltica due to the presence of *Broeggerolithus nicholsoni* in Sweden (Bowdler-Hicks et al. 2002).

Material and methods

The bulk of the studied material was collected by T. Dean and F. Martin in the 1970s and is stored at the Royal Belgian Institute of Natural Sciences (prefixed RBINS), where it is complemented by specimens belonging to the C. Malaise and R. Roncart collections belonging to the same institution. Malaise's collections were acquired by the RBINS in July 1902 (I.G. 6887 with I.G. meaning *Inventaire général*) and April 1930 (I.G. 9340; 14 years after his death) whereas the material collected by R. Roncart (I.G. 13394) were donated to the RBINS in December 1941. In addition, material from the palaeontological collections of the University of Liège (prefixed PA.ULg.; G. Dewalque's (Fond d'Oxhe) and E. Poty's (Sart-Bernard) collections), was also included in the present study.

The material was coated with ammonium chloride and photographed using an Olympus OM-D E-M10 Mark II digital camera, equipped with the Olympus M.Zuiko Digital ED 60 mm macro lens. Specimens selected for scanning electron microscopy were imaged with an ESEM FEI Quanta 200, under low vacuum; specimens were uncoated.

Brachiopods from the Oxhe Formation exclusively occur as internal moulds (except for the only linguliformean available), most commonly of disarticulated valves and are frequently deformed by tectonics. A few articulated moulds of rhynchonelliformeans have been recovered.

Further comments on the brachiopod faunas

Huy Formation

Brachiopods were first reported by Lecrenier (1887) at Statte, who noted, besides the presence of numerous graptolites (see above), the discovery of three species of lingulides at Huy, but they have never been published (see Malaise 1887a) and the material has not been traced in the palaeontological collections of the Liège University. Other reports of lingulides ('*Lingula* sp.') in the Huy Formation in the Central Condroz Inlier and in the Oxhe Inlier are those of Malaise (1900a, 1901a, 1901b, 1911) and Dean (1991) but remain unrevised as the specimens were not traced in the RBINS collections. Consequently, further field work is needed to assess the brachiopod diversity of this unit.

Vitrival-Bruyère Formation (Sart-Bernard Member)

In addition to the orthide illustrated by Maillieux (1939), some well-preserved internal moulds of strophomenides and orthides are described below. The data presented here should be regarded as preliminary pending further collections of material.

Oxhe Formation

The brachiopod fauna from the Oxhe Formation is of low diversity including essentially orthides and strophomenides with the former, clearly predominant. The presence of Lingulida and Craniopsida is purely anecdotal; there is currently no evidence for their occurrence. Brachiopods are mainly preserved as disarticulated valves, and ventral valves largely predominate over dorsal ones; a few articulated orthide specimens have been also recovered. As already pointed out by Schallreuter et al. (2000), brachiopods are preserved in coquinas that reflect the influence of tempestites in the formation of these beds. One external mould of a dorsal valve of *Kjaerina* cf. *bipartita* (Pl. 2, fig. 9) displays a scar from the repaired shell at a short distance from the anterior margin, which is marked by the deviation of the radial ornamentation. Such a scar may reflect an unsuccessful predatory attack and is slightly older than those recognized in the Upper Ordovician succession of the Brabant Massif by Candela & Mottequin (2023).

Plate 1

Echinoderm (1), machaeridian (2), molluscs (3-7), ostracod (7) and trilobites (8-14) from the Oxhe Formation, Oxhe Inlier, Belgium.

1) RBINS a14108 (I.G. 6887), external moulds of pentameric stems of crinoids.
2) RBINS a14109, a machaeridian plate (SEM) possibly *Lepidocoleus* sp., locality I in Dean (1991; FM-77-2-2).
3) RBINS a14110 (I.G. 6887), internal mould of an isolated valve of an unidentified bivalve.
4) RBINS a14111 (I.G. 6887), right valve of an articulated unidentified bivalve.
5) RBINS a14112 (I.G. 9340), flattened internal mould of an unidentified bellerophontid (possibly *Sinuites* according to Dean, 1991).
6) RBINS a14113 (I.G. 6887), incomplete internal mould of an orthoconic cephalopod.
7) RBINS a14114 (I.G. 6887), internal mould of the ostracod *Harperopsis ohensis* Schallreuter et al., 2000 enclosed in the apical portion of an internal mould of an orthoconic cephalopod.
8-10) *Broeggerolithus nicholsoni* (Reed, 1910); 8a-b) RBINS a2988 (I.G. 6887), internal mould of a cranidium in dorsal, lateral and dorsal views (Dean, 1991, pl. 1, fig. 8); 9a-b) RBINS a2985 (I.G. 6887), internal mould of cephalon in dorsal and left oblique views (Dean, 1991, pl. 1, fig. 4); 3a-c) RBINS a2991 (I.G. 6887), incomplete internal mould of a pygidium in dorsal, lateral and posterior views (Dean, 1991, pl. 1, fig. 14).
11-14) *Brongniartella minor minor* (Salter, 1852); 11) RBINS a14115, incomplete internal mould of a cranidium, locality OXH 4 in Martin (1969, FM-75-3a); 12a-c) RBINS a3002 (I.G. 9340), pygidium preserved mainly as internal mould in dorsal, lateral and posterior views (Dean, 1991, pl. 2, fig. 9); 13) RBINS a14116, internal mould of a pygidium with partly preserved thorax in dorsal view, locality J in Dean (1991; FM-77-1); 14a-b) RBINS a2999 (I.G. 6887), almost complete internal mould of a pygidium and part of enrolled thorax in dorsal, lateral and posterior (Dean, 1991, pl. 2, fig. 6).

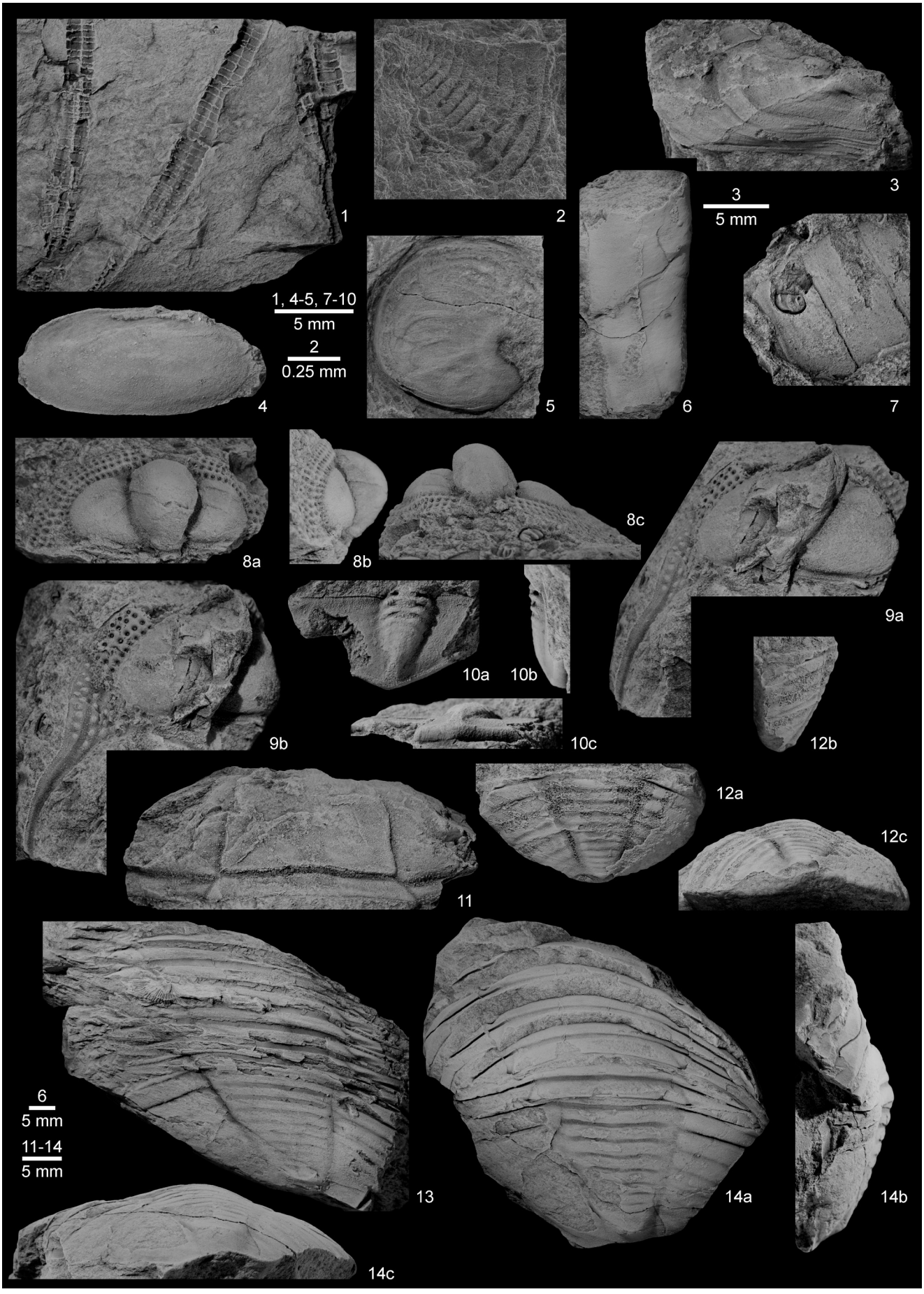
1
2
3
3
5 mm
1, 4-5, 7-10
5 mm
2
0.25 mm
4
5
6
7
8a
8b
8c
9a
9b
10a
10b
10c
12a
12b
12c
11
6
5 mm
11-14
5 mm
13
14a
14b
14c

Plate 1

Stratigraphic summary

The geographic and stratigraphic distributions of the Ordovician brachiopod species recognized herein in the Central Condroz and Oxhe inliers are presented in Figure 4.

Systematic palaeontology

Subphylum **LINGULIFORMEA** Williams et al., 1996
Class **LINGULATA** Gorjansky & Popov, 1985
Order **Lingulida** Waagen, 1885
Superfamily Linguloidea Menke, 1828

Linguloidea indet.

Pl. 2, fig. 1

1939 *Lingula* aff. *impar*; Maillieux, p. 4, 17, pl. 1, fig. 11.

Material: One external mould of an undifferentiated valve.

Remarks. Spe cimen RBINS a9758 was illustrated by Maillieux (1939, pl. 1, fig. 11) but has unfortunately not been traced in the RBINS collections: it is therefore considered lost. However, the box where this specimen was kept, also contains an incomplete external mould (of comparable size to the missing specimen) that might be the counterpart of the specimen described and figured by Maillieux (1939). The number '11' is also written in white paint on the external mould: this number corresponds to the figure number of the missing specimen in Maillieux (1939). It is nevertheless impossible to confirm this: the external mould is figured here for information. Maillieux (1939) tentatively assigned specimen RBINS a9758 to *Lingula* aff. *impar* based on its similarities with the Bohemian species *Lingula impar* described by Barrande (1879) from the Darriwilian of Santa Benigna (now Svatá Dobrotivá) based on the size, the outline and the ornamentation of the Belgian specimen. *Lingula impar* was designated by Havlíček (1980) as type species for the genus *Rafanoglossa* Havlíček, 1980 (see also Havlíček 1982 and Mergl 2002). Maillieux's (1939) identification cannot be validated here based on the paucity of the material originally collected and the subsequent loss of this material. The putative counterpart does not show any diagnostic features that could help with identification. Therefore, the specimen is best retained under open nomenclature, at the superfamily level.

Occurrence. Sart-Bernard (Naninne 1) (Figs. 1-2), Huy Formation (Fig. 4).

Linguliformea indet. 1

Pl. 2, fig. 2

? 1900a *Lingula* sp.; Malaise, p. 203.
? 1901b *Lingula* sp.; Malaise, p. 568
? 1900a *Lingula*; Malaise, p. 203.
? 1901a *Lingula* sp. [Arenig]; Malaise, p. 219.
1992 lingulid brachiopods, brachiopod fragments; Servais & Maletz, p. 269, pl. 2, fig. 1.

Material: Two poorly preserved moulds (RBINS a3385; Servais & Maletz 1992, pl. 2, fig. 1).

Description. External mould of undetermined valve; only concentric ornament (growth lines) are visible, numbering 42 per mm, intersected by wavy radial lines laterally on the valve surface. Interior of dorsal valve characterized by a broad median ridge broadening anteriorly, about 9% as wide as valve width and extending for 60% of valve length; anterior and lateral rim of the valve flattened; posterior end of the valve obscured by matrix.

Remarks. Both specimens display very few diagnostic features that could help identification. The posterior ends of the valves are broken and the presence of a median ridge indicates these may possibly be dorsal valves. These specimens are best retained under open nomenclature as Linguliformea indet. 1.

Occurrence. Sart-Bernard 72270a (Figs 1-2), Huy Formation (Fig. 4).

Linguliformea indet. 2

Pl. 2, fig. 3

Material: One incomplete undetermined valve.

Remarks. This specimen is impossible to identify more precisely than at the subphylum level. The fragment (about 5 mm by 3 mm in its longest and shortest, perpendicular axis) is simply characterized by a fine concentric ornament (growth lines), numbering 20 per mm. No comparison can be made with any other taxa.

Occurrence. Fond d'Oxhe (Figs. 1-3), Oxhe Formation (Fig. 4).

Subphylum **CRANIIFORMEA** Popov et al., 1993
Class **CRANIATA** Williams et al., 1996

Order **Craniopsida** Gorjansky & Popov, 1985
Superfamily Craniopsoidea Williams, 1963
Family Craniopsidae Williams, 1963

Genus *Paracraniops* Williams, 1963

Type species: *Craniops pararia* Williams, 1962, by original designation, from the Kiln Mudstones (Katian), Girvan, Scotland.

Paracraniops cf. ***doyleae*** Hurst, 1979a

Pl. 2, fig. 4

cf. 1979a *Paracraniops doyleae* Hurst, p. 227, figs. 64-69.
1986 *Paracraniops doyleae* Hurst; Popov & Pushkin, p. 18, figs 9, 10.

Material: One near complete dorsal internal mould (and counterpart).

Description. Valve suboval, 80% as wide as long, with narrow limbus, 5% as wide as valve; two elongated oval depressions situated postero-laterally possibly for insertion of oblique internal muscles.

Remarks. A single, damaged and poorly preserved valve is available. Nevertheless, some features (valve shape, limbus and oblique internal muscle impressions) indicate affinity with *Paracraniops*. The genus is common in the Ordovician around the Iapetus Ocean, in particular in marginal Laurentia (Williams 1962) and Avalonia (Williams, 1963, Hurst 1979a, Lockley 1980). The specimen from Belgium is similar to *P. doyleae* Hurst, 1979a from the Cheney Longville Formation (Katian) of Shropshire, England, based on the valve shape and outline and size of the limbus. *Paracraniops dolyleae* is also recorded from the lower Katian of Lithuania and Estonia (Popov & Pushkin 1986, p. 18). *Paracraniops glaber* Lockley, 1980 from the Allt Ddu Formation (upper Sandbian) in North Wales, and *P. pararius* (Williams, 1962) from the Kiln Mudstone Member (lower Katian), Craighead, SW Scotland, are more circular and with a wider limbus. More material requires study to validate the comparisons.

Occurrence. Fond d'Oxhe (Figs. 1-3), Oxhe Formation (Fig. 4).

Subphylum **RHYNCHONELLIFORMEA** Williams et al., 1996
Class **STROPHOMENATA** Williams et al., 1996
Order **Strophomenida** Öpik, 1934
Superfamily Plectambonitoidea Jones, 1928
Family Subfamily Rafinesquinidae Schuchert, 1893
Family Subfamily Rafinesquininae Schuchert, 1893

Genus *Colaptomena* Cooper, 1956

Type species: *Colaptomena leptostrophoidea* Cooper, 1956 by original designation, from the Martinsburg Formation (Katian), Virginia, USA.

Colaptomena cf. ***delicata*** Williams, 1974

Pl. 2, figs. 5-6

cf. 1974 *Rafinesquina delicata* Williams, p. 141, pl. 25, figs 6-13.
cf. 1978 *Rafinesquina delicata* Williams; Cocks, p. 110.
cf. 2008 *Colaptomena delicata* (Williams); Cocks, p. 51.

Material: One ventral valve, and a broken dorsal valve.

Description. Ventral valve gently convex, 73% as long as wide, cardinal angles perpendicular; maximum width posteriorly; anterior commissure rectimarginate. Ornamentation impressed on internal mould, consisting of unequal parvicostellae, with 7-8 costellae per mm at the 10 mm growth stage; 5 weaker costellae between two stronger costellae.

Interior with flabellate muscle scar, 88% as long as wide, extending anteriorly for 35% of valve length; muscle scar feebly impressed and not confined laterally and anteriorly by bounding ridges; dental plates short, widely divergent at right angle, extending anteriorly for 15% of valve length; interarea flat, apsacline extending for 8% of valve length; faint subperipheral rim extending for less than 10% of valve length.

Dorsal valve broken, estimated 77% as long as wide; valve appears very faintly concave with impression of median septum estimated to extend less than a third of valve length; adductor muscle scar faintly impressed.

Remarks. The genera *Rafinesquina* Hall & Clarke and *Colaptomena* Cooper are similar and usually separated by features in the dorsal valve. Nevertheless, these two specimens are assigned to the genus *Colaptomena* Cooper on the basis of the ventral valve being gently convex and possessing small dental plates orientated at right angles, rather than more obtuse as in *Rafinesquina*; and the dorsal valve is gently concave, with a shorter median septum and faint adductor scars. Moreover, this ventral valve appears similar to *Rafinesquina delicata* Williams, 1974 [reassigned to *Colaptomena* by Cocks 2008], described from the upper Darriwilian Meadowtown Formation

in Shropshire, England. It possesses similar unequiparvicostellate ornament, muscle scar, dental plates diverging at right angles and a faint subperipheral rim. However, the single valve cannot alone validate a species assignment and more material, especially dorsal valve interiors showing the cardinalia, is needed to identify this Belgian stock with confidence.

Occurrence. Sart-Bernard (Naninne 2a) (Figs. 1-2), Vitrival-Bruyère Formation (Sart-Bernard Member) (Fig. 4).

Genus *Kjaerina* Bancroft, 1929

Type species: *Kjaerina typa* Bancroft, 1929, by original designation, from the Cheney Longville Formation (Katian) of Burrell's Coppice, Cheney Longville, Shropshire, England.

Kjaerina cf. ***bipartita*** (Salter in Salter & Aveline, 1854)

Pl. 2, figs. 7-11; Fig. 5.1

cf. 1854 *Strophomena bipartita* Salter *in* Salter & Aveline, p. 74.
cf. 1929 *Kjaerina bipartita* (Salter) Bancroft, p. 52, pl. 1, fig. 14.
cf. 1978 *Kjaerina bipartita* (Salter); Cocks, p. 112.
cf. 1979a *Kjaerina bipartita* (Salter); Hurst, p. 284, figs. 467-476.
cf. 1994 *Kjaerina bipartita* (Salter); Rong & Cocks, pl. 3, figs. 3-5.
cf. 1996 *Kjaerina bipartita* (Salter); Harper & Wright, p. 88, pl. 14, figs. 6-8.

Material: Three ventral and three dorsal valves.

Description. Shell concavo-convex, semi oval, with cardinal angles acute; maximum width at hinge line; maximum convexity/concavity sagittally, with shell flattening laterally and posterolaterally; anterior commissure rectimarginate. Ornamentation parvicostellate with 5 costellae at the 10 mm growth stage; accentuated median costella; rugae developed laterally along the hinge line (on dorsal valves).

Ventral valve 65-70% as long as wide; ventral interior with dental plates, short, extending anteriorly for 10% of valve length and almost at right angles; interarea short, apsacline; ventral muscle scar weakly impressed, suboval and triangular, slightly longer than wide, extending anteriorly for 25% of valve length. Dorsal valve 55% as long as wide; dorsal interior characterized by delicate bifid cardinal process on slightly elevated cardinal platform, with subparallel, elongate flattened lobes; socket ridges slender, diverging at right angle; short but broad median septum originating from anterior end of cardinal platform; interarea flat, short and anacline.

Remarks. Cocks (2008) listed this species in his revised review of the British and Irish Lower Palaeozoic brachiopods and included all the *Kjaerina* species named by Bancroft (1929; 1945). Seven valid species of *Kjaerina*, and a species in open nomenclature, were reviewed. However, Cocks (2010) revised his previous assessment and due to the plasticity of the genus, decided to retain only five recognizable species (Cocks 2010, p. 1167). These species are, listed from the earlier to the later, *K. complanata* (J. de C. Sowerby, 1839), *K. jonesi* Bancroft, 1929, *K. hedstroemi* Bancroft, 1929, *K. bipartita* (Salter in Salter & Aveline, 1854) and *K. typa* Bancroft, 1929. The Belgian material is different from *K. jonesi* [= *K. horderleyensis* Bancroft, 1929; = *K. latericostata* Bancroft, 1929] and from *K. complanata* as these possess more circular shells, longer dental plates and larger cardinal process lobes. Moreover, *K. complanata* also lacks well pronounced a median costellae (Cocks 2010). The upper Sandbian *K. hedstroemi* is also different in its more circular shell, longer ventral muscle field and dental plates with respect to valve length, and less divergent dental plates (average 58°, see Cocks 2010). *Kjaerina typa* does not possess a pronounced median costella, but significantly differs from the Belgian sample in its geniculate shell and longer ventral muscle field (extending anteriorly for up to half valve length). The Belgian specimens are closer

---

Plate 2

1) Linguloidea indet., RBINS a9758, incomplete external mould of undetermined valve, from Naninne 1, Huy Formation (SEM).
2) Linguliformea indet. 1, RBINS a3385, dorsal valve interior, from Sart-Bernard, Huy Formation (SEM).
3) Linguliformea indet. 2, RBINS a14117, incomplete external mould of undetermined valve, from the Fond d'Oxhe (I.G. 6687), Oxhe Formation (SEM).
4a-b) *Paracraniops* cf. *doyleae* Hurst, 1979a, RBINS a14118 (I.G. 6887), external and internal moulds of dorsal valve, from the Fond d'Oxhe, Oxhe Formation (SEM).
5-6) *Colaptomena* cf. *delicata* Williams, 1974 from Sart-Bernard, Vitrival-Bruyère Formation (Sart-Bernard Member); 5a-c) PA.ULg.2024.09.06-1a, ventral valve interior and close up (SEM) of the muscle field and dental plates (artificial cast) in oblique lateral views; 6) PA.ULg.2024.09.06-1b, incomplete dorsal valve interior.
7-11) *Kjaerina* cf. *bipartita* (Salter in Salter & Aveline, 1854) from the Fond d'Oxhe, Oxhe Formation; 7a-b) PA.ULg.1482, ventral exterior and artificial cast; 8) PA.ULg.319, incomplete dorsal exterior; 9) PA.ULg.1479, dorsal exterior with reparation scar on the anterior part; 10) RBINS a14119, ventral interior, locality OXH 4 in Martin (1969; FM-75-3b); 11) RBINS a14120, ventral interior, locality OXH 4 in Martin (1969; FM-75-3b).

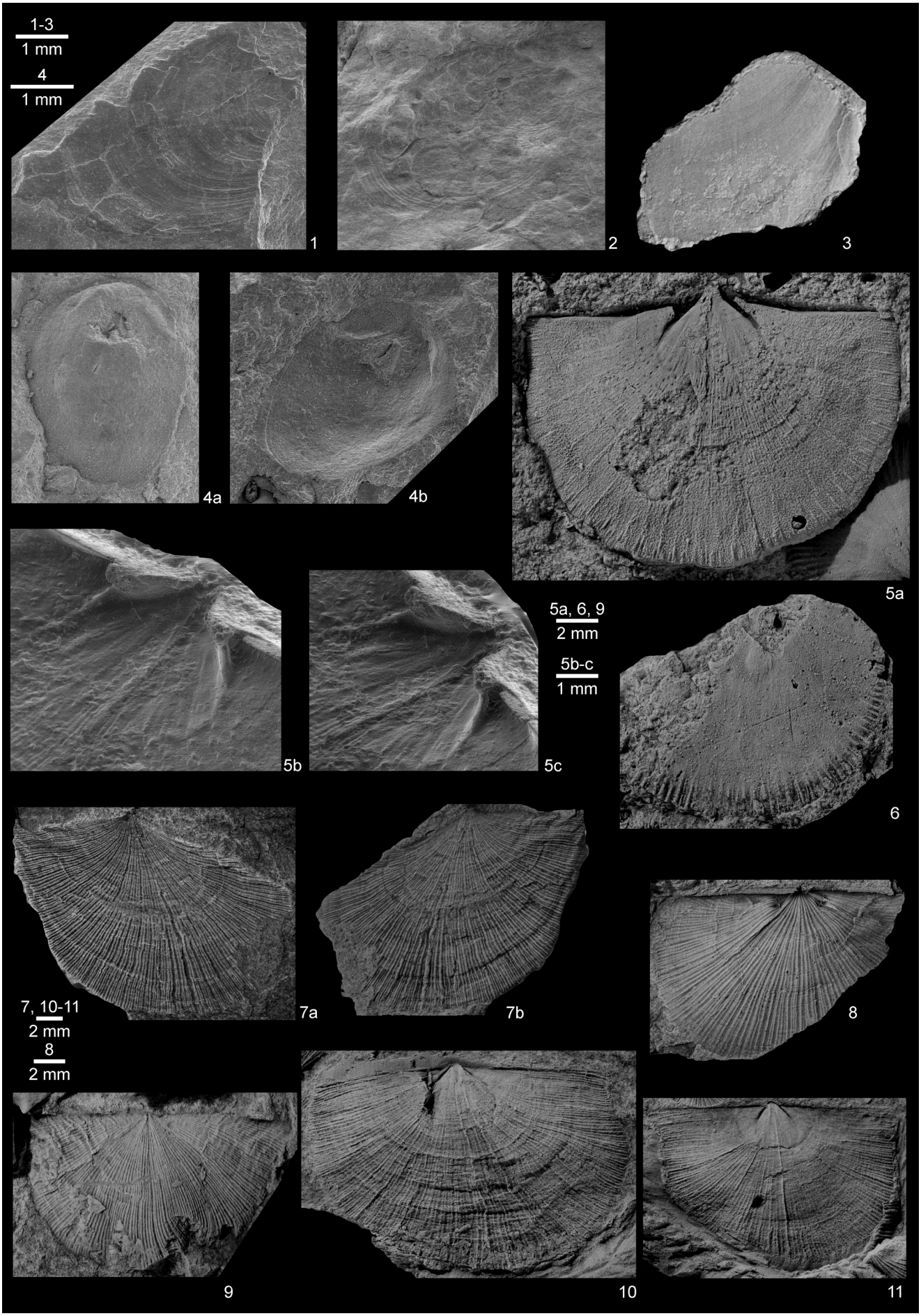
1-3
1 mm
4
1 mm
1
2
3
4a
4b
5a
5a, 6, 9
2 mm
5b-c
1 mm
5b
5c
6
7, 10-11
2 mm
8
2 mm
7a
7b
8
9
10
11

PLATE 2

to *K. bipartita* based on shell outline, ventral muscle field, presence of an accentuated median costellae and length of dental plates. More Belgian material is necessary to assess whether it is identical to *K. bipartita*.

Occurrence. Fond d'Oxhe (Figs. 1-2) and locality OXH 4 of Martin (1969; FM-75-3b) (Fig. 3), Oxhe Formation (Fig. 4).

Family Sowerbyellidae Öpik, 1930
Subfamily Sowerbyellinae Öpik, 1930

Genus *Sowerbyella* Jones, 1928

Type species: *Leptaena sericea* J. de C. Sowerby, 1839, by original designation, from the Alternata Limestone Formation (lower Katian) of Shropshire, England.

Sowerbyella aff. ***sladensis*** Jones, 1928

Fig. 5.2-5

1871 *Leptaena sericea* J. de C. Sowerby; Davidson, p. 323 *pars*, pl. 48, figs. 14, *non* 10-13, 15-22.
1896 *Leptaena sericea*; Destinez, p. 118.
1896 *Chonetes* se rapprochant beaucoup de *Chonetes tenuissime-striata*; Destinez, p. 118.
1899 *Leptaena sericea*; Forir, p. 159.
1899 *Chonetes tenuissime-striata*; Forir, p. 159.
1900a *Leptaena sericea*; Malaise, p. 203.
1900a *Chonetes tenuissime-striata*; Malaise, p. 204.
1901a *Leptaena sericea*; Malaise, p. 218.
1901a *Chonetes tenuissime-striata*; Malaise, p. 219.
aff. 1928 *Sowerbyella sladensis* Jones, p. 421, pl. 21, figs. 14-17.
aff. 1928 *Sowerbyella sladensis* var. *simulans* Jones, p. 423, pl. 21, figs. 18-20.
aff. 1978 *Sowerbyella sladensis* Jones; Cocks, p. 98.
aff. 1989 *Sowerbyella (Sowerbyella) sladensis* Jones; Cocks & Rong, p. 141.
1991 *Sowerbyella*; Dean, p. 139.

Material: Nine ventral and nine dorsal valves.

Description. Shell semi-circular, concavo-convex, with maximum width at hinge line; cardinal angles perpendicular to slightly acute, anterior commissure rectimarginate. Ventral valve 50% as long as wide, maximum convexity at mid valve length; interarea flat, short and apsacline, about 10% as long as valve length. Dorsal valve 45% as long as wide; interarea flat, short and anacline, 5% as long as valve length. Ornament of fine parvicostellae numbering 10-12 per mm at the 5 mm growth stage.

Ventral interior with bilobed muscle field, 70% as long as wide and extending anteriorly for 35% of valve length; minute adductor scars enclosed anteriorly by a pair of large, diverging diductor scars; myophore extending anteriorly for 20% of valve length, dividing the adductor and diductor scars, extending anteriorly for half the diductor scars length; short dental plates extending anteriorly to a faint muscle (diductor) bounding ridge; *vascular media* diverging from anterior tip of the diductor scars.

Dorsal valve with small cardinalia characterized by widely divergent socket ridges (130°), extending anteriorly for 12% of valve length, and laterally for 25% of valve width; cardinal process not preserved; pair of submedian septa, originating from sagittal base of socket ridges, diverging at an angle of 20° and extending anteriorly for mid valve length; septa representing the internal sides of the faintly developed bema, 75% as long as wide, characterized by intra-muscle septa; adductor muscle scars faint on bema.

Remarks. Juvenile specimens were identified as *Orthis tenuissimestriata* M'Coy, 1846 in the collections of the RBINS. This is a poorly known and obscure species (Davidson 1871), from the Upper Ordovician of County Wicklow, Republic of Ireland, probably belonging to the genus *Sowerbyella* (see discussion in Cocks 1978, 2008, 2010). The species *S. tenuissimestriata* is only known from an external mould, and some of M'Coy's type material does not seem to all belong to the same genus (Davidson 1871). Cocks & Rong (1989, p. 142) listed the species as questionably assigned to the genus, whereas Cocks (2010) suggested more topotypic material should be collected and studied in order to validate (or not) this species.

The genus *Sowerbyella* Jones, 1928 is characterized by numerous species. Indeed, Cocks & Rong (1989) listed over 60 species, some of which from the Upper Ordovician – Caradoc of the Anglo-Welsh area are briefly discussed by Cocks (2010), as closely related. Nevertheless, only six species from Avalonia were recorded (Cocks & Rong 1989; Cocks 2010) which narrows down comparisons. *Sowerbyella antiqua* Jones, 1928 from upper Darriwilian beds in Wales and from SE Ireland (Liljeroth et al. 2017), as well as *S. multipartita* Williams in Cocks, 1978 from the Spy Wood Sandstone Formation (lower Sandbian) of Shropshire, England, are species characterized by strong transmuscle septa scarring the bema, a feature absent in the Belgian material. *Sowerbyella musculosa* Williams,

Fig. 5 - 1a-d) *Kjaerina* cf. *bipartita* (Salter in Salter & Aveline, 1854), PA.ULg.1478, dorsal interior and artificial cast and close up of the cardinalia in oblique lateral and oblique posterior views, from the Fond d'Oxhe, Oxhe Formation. 2-5) *Sowerbyella* aff. *sladensis* Jones, 1928, from the Fond d'Oxhe, Oxhe Formation; 2) RBINS a14121, ventral interior, locality H in Dean (1991; FM-77-2-3); 3) RBINS a14122 (I.G. 13394), ventral interior; 4a-c) RBINS a14123 (I.G. 6887), dorsal interior and artificial cast and detail of the muscle field and cardinalia in oblique lateral view; 5) RBINS a14125 (I.G. 13994), almost complete dorsal exterior. 6a-c) *Dalmanella* sp., PA.ULg.2024.09.06-1c, ventral interior and detail of artificial cast in oblique lateral and anterior views, from Sart-Bernard, Vitrival-Bruyère Formation (Sart-Bernard Member).

1963 from the Allt Ddu Group (Sandbian) of Bala, Wales differs from the Belgian specimens in their acute cardinal angles (in both juveniles and adults), more transverse shells and less transverse cardinalia. *Sowerbyella sericea* (J. de C. Sowerby, 1839) from the Alternata Limestone (Sandbian) and *S. soudleyensis* Jones, 1928 from the Horderley Sandstone (lower Katian), both from Shropshire, are species that differ little from each other (Cocks 2010). Cocks (2010) differentiated them on the basis of the more suboval and subparallel dorsal adductor muscle scars in *S. soudleyensis*. Furthermore, until more data are available, he referred the upper Sandbian (Burrelian) population to *S. soudleyensis*, whereas the lower Katian (Cheneyan) population was referred to *S. sericea*. Finally, *S. sladensis* Jones, 1928 from the Slade and Redhill Formation (upper Katian) of Dyfed, Wales is similar to the previous two species, but differs in a relatively narrower bema, small cardinal process and concave socket plates. Moreover, the ventral diductor muscle scar is shorter, relative to its width, in *S. sladensis* than in both *S. soudleyensis* and *S. sericea*. In this respect, the Belgian specimens are more similar to *S. sladensis* than to *S. soudleyensis*

and *sericea*. More specimens are needed to confirm the conspecificity with *S. sladensis* or potentially the presence of a new species.

Occurrence. Fond d'Oxhe (Figs. 1-2), including the locality H of Dean (1991; FM-77-2-3) (Fig. 3), Oxhe Formation (Fig. 4).

Class **RHYNCHONELLATA** Williams et al., 1996
Order **Orthida** Schuchert & Cooper, 1932
Suborder **Dalmanellidina** Moore, 1952
Superfamily Dalmanelloidea Schuchert, 1913
Family Dalmanellidae Schuchert, 1913

Remarks. Some dalmanellid specimens from the Oxhe Formation were identified in the RBINS and PA.ULg. collection as *Orthis testudinaria* Dalman, 1828 (type species of *Dalmanella* Hall & Clarke, 1892), *Orthis redux* Barrande, 1848 (type species of *Drabovia* Havlíček, 1950) and *Orthis redux* var. *budleighensis* Davidson, 1870 [placed in synonymy with *Tafilaltia valpyana* (Davidson, 1869) by Cocks & Lockley (1981)]. Comparison with the type material of these species clearly demonstrated that the Belgian material undoubtedly differs from these taxa. The differences between dalmanellid genera are finely drawn and accurate identifications generally require complete and well-preserved material. It is not uncommon to express doubt in assignments to genera and species within this family. The specimens identified as *Orthis testudinaria* and *Orthis redux budleighensis* are here identified as *Howellites antiquior* and *Bancroftina* sp., respectively.

Subfamily Dalmanellinae Schuchert, 1913

Genus *Dalmanella* Hall & Clarke, 1892

Type species: *Orthis testudinaria* Dalman, 1828, by original designation, from the Loka Formation (Hirnantian) of Borenshult, Västergötland, Sweden.

Dalmanella sp.
Fig. 5.6

Material: One ventral valve.

Description. Ventral valve convex, suboval, transverse, 73% as long as wide; interarea flat and apsacline, extending for 10% of valve length. Ornament expressed at the anterior commissure, numbering 6-7 per mm.

Interior with elongate, bilobed muscle scar, 124% as long as wide and extending anteriorly for 39% of valve length; dental plates short extending anteriorly for 17% of valve length; muscle field bounded laterally by faint ridges not extending anteriorly.

Remarks. This single specimen possesses a characteristic *Dalmanella* bilobed ventral muscle scar as illustrated in the Treatise (Harper 2000: fig. 518.4), with each diductor scar (left and right) divided into two strands. The genus *Dalmanella* is very common in Avalonia (see Cocks 2008 for example). A single valve is not sufficient for meaningful comparisons with other species; therefore, this specimen is left in open nomenclature.

Occurrence. Sart-Bernard (Naninne 2a) (Figs. 1-2), Vitrival-Bruyère Formation (Sart-Bernard Member) (Fig. 4).

Genus *Bancroftina* Sinclair, 1946

Type species: *Raymondella typa* Whittington, 1938; by original designation, from the Horderley Sandstone Formation (Sandbian–Katian) of Shropshire, England.

Bancroftina cf. ***typa*** (Whittington, 1938)
Pl. 3, figs. 1-6

cf. 1938 *Raymondella typa* [Bancroft MS] Whittington, p. 249 *pars*, pl. 10, fig. 13, *non* figs. 12, 14.

Plate 3

1-6) *Bancroftina* cf. *typa* (Whittington, 1938), from the Fond d'Oxhe, Oxhe Formation. 1) RBINS a14126 (I.G. 6887), artificial cast of an incomplete ventral valve exterior; 2) RBINS a14128, dorsal valve exterior, locality OXH 4 in Martin (1969; FM-75-3a); 3) RBINS a14127, artificial cast of an distorted dorsal exterior, locality OXH 4 in Martin (1969; FM-75-3a); 4a-e) RBINS a14129 (I.G. 6887), articulated internal mould in ventral, dorsal, lateral, posterior and anterior views; 5a-c) RBINS a14130, ventral interior and artificial cast in ventral and ventro-lateral views, locality OXH 4 in Martin (1969; FM-75-3b); 6a-e) PA.ULg.6664, dorsal interior and artificial cast in dorsal, oblique lateral view showing the gentle sulcus and close up of the cardinalia in dorsal and inclined posterior views.

7-8) *Howellites antiquior* (M'Coy, 1852), from the Fond d'Oxhe, Oxhe Formation; 7) RBINS a14131, dorsal valve exterior, locality G in Dean (1991; FM-77-2-4); 8a-c) RBINS a14133–14135 (I.G. 9340), group with three ventral valve interiors, and latex cast in ventral view and ventro-lateral view with detail of dental plates of the valve on the lower left corner of figure (RBINS a14133).

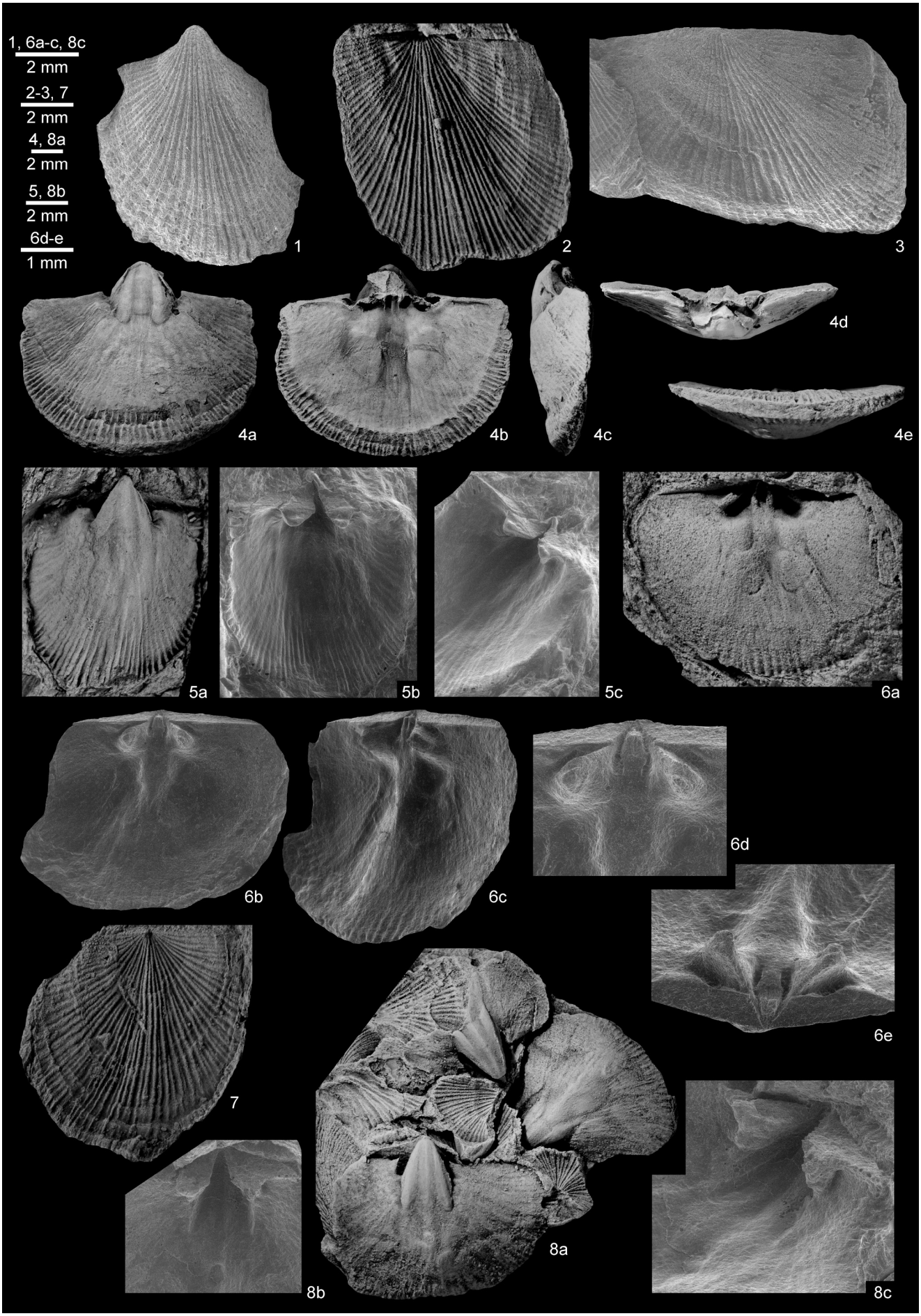
1, 6a-c, 8c
2 mm
2-3, 7
2 mm
4, 8a
2 mm
5, 8b
2 mm
6d-e
1 mm
1
2
3
4a
4b
4c
4d
4e
5a
5b
5c
6a
6b
6c
6d
6e
7
8a
8b
8c

PLATE 3

1945 *Raymondella robusta* Bancroft, p. 201, pl. 25, figs. 11, 12, pl. 26, figs. 1-3.
cf. 1959 *Bancroftina typa* (Whittington); Cave & Dean, p. 294, pl. 53, figs. 5, 6.
1978 *Bancroftina robusta* (Bancroft); Cocks, p. 63.
cf. 1978 *Bancroftina typa* (Whittington); Cocks, p. 64 *pars*.
1978a *Bancroftina robusta* (Bancroft); Hurst, p. 548, pl. 59, figs. 15, 16.
1978b *Bancroftina robusta* (Bancroft); Hurst, p. 247, fig. 1d.
cf. 1979a *Bancroftina typa* (Whittington); Hurst, p. 252, figs. 234-246.
cf. 2000 *Bancroftina typa* (Whittington); Harper, p. 785, fig. 566, 1a-d.
2000 *Bancroftina robusta* (Bancroft); Harper, p. 785, fig. 566, 1e.

Material: Sixteen ventral and six dorsal valves.

Description. Shell subcircular, slightly transverse, ventribiconvex, anterior commissure sulcate, with wide shallow sulcus; hinge line straight; maximum width at mid valve length. Ornament consisting of fine parvicostellae, numbering 5–6 per mm at the 5 mm growth stage.

Ventral valve over 90-95% as long as wide; interarea curved, apsacline, 17% as long as valve length; cardinal angles at right angle to obtuse, often with preserved anterior ends of costellae; delthyrium open. Dorsal valve 90% as long as wide; interarea short extending for 5–8% of valve length; notothyrium open, filled with cardinal process.

Ventral interior with bilobed muscle scar, extending forward for 30% of valve length; diductor scars subparallel, flanking the adductor scar laterally but not enclosing it anteriorly; recessive dental plates; *vascula media*, when preserved, continuing anteriorly from the diductor muscle scar, with the two tracks subparallel; vascular pattern possibly lemniscate.

Dorsal interior with cardinal process supported on a blade-like shaft, extending the whole length of the notothyrial cavity; brachiophores short, extending for less than 20% of valve length, supported by plates from the notothyrial platform; brachiophore tops narrowly divergent (40° angle), while bases widely divergent (70°–80° angle); presocket lines obtusely convergent; median ridge extending anteriorly for mid valve length, separating the quadripartite adductor muscle scars; anterior and posterior scars separated by a low ridge; adductor scars not developed anterior to the median ridge.

Remarks. The two genera *Howellites* and *Bancroftina* are very similar externally and also internally. Only few features differentiate these. *Bancroftina* possesses a broader and shallower dorsal valve sulcus (about 50% of valve width) than *Howellites* (about 30% of valve width); the ventral muscle scar in *Bancroftina* extends anteriorly for less than 1/3 of valve length, whereas it extends for 40% on average in *Howellites*; Williams & Wright (1963, p. 25, text-fig. 10) have differentiated the position and angle of their brachiophore bases, being "almost subparallel with the hinge line" (op. cit., p. 27) in *Bancroftina*, and "greatly divergent" (op. cit., p. 29) in *Howellites*.

Whittington (1938) described the type species *B. typa* and later Bancroft (1945) erected another species *robusta*, from Horderley, Shropshire, England. However, Hurst (1979a) synonymized Bancroft's (1945) species, an opinion followed by Cocks (2008). Harper (2000) did not follow these previous authors and left the two species separate. We follow Hurst's (1979a) opinion and synonymise *B. typa* and *B. robusta*. In addition, Hurst (1979a) described another two species, *B. hewitti* and *B. whittingtoni*, from Shropshire and the Berwyn Hills, North Wales, respectively. *Bancroftina hewitti* is, among other features, characterized by coarser ornament than the other species; the Belgian specimens are more similar to the type species in the fine ornament, but not as fine as *B. whittingtoni*. Moreover, *B. typa* has more circular ventral valves than the other species, which is more similar to the Belgian specimens studied here. These are also characterized by a cardinal process as long and divergent, relative to the valve dimensions, than in *B. typa*. Wright (1964) described a limited number of specimens of *Bancroftina* sp. from the upper Katian Portrane Limestone in Ireland; these are characterized by a coarse ornament different from that of the Belgian material. Other species in open nomenclature include two collections from the Bala District, Wales, described by Williams (1963) and Lockley (1980). The specimens described by Williams (1963) show some similarities to our specimens, in ornament, ventral interarea size, and the proportion of valves, but the cardinal process is here longer and less divergent than in the Belgian specimens. Lockley (1980) collected a single dorsal valve. No comparisons can be made with his material.

The Belgian specimens are therefore closely comparable with *B. typa* but more material is needed to verify the identification.

Occurrence. Fond d'Oxhe (Figs. 1-2), including locality OXH 4 in Martin (1969; FM-75-3a and FM-75-3b) (Fig. 3), Oxhe Formation (Fig. 4).

Genus *Howellites* Bancroft, 1945

Type species: *Resserella* (*Howellites*) *striata* Bancroft, 1945, by original designation, from the Allt Ddu Formation (Sandbian) of Bala, Wales.

Howellites antiquior (M'Coy in Sedgwick & M'Coy, 1852)

Pl. 3, figs. 7-8; Pl. 4, figs. 1-5

1839 *Orthis canalis* J. de C. Sowerby, p. 640 *pars*, pl. 20, fig. 8, *non* p. 630, pl. 13, fig. 12a.
1852 *Orthis canalis* J. de C. Sowerby var. *antiquior* M'Coy *in* Sedgwick & M'Coy, p. 217.
1959 *Paucicrura sowerbyii* Cave & Dean, p. 295, pl. 53, figs. 7-11.
1963 *Howellites antiquior* (M'Coy) Williams, p. 389, pl. 6, figs. 13-19, pl. 7, figs. 1, 2, 5, 6.
1978 *Howellites antiquior* (M'Coy); Cocks, p. 64.
2008 *Howellites antiquior* (M'Coy); Cocks, p. 148.

Material: Fifteen ventral and 20 dorsal valves.

Description. Shell ventribiconvex; anterior commissure variably sulcate; cardinal angles at right angle. Ventral valve subcircular, deeply convex, about 40% as deep as long; interarea apsacline, convex, extending for 15% of valve length. Dorsal valve semicircular, 70-80% as long as wide; maximum width at hinge line; interarea anacline, extending for 10% of valve length.

Ventral interior with large teeth supported by slender, but well-developed, subparallel dental plates, extending anteriorly for 40% of valve length; muscle scar extending anteriorly for 40% of valve length, about 80% as wide as long; diductor scars extending anteriorly to the adductor scar, not enclosing it anteriorly.

Dorsal interior with cardinal process bladelike restricted to the posterior end of the notothyrial cavity; brachiophores short, extending for 20% of valve length, and narrowly divergent, 50% as long as wide; fulcral plates occasionally present; wide median ridge extending for over half of valve length, separating the quadripartite adductor scars; adductor scars elongately oval, with transverse posterior scar smaller than subcircular anterior scar.

Remarks. Williams & Wright (1963) reviewed the taxonomy of the Dalmanellidae and Williams (1963), in particular, focused on species from North Wales of *Howellites*: *striata, intermedia, ultima* and *antiquior*. Whittington (1938) also described a species from North Wales, namely *H. cruralis*. All the Welsh material was retrieved from Sandbian rocks. The Belgian material is characterized by deep ventral valves, well-developed dental plates, diductor scars extending anteriorly to the adductor scars, not enclosing them, brachiophore bases more divergent than their tops, which are diagnostic of the genus *Howellites*. Williams (1963) compared the different species of *Howellites* listed above; *H. antiquior* is characterized by a deeper ventral valve and brachiophores half as long as wide. The other species have similar ventral and dorsal valves in outline and profile, similar brachiophores about two-thirds as long as wide. On the other hand, *H. cruralis* although possessing a deep ventral valve, differs from the other species in a more circular dorsal valve, shorter dorsal adductor muscle scars and shorter brachiophores. The Belgian specimens are identified as *H. antiquior*, based on the deep ventral valve, deeper than *H. cruralis*, the brachiophores being half as long as wide, and the dorsal adductors extending for over half valve length.

Occurrence. Fond d'Oxhe (Figs. 1-2), including the localities OXH 4, G and H (Fig. 3), Oxhe Formation (Fig. 4).

Genus *Onniella* Bancroft, 1928

Type species: *Onniella broeggeri* Bancroft, 1928, by original designation, from the Acton Scott Formation (Sandbian), Shropshire, England.

Onniella sp.

Pl. 4, figs. 6-8

Material: Three ventral and three dorsal valves.

Description. Shell transverse suboval, ventribiconvex, with anterior commissure sulcate; maximum width at mid valve length. Ornament fascicostellate with 6 costellae per mm at the 3 mm growth stage.

Ventral valve 80% as long as wide; interarea apsacline, gently convex, extending for 15% of valve length; delthyrium open.

Dorsal valve 70% as long as wide; interarea short, anacline, extending for less than 5% of valve length; notothyrium open.

Ventral interior with teeth supported by subparallel dental plates extending for 25% of the valve length, flanking laterally the muscle field; muscle scar triangular with diductors extending laterally to and anteriorly from the adductor for 30% of valve length.

Dorsal interior with stout cardinal process filling the notothyrium; brachiophores widely divergent, extending for 18% of valve length, with bases ankylosed with thick median ridge, separating the quadripartite adductor scars; adductor scars extending forward for 45% of valve length.

Remarks. This small sample is not very well preserved but presents some features that are identified as diagnostic of *Onniella*, such as the swollen cardinal process and recessive dental plates. However, better preserved material is needed to expand on the generic identification. *Onniella* is a cosmopolitan taxon and, in the upper Sandbian–lower Katian, it was widespread in high latitude Gondwana, Shropshire and South Wales, Anglesey, Baltica (see Liljeroth et al. 2017) and present in SE Ireland (Harper et al. 2017). Hurst (1979a) recognized that several species of *Onniella* from Shropshire were conspecific, as these were originally defined based on their ribbing patterns. Hurst (op. cit.) only recognized *O. reuschi, O. depressa* and *O. broeggeri*. The Belgian specimens are similar to *O. broeggeri* Bancroft from the Katian of Shropshire in having a swollen cardinal process, widely divergent brachiophores with bases ankylosed to a median ridge, subparallel dental plates and ventral muscle field. However, the paucity of material does not permit statistically meaningful comparisons.

Occurrence. Fond d'Oxhe (Figs. 1-2), including the locality G (Fig. 3), Oxhe Formation (Fig. 4).

Dalmanelloidea fam., gen. et sp. indet.

1938a *Pionodema redux* (Barrande, 1848); Maillieux, p. 23.
1938b *Pionodema redux* (Barrande, 1848); Maillieux, p. 339.
1939 *Pionodema redux* (Barrande, 1848); Maillieux, pp. 21-22, pl. 1, fig. 18-18a.

Remarks. The single specimen, comprising a single ventral valve (internal mould and external counterpart), illustrated by Maillieux (1939) is lost. This author identified it as the Bohemian species *Pionodema redux* (Barrande), designated as the genotype of *Drabovia* by Havlíček (1951). Havlíček (1977) described the species with a rounded carinate ventral valve, a weakly unisulcate anterior commissure, moderately diverging dental plates (75-90°), and subequal poorly differentiated ventral muscle scars. These features are not represented in the Sart-Bernard specimen, the ventral valve looks simply convex, with a rectimarginate anterior commissure, short, very divergent dental plates (see Maillieux 1939, p. 21), and an adductor scar wider than the diductors. Therefore, we regard this identification as very tentative, since there are no dorsal valve interiors available. Nevertheless, based on the limited illustrations, it is plausible that this valve belongs to the Dalmanelloidea.

Occurrence. Sart-Bernard (Naninne 2a) (Figs. 1-2), Vitrival-Bruyère Formation (Sart-Bernard Member) (Fig. 4).

Superfamily Enteletoidea Waagen, 1884
Family Draboviidae Havlíček, 1950
Subfamily Draboviinae Havlíček, 1950

Genus *Oanduporella* Hints, 1975

Type species: *Oanduporella reticulata* Hints, 1975, by original designation, from the Hirmuse Formation (Katian) of Oandu, Estonia.

Oanduporella aff. ***alamensis*** Benedetto, 1995

Fig. 6.1-5

aff. 1995 *Oanduporella alamensis* Benedetto, p. 244, pl. 1, figs. 14-26.

Material: Two ventral, two dorsal valves and a conjoined valve.

Plate 4

1-5) *Howellites antiquior* (M'Coy, 1852), from the Fond d'Oxhe, Oxhe Formation; 1a-e) RBINS a14136 (I.G. 13394), distorted articulated internal mould in ventral, dorsal, lateral, posterior and anterior views; 2a-c) RBINS a14137 (I.G. 13394), distorted incomplete articulated internal mould in ventral and dorsal views, showing the vascular pattern on the ventral valve and partially on the dorsal valve, and dorsal external mould; 3) RBINS a14124 (I.G. 6887), incomplete dorsal interior showing the *vascula genitalia*; 4a-b) RBINS a14138, dorsal valve interior and artificial cast, locality OXH 4 in Martin (1969; FM-75-3a); 5a-d) RBINS a14139, almost complete dorsal valve interior and artificial cast in dorsal and dorsal oblique lateral views, and detail of the cardinalia in oblique posterior view, locality H in Dean (1991; FM-77-3).
6-8) *Onniella* sp., from the Fond d'Oxhe, Oxhe Formation; 6) RBINS a14132, ventral valve exterior, locality G in Dean (1991; FM-77-2-4); 7a-c) RBINS a14140 (I.G. 6887), ventral valve interior with artificial cast in ventral and antero-lateral views; 8a-d) RBINS a14141 (I.G. 6887), dorsal valve interior with artificial cast in dorsal and antero-dorsal views and detail of the cardinalia.

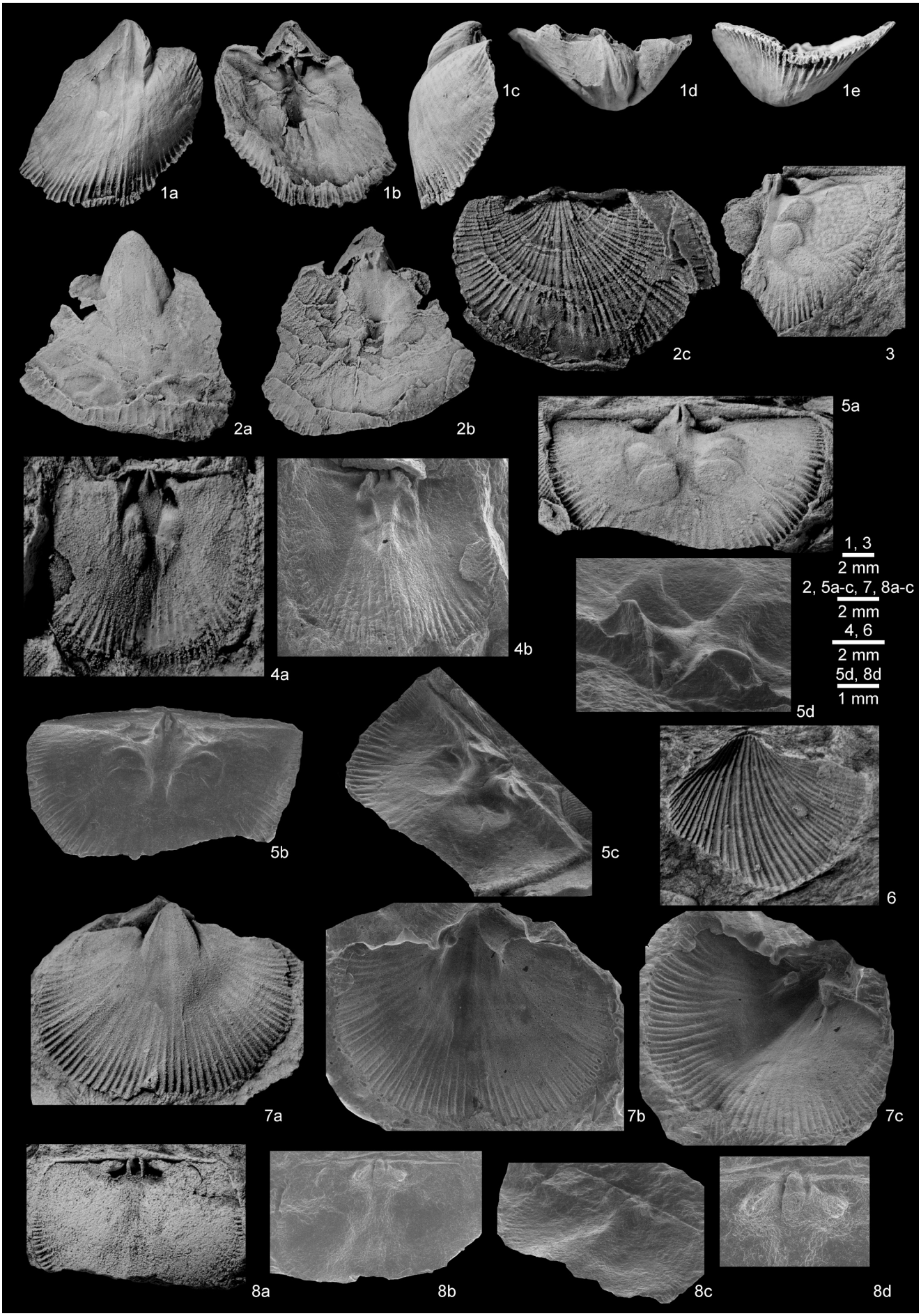
1a
1b
1c
1d
1e
2a
2b
2c
3
4a
4b
5a
5b
5c
5d
6
7a
7b
7c
8a
8b
8c
8d
1, 3
2 mm
2, 5a-c, 7, 8a-c
2 mm
4, 6
2 mm
5d, 8d
1 mm

Plate 4

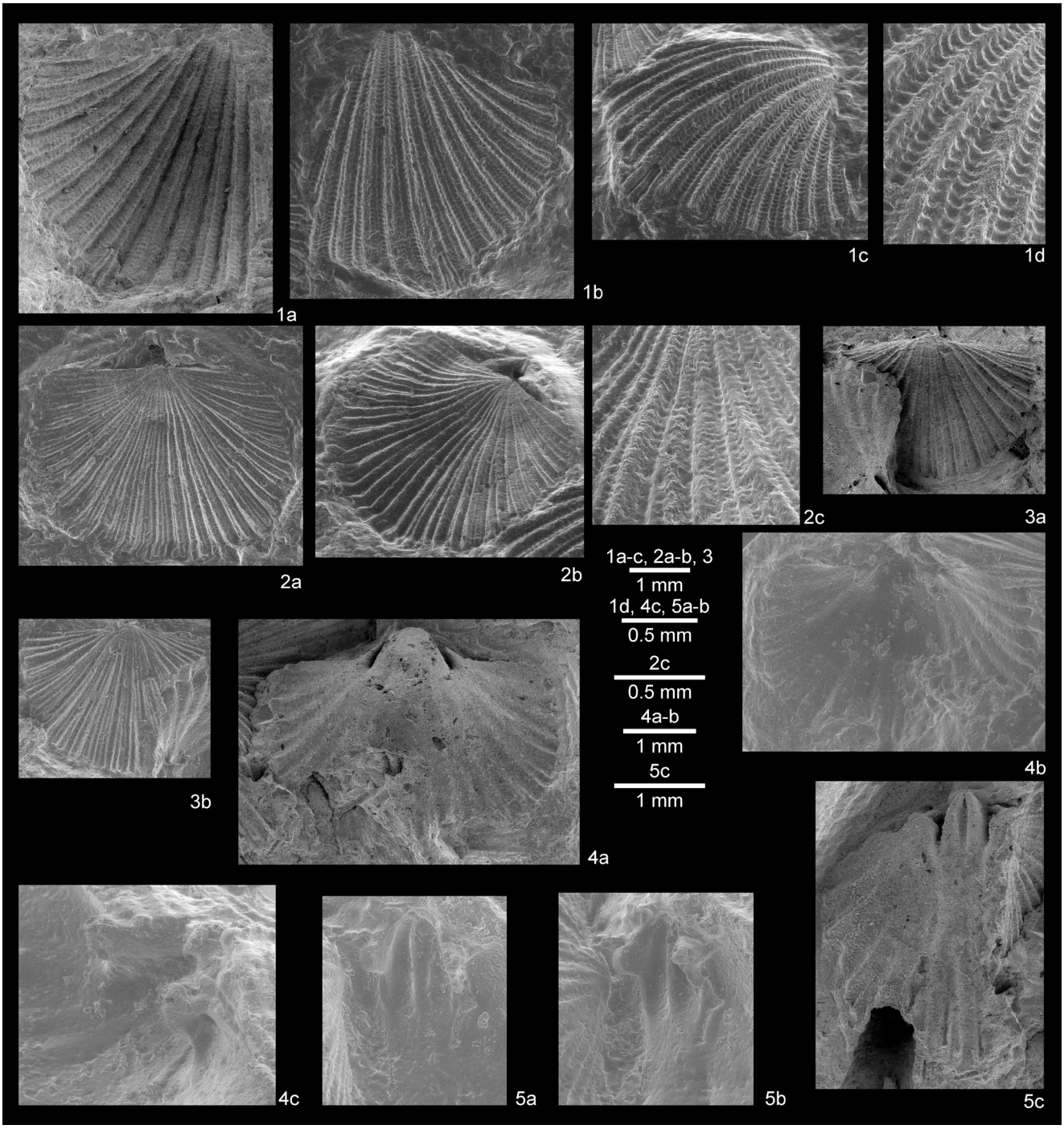

Fig. 6 - *Oanduporella* aff. *alamensis* Benedetto, 1995, from Sart-Bernard, Vitrival-Bruyère Formation (Sart-Bernard Member); 1a-d) PA.ULg.2024.09.06-1d, ventral valve exterior and artificial cast in ventral and oblique lateral views and detail of the reticulate ornament; 2a-c) PA.ULg.2024.09.06-1e, artificial cast of an articulated specimen with ventral valve enclosed in matrix in dorsal and oblique dorso-lateral views and detail of the reticulate ornament on the dorsal valve; 3a-b) PA.ULg.2024.09.06-1f, ventral valve exterior and artificial cast; 4a-c) PA.ULg.2024.09.06-1g, incomplete ventral valve interior, artificial cast and detail of the dental plates in oblique lateral view; 5a-c) PA.ULg.2024.09.06-1h, detail of cardinalia (artificial cast) in dorsal and oblique lateral views and incomplete dorsal interior.

Description. Shell ventribiconvex; anterior commissure sulcate; cardinal angles obtuse. Ventral valve subcircular, 80-90% as long as wide, with maximum width at mid valve length; interarea slightly concave, apsacline, 15% as long as valve length. Dorsal valve subcircular to transverse, 75-90% as long as wide; interarea anacline, flat, short, extending for 5% of valve length. Ornament of angular costae and costellae numbering 11-12 per 2 mm at the 3 mm growth stage, intersected by filae numbering 14 per mm at the commissure; inter-costae space wider than costae; pseudopunctae transverse-

ly oval, the pits forming rows in intercostal spaces, numbering 11-12 per mm.

Ventral interior with short dental plates, extending for 20% of valve length and diverging at an angle of 65°; muscle scar broad and triangular, faintly impressed, 65% as long as wide and extending anteriorly for 22% of valve length; small teeth supported by divergent dental plates.

Dorsal interior with simple cardinal process on a shaft extending anteriorly for 20% of valve length; brachiophores divergent, short and stout, supported by thin subparallel bases flanking elongated notothyrial platform; bases extending anteriorly for 20% of valve length.

Remarks. The genus *Oanduporella* Hints, 1975 is recorded from the Sandbian of Gondwana (Bolivia, Peru and Argentina: Havlíček & Branisa 1980, Suárez-Soruco 1992, Benedetto 1995), Laurentia (Illinois, Alaska, Scotland, Northern Ireland: Potter & Boucot 1992, Rasmussen et al. 2012, Candela & Harper 2010, Candela 2003), Avalonia (eastern Ireland: Harper et al. 1985, Parkes 1994), and the Katian of Estonia (from where it was first recognized) and Lithuania (Hints 1975, Paškevičius 1994). This genus is characterized by its pseudopunctae in the costellae interspaces. The pseudopunctae are often distributed in a honey-comb pattern (pseudopunctae in a zig-zag pattern), but some species display a more regular reticulate pattern, with the pseudopunctae in parallel rows (see Benedetto, 1995). The shape, arrangement in parallel row, and number of pseudopunctae in the present Belgian specimens most resemble *O. alamensis* Benedetto, 1995 from the Las Plantas Formation (lower Caradoc, Sandbian) in the Argentinean Cordillera. Rasmussen (2011) hypothesized that the stock from the Cordillera migrated eastward towards Avalonia at the end of the Sandbian. The morphological closeness with the Belgian specimens indicates that these might be related. However, the two samples differ in the shape of the ventral valve (more transverse in the Belgian stock), the shape of the ventral muscle scar (wider than long in the Belgian stock and as long as wide in *O. alamensis*), and less divergent brachiophores (Belgian sample). It is possible that this Belgian sample belongs to a new species, but more material is needed in order to confirm this.

Occurrence. Sart-Bernard (Naninne 2a) (Figs. 1-2), Vitrival-Bruyère Formation (Sart-Bernard Member) (Fig. 4).

Palaeoecological and palaeobiogeographical interpretations of the fauna

Brachiopod-dominated associations have been reported from well-documented areas in Wales and western England (for example, Hurst 1979b; Pickerill & Brenchley, 1979; Lockley 1980, 1983), based on the substantial taxonomic work published by Williams (1963, 1974) Hurst (1979a) and Lockley (1980). The Upper Ordovician fauna (Oxhe and Vitrival-Bruyère (Sart-Bernard Member) formations) is dominated by *Howellites* (36% of the assemblage), *Bancroftina* (22%) and *Sowerbyella* (18%), with additional taxa such as *Kjaerina* and *Onniella* (both 6%), *Oanduporella* (5%), *Colaptomena* (2%) and *Paracraniops*, *Dalmanella*, and an indeterminate dalmanelloid and linguliform (each representing 1%). This assemblage has taxonomic similarities with the *Bancroftina* Association of Hurst (1979b, c) from England and with the *Dalmanella* Community of Pickerill & Brenchley (1979) from Wales, although it shows some variations. The former is dominated by *Bancroftina* and *Kjaerina* (both totalling 75% of the assemblage) with additional taxa such as *Sowerbyella* (6%) and *Paracraniops* (<1%). The latter is characterized by *Dalmanella* (31%), *Howellites* (27%) and *Sowerbyella* (16%), with additional taxa such as *Kjaerina* (<3%), *Paracraniops* and a linguliform brachiopod (both <1%). These associations reflect some regional and stratigraphic differences. *Howellites* is a common taxon in Bala, Wales and therefore a component of the community described by Pickerill & Brenchley (1979) but absent from Shropshire and the Shelve District in England and absent from the association described by Hurst (1979b). Similarly, *Bancroftina* is abundant in England but rarer in Wales, which is reflected in the publications of Pickerill & Brenchley (1979) and Hurst (1979b). Additionally, Pickerill & Brenchley (1979) described a *Howellites* Community from Wales but, although the taxonomic composition is similar to that of the Belgian assemblage, with taxa such as *Howellites, Sowerbyella, Paracraniops, Onniella, Dalmanella* and *Kjaerina,* the relative abundance of these taxa is very different in the Welsh and Belgian faunas.

The *Dalmanella* Community is described as living in a moderately deep-water environment, transitional between nearshore and offshore environments, and characterized by a water depth of less than 25 meters (see Pickerill & Brenchley 1979),

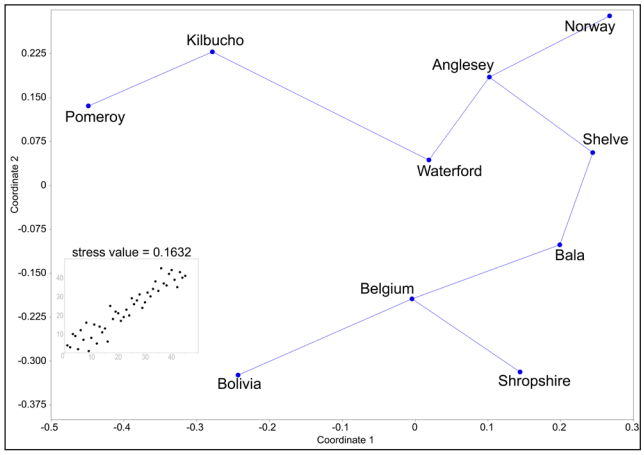

Fig. 7 - Non-metric multidimensional scaling (NMDS) plot of the Upper Ordovician brachiopod fauna of the Oxhe and Vitrivial-Bruyère (Sart-Bernard Member) formations with coeval brachiopod assemblages from Laurentia, Baltica, Avalonia and Gondwana, using the software package PAST (Hammer et al. 2001), with the Raup-Crick similarity coefficient.

certainly above the storm-wave base (40 m depth maximum). It is characterized by more arenaceous environments (Lockley 1983). It is described as equivalent to Boucot's (1975) Benthic Assemblage 3 (Pickerill & Brenchley 1979). The *Bancroftina* Association is interpreted as representing a nearshore environment subjected to distal storm events positioned above the fair-weather-wave base (Hurst 1979b). The Belgian fauna is characterized by the combination of taxa from relatively deep-water (e.g., *Howellites*, *Oanduporella, Colaptomena*) and shallower (e.g., *Bancroftina*, *Onniella, Dalmanella, Sowerbyella*) environments, with *Howellites, Bancroftina* and *Sowerbyella* representing three-quarters of the total assemblage. The Belgian fauna may represent a regional variation of these assemblages from Wales and England, occupying similar bathymetry and substrates.

The palaeobiogeographical relationships of the Belgium fauna from the Oxhe Formation with coeval faunas from peri-Iapetus localities in marginal Laurentia (Pomeroy, Northern Ireland: Candela 2003; Kilbucho, Scotland: Candela & Harper 2010), Baltica (Norway: Hansen 2008), Western Gondwana (Bolivia: Waisfeld & Henry 2003), Ganderia (Waterford, Republic of Ireland: Harper et al. 2017; Anglesey, Wales: Bates 1968) and Avalonia (Bala, Wales: Williams 1963; Shropshire, England: Hurst 1979a; Shelve, England: Williams 1974) are represented in the Nonmetric Multidimensional Scaling analysis (NMDS) on Figure 7, using the Raup-Crick similarity index, and in the network analysis (NA) (Fig. 8). The study is restricted to peri-Iapetus faunas to test the affinities of the Belgian fauna at a regional scale. The Belgian fauna is not very diverse with nine taxa identified at the generic level; an undetermined linguliform valve and a dalmanelloid valve are also recorded. The NMDS and NA plots clearly show the strong relationship of the Belgian fauna with the faunas from Avalonia and Ganderia; the fauna is dominated by *Howellites* (36% of the total assemblage) and *Bancroftina* (22%), both taxa restricted to Avalonia in the Upper Ordovician. Moreover, in the upper Sandbian-lower Katian, *Paracraniops*, a taxon found in Britain, Kazakhstan, Turkey, China, North America, Estonia, Lithuania, and *Kjaerina*, endemic to Britain, are also part of the Belgian fauna. The Belgian fauna is distinct from the deep-water (BA 4-5) Scoto-Appalachian fauna of marginal Laurentia (Candela 2003, 2006; Candela & Harper 2010), as the oceanic gyres configuration does not facilitate north-south faunal exchanges (see Liljeroth et al. 2017, redrawn from Pohl et al. 2016), and from Baltica. In the latter, the upper Katian main immigration from the west into the Oslo Region (Hansen & Harper 2008) seemed to have taken place preferably from Ganderia as shown by the closer link with Anglesey and Waterford (Figs 7 and 8), which could be explained by the oceanic gyre paths as proposed by Liljeroth et al. (2017). Similarly, the closer connection of Bolivia (Western Gondwana) with the Belgian fauna can be interpreted by the eastward direction of the oceanic gyre (Rasmussen 2011; Liljeroth et al. 2017).

Conclusions

The present study has documented for the first time a detailed taxonomic description and numerical analysis of the Upper Ordovician brachiopod fauna of the Oxhe Formation, including some preliminary data for the Vitrivial-Bruyère Formation (Sart-Bernard Member). The material described here includes the oldest record of rhynchonelliformean brachiopods in Belgium. A varied associated invertebrate fauna (e.g. trilobites, molluscs) is also included and figured. Analyses of this low-diversity assemblage have suggested habitats in deeper-water environments and have confirmed

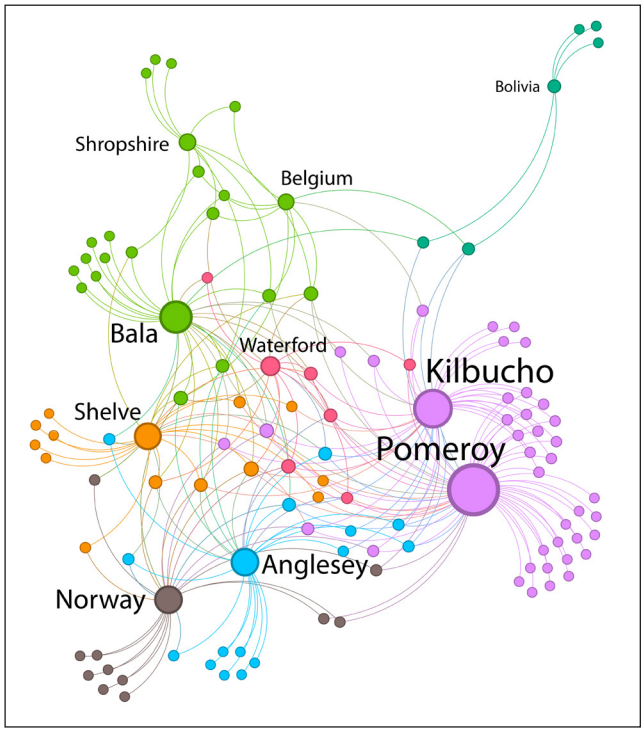

Fig. 8 - Graphical output of network analysis using GEPHI (Bastian et al. 2009) of the Upper Ordovician brachiopod fauna of the Oxhe and Vitrivial-Bruyère (Sart-Bernard Member) formations with coeval brachiopod assemblages from Laurentia, Baltica, Avalonia and Gondwana. The diameter of circles reflects the relative diversity of the faunas.

close comparison with other brachiopod faunas from Avalonia. This study is the continuation of our work revising the Ordovician and Silurian brachiopod faunas from Belgium. This work clearly shows the shift in brachiopod assemblages from linguliformean-dominated in the Lower Ordovician to rhynchonelliformean-dominated here, in the Middle to Upper Ordovician.

Further work is in progress investigating the brachiopod fauna from the Huet Formation (Upper Ordovician, Katian) of the Brabant Massif described by Malaise (1873).

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding author to obtain access

Acknowledgments: We thank Nathan Vallée Gillette for his technical support, Laetitia Despontin who did the SEM photographic work, Bertrand Lefebvre for comments on Crinoidea, and Valentin Fischer for access to the palaeontological collections of the University of Liège. We thank both reviewers, Lars Holmer and Leonid Popov, for comments and suggestions that greatly improved the manuscript. We thank the editor, Lucia Angiolini, for careful editing of this manuscript. This research (Project Acronym BETAF-C3-CANDELA), received support from the SYNTHESYS+ Project, which is financed by European Community Research Infrastructure Action under the H2020 Integrating Activities Programme, Project number 823827. Harper thanks the Leverhulme Trust for support. This is a contribution to IGCP project 735 "Rocks and the Rise of Ordovician Life: Filling knowledge gaps in the Early Palaeozoic Biodiversification".

References

Bancroft B.B. (1928) - On the notational representation of the rib-system in Orthacea. *Manchester Literary and Philosophical Society, Memoirs and Proceedings*, 72: 53-90.

Bancroft B.B. (1929) - Some new genera and species of Strophomenacea from the Upper Ordovician of Shropshire. *Memoirs and Proceedings of the Manchester Literary and Philosophical Society*, 73: 33-65.

Bancroft B.B. (1945) - The brachiopod zonal indices of the stages Costonian to Onnian in Britain. *Journal of Paleontology*, 19: 181-252.

Barrande J. (1848) - Über die Brachiopoden der silurischen Schichten von Böhmen. *Naturwissenschaftliche Abhandlungen*, 2: 155-256.

Barrande J. (1879) - Système Silurien du centre de la Bohême. 1re partie. Recherches paléontologiques, Vol. 5, Classe de Mollusques, Ordre des Brachiopodes. Published by the Author, Prague and Paris, 226 pp.

Bastian M., Heymann S. & Jacomy M. (2009) - Gephi: an open source software for exploring and manipulating networks. *Proceedings of the international AAAI conference on web and social media*, 3(1): 361-362.

Bates D.E.B. (1968) - The Lower Palaeozoic brachiopod and trilobite faunas of Anglesey. *Bulletin of the British Museum (Natural History), Geology*, 16(4): 125-199.

Belanger I., Delaby S., Delcambre B., Ghysel P., Hennebert M., Laloux M., Marion J.-M., Mottequin B. & Pingot J.-L. (2012) - Redéfinition des unités structurales du front varisque utilisées dans le cadre de la nouvelle Carte géologique de Wallonie (Belgique). *Geologica Belgica*, 15(3): 169-175.

Benedetto J.L. (1995) - La fauna de braquiópodos de la Formación Las Plantas (Ordovícico tardío, Caradoc), Precordillera Argentina. *Revista Española de Paleontología*, 10(2): 239-258.

Béthune P. de (1954) - Carte géologique de Belgique. 1/500 000. Atlas de Belgique, planche 8. In: Fourmarier P. (Ed.), Prodrome d'une description géologique de la Belgique: Annexe 1. Société géologique de Belgique, Liège.

Boucot A.J. (1975) - Evolution and extinction rate controls. Elsevier, Amsterdam, 427 pp.

Bowdler-Hicks A., Ingham J.K. & Owen A.W. (2002) - The taxonomy and stratigraphical significance of the Anglo-Welsh Cryptolithinae (Trinucleidae, Trilobita). *Palaeontology*, 45: 1075-1105.

Candela Y. (2003) - Late Ordovician brachiopods from the Bardahessiagh Formation of Pomeroy, Co. Tyrone, Northern Ireland. *Monograph of the Palaeontographical Society*, 156(618): 1-95.

Candela Y. (2006) - Late Ordovician brachiopod faunas from Pomeroy, Northern Ireland: a paleoenvironmental synthesis. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 96: 317-325.

Candela Y. & Harper D.A.T. (2010) - Late Ordovician (Katian)

brachiopods from the Southern Uplands of Scotland: Biogeographic patterns on the edge of Laurentia. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 100: 253-274.

Candela Y. & Mottequin B. (2022) - Tremadocian and Floian (Ordovician) linguliformean brachiopods from the Stavelot–Venn Massif (Avalonia; Belgium and Germany). *Geologica Belgica*, 22(1/2): 1-15.

Candela Y. & Mottequin B. (2023) - Middle and Upper Ordovician linguliformean and craniiformean brachiopods from the Brabant Massif, Belgium: infaunal giants, encrusting forms and durophagy. *Geobios*, 81: 101-119.

Candela Y., Marion J.-M., Servais T., Wang W., Wolvers M. & Mottequin B. (2021) - New linguliformean brachiopods from the lower Tremadocian (Ordovician) of the Brabant Massif, Belgium, with comments on contemporaneous faunas from the Stavelot–Venn Massif. *Rivista Italiana di Paleontologia e Stratigrafia*, 127(2): 383-395.

Cave R. & Dean W.T. (1959) - Four British Ordovician species of dalmanelloid brachiopod. *Palaeontology*, 1: 292-297.

Cluysenaar P.-G. & Lecrenier A. (1887) - Etude des fossiles siluriens de Huy et d'Ombret. Première communication. *Bulletin du Cercle des Naturalistes hutois*, 1887(2): 47-54.

Cocks L.R.M. (1978) - A review of British Lower Palaeozoic brachiopods, including a synoptic revision of Davidson's monograph. *Monographs of the Palaeontographical Society*, 131(549): 2-228.

Cocks L.R.M. (2008) - A revised review of British Lower Palaeozoic brachiopods. *Monograph of the Palaeontographical Society*, 161(629): 1-276.

Cocks L.R.M. (2010) - Caradoc strophomenoid and plectambonitoid brachiopods from Wales and the Welsh Borderland. *Palaeontology*, 53: 1155-1200.

Cocks L.R.M. & Lockley M.G. (1981) - Reassessment of the Ordovician brachiopods form the Budleigh Salterton Pebble Bed, Devon. *Bulletin of the British Museum (Natural History), Geology*, 35(3): 111-124.

Cocks L.R.M. & Rong Jia-Yu (1989) - Classification and review of the brachiopod superfamily Plectambonitacea. *Bulletin of the British Museum* (*Natural History*)*, Geology*, 45: 77-163.

Cocks L.R.M. & Torsvik T.H. (2002) - Earth geography from 500 to 400 million years ago: a faunal and palaeomagnetic review. *Journal of the Geological Society, London*, 159: 631-644.

Cocks L.R.M. & Torsvik T.H. (2021) - Ordovician palaeogeography and climate change. *Gondwana Research*, 100: 53-72.

Cooper G.A. (1956) - Chazyan and related brachiopods. *Smithsonian Miscellaneous Collections*, 127(I/II): 1-1245.

Dalman J.W. (1828) - Uppställning och Beskrifning af de i Sverige funne Terebratuliter. *Kongliga Svenska Vetenskapsakademien*, Handlingar for 1827: 85-155.

Davidson T. (1869) - A Monograph of the British Fossil Brachiopoda. Part 7, no. 3. The Silurian Brachiopoda. *Monograph of the Palaeontographical Society*, 22(96): 169-248.

Davidson T. (1870) - Notes on the Brachiopoda hitherto obtained from the 'Pebble-bed' of Budleigh Salterton, near Exmouth, in Devonshire. *Quarterly Journal of the Geological Society London*, 26: 70-90.

Davidson T. (1871) - A Monograph of the British Fossil Brachiopoda. Part 7, no. 4. The Silurian Brachiopoda. *Monograph of the Palaeontographical Society*, 24(108): 249-397.

Dean W.T. (1991) - Ordovician trilobites from the inlier at Le Petit Fond d'Oxhe, Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 61: 135-155.

Denayer J. & Mottequin B. (2024) - The Lower Devonian lithostratigraphy of Belgium. *Geologica Belgica*, 27(3/4): 115-154. https://doi.org/10.20341/gb.2024.004

Destinez P. (1896) - Quelques nouveaux fossiles siluriens à Ombret. *Annales de la Société géologique de Belgique*, 23 (Bulletin): 118-119.

Dewalque G. (1894) - Un nouveau gîte de fossiles siluriens à Ombret. *Annales de la Société géologique de Belgique*, 21 (Bulletin): 80-81.

Forir H. (1899) - Compte rendu de la session extraordinaire de la Société géologique de Belgique, tenue à Huy, du 2 au 5 octobre 1897. *Annales de la Société géologique de Belgique*, 24 (pro 1897) (Bulletin): 149-203.

Fortey R.A., Harper D.A.T., Ingham J.K., Owen A.W. & Rushton A.W.A. (1995) - A revision of Ordovician series and stages from the historical type area. *Geological Magazine*, 132: 15-30.

Fortey R.A., Harper D.A.T., Ingham J.K., Owen A.W., Parkes, M.A., Rushton A.W.A. & Woodcock N. (2000) – Revised correlation of Ordovician rocks in the British Isles. Geological Society of London, London, 86 pp.

Gorjansky V.Iu. & Popov L.E. (1985) - Morfologiia, systematicheskoe polozhenie I proiskhozhdenie bezzamkovykh brakhiopods karbonatnoi rakovinoi [Morphology, systematic position and origin of the inarticulate brachiopods with calcareous shells]. *Paleontologicheskii Zhurnal*, 1985(3): 3-14 [in Russian].

Hall J. & Clarke J.M. (1892) - An introduction to the study of the genera of Palaeozoic Brachiopoda, Natural History of New York, Palaeontology, vol. 8, part 1. New York Geological Survey. Charles van Benthuysen & Sons, Albany, 367 pp.

Hammer Ø., Harper D.A.T. & Ryan P.D. (2001) - PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4. http://palaeo-electronica.org/2001-1/past/issue1_01.htm

Hansen J. (2008) - Upper Ordovician brachiopods from the Arnestad and Frognerkilen formations in the Oslo-Asker district, Norway. *Palaeontos*, 13: 1-99.

Hansen J. & Harper D.A.T. (2008) - The late Sandbian-earliest Katian (Ordovician) brachiopod immigration and its influence on the brachiopod fauna in the Oslo Region, Norway. *Lethaia*, 41: 25-35.

Harper D.A.T. (2000) - Dalmanellidina. In: Kaesler R.L. (Ed.) - Treatise on Invertebrate Paleontology, part H, Brachiopoda, Revised, Volume 3: Rhynchonelliformea (part): 782-844. The Geological Society of America and The University of Kansas. Boulder, Colorado and Lawrence, Kansas.

Harper D.A.T., Mitchell W.I., Owen A.W. & Romano M. (1985) - Upper Ordovician brachiopods and trilobites from the Clashford House Formation, near Herbertstown, Co. Meath, Ireland. *Bulletin of the British Museum (Natural History), Geology Series*, 38(5): 287-308.

Harper D.A.T., Parkes M.A. & Zhan Ren-Bin (2017) - Late Ordovician deep-water brachiopod fauna from Raheen, Waterford Harbour, Ireland. *Irish Journal of Earth Sciences*, 35: 1-18.

Harper D.A.T. & Wright A.D. (1996) - Brachiopods: 63–94. In: Harper D.A.T. & Owen A.W. (Eds) - Fossils of the Upper Ordovician. Palaeontological Association Field Guides to Fossils, 7: 63-94. The Palaeontological Asso-

ciation, London.
Havlíček V. (1950) - Ramenonožci českého ordoviku. *Rozpravy Ústředního ústavu geologického*, 13: 1-72.
Havlíček V. (1951) - The Ordovician Brachiopoda from Bohemia. *Rozpravy Ústředního ústavu geologického*, 12: 1-135.
Havlíček V. (1977) - Brachiopods of the order Orthida in Czechoslovakia. *Rozpravy Ústředního ústavu geologického*, 44: 1-327.
Havliček V. (1980) - Inarticulate brachiopods in the Lower Ordovician of the Montagne Noire. (South France). *Mémoire de la Société d'Études scientifiques de l'Aude*, 1980: 3-11.
Havliček V. (1982) - Lingulacea, Paterinacea, and Siphonotretacea (Brachiopoda) in the Lower Ordovician sequence of Bohemia. *Sbornik geologickych věd, Paleontologie*, 25: 9-82.
Havlíček V. & Branisa L. (1980) - Ordovician brachiopods of Bolivia (Succession of assemblages, climate control, affinity to Anglo-French and Bohemian provinces). *Rozpravy Československé akademie věd*, 90: 1-54.
Herbosch A. & Verniers J. (2014) - Stratigraphy of the Lower Palaeozoic of the Brabant Massif, Belgium. Part II: The Middle Ordovician to lowest Silurian of the Rebecq Group. *Geologica Belgica*, 17: 115-136.
Hints L. (1975) - Ordovician brachiopods: Enteletacea of the East Baltic area. Eesti NSV Teaduste Akadeemia Geoloogia, Tallinn, 117 pp. [in Russian].
Hurst J.M. (1978a) - A phenetic strategy model for dalmanellid brachiopods. *Palaeontology*, 21(3): 535-554.
Hurst J.M. (1978b) - Morphological variation in some Lower Palaeozoic dalmanellid brachiopods. *Paleontologicheskii Zhurnal*, 52: 246-256.
Hurst J.M. (1979a) - The stratigraphy and brachiopods of the upper part of the type Caradoc of south Salop. *Bulletin of the British Museum* (*Natural History*), *Geology*, 32: 183-304.
Hurst J.M. (1979b) - The environment of deposition of the Caradoc Alternata Limestone and contiguous deposits of Salop. *Geological Journal*, 14(1): 15-40.
Jones C.R. & Siveter D.J. (1983) - On *Harperopsis scripta* (Harper). *Stereo-atlas of ostracod shells*, 10: 5-12.
Jones O.T. (1928) - *Plectambonites* and some allied genera. *Memoirs of the Geological Survey of Great Britain, Palaeontology,* 12(5): 367-527.
Lecrenier A. (1887) - Sur des fossiles siluriens de Huy. *Annales de la Société géologique de Belgique*, 14 (Bulletin): 182-183.
Lefebvre B., Javier Álvaro J., Casas J.M., Ghienne J.-F., Herbosch A., Loi A., Monceret E., Verniers J., Vidal M., Vizcaïno D. & Servais T. (2023) - The Ordovician of France and neighbouring areas of Belgium and Germany. *Geological Society, London, Special Publications*, 532: 375-408.
Liljeroth M., Harper D.A.T., Carlisle H. & Nielsen A.T. (2017) - Ordovician rhynchonelliformean brachiopods from Co. Waterford, SE Ireland: Palaeobiogeography of the Leinster Terrane. *Fossils and Strata*, 62: 1-164.
Lockley M.G. (1980) - The Caradoc faunal associations of the area between Bala and Dinas Mawddy, north Wales. *Bulletin of the British Museum* (*Natural History*), *Geology*, 33: 165-235.
Lockley M.G. (1983) - A review of brachiopod dominated palaeocommunities from the type Ordovician. *Palaeontology*, 26(1): 111-145.
Lohest M. & Forir H. (1900) - Quelques découvertes intéressantes faites pendant les excursions du cours de géologique de l'Université de Liége. *Annales de la Société géologique de Belgique*, 27 (Bulletin): 161-163.
Maillieux E. (1926) - Remarques sur l'Ordovicien de la Belgique. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 27 (Procès-verbaux): 67-85.
Maillieux E. (1933) - Terrains, roches et fossiles de la Belgique. Deuxième édition revue et corrigée. Patrimoine du Musée royal d'Histoire naturelle de Belgique, Bruxelles, 217 pp.
Maillieux E. (1938a) - Observations nouvelles sur l'Ordovicien de la Belgique. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 48 (Procès-verbaux): 22-23.
Maillieux E. (1938b) - Compte rendu de l'excursion de la Société belge de Géologie à Sart-Bernard et à Naninne, le 30 juin 1938. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, 48 (Procès-verbaux): 338-341.
Maillieux E. (1939) - L'Ordovicien de Sart-Bernard. *Mémoires du Musée royal d'Histoire naturelle de Belgique*, 86: 1-59.
Malaise C. (1873) - Description du terrain silurien du centre de la Belgique. *Mémoires couronnés et mémoires des savants étrangers publiés par l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 37: 1-122.
Malaise C. (1887a) - Observations sur la lettre précédente. *Annales de la Société géologique de Belgique*, 14 (Bulletin): 183.
Malaise C. (1887b) - Observations sur quelques graptolithes de la bande silurienne de Sambre-et-Meuse. *Annales de la Société géologique de Belgique*, 14 (Bulletin): 183-184.
Malaise C. (1888a) - Découverte de la faune de la base du Silurien en Belgique. *Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 3e série, 15: 365-367.
Malaise C. (1888b) - Les schistes siluriens de Huy et leur signification géologique. *Annales de la Société géologique de Belgique*, 15 (Bulletin): 39-44.
Malaise C. (1888c) - A propos des schistes siluriens de Huy. *Annales de la Société royale malacologique de Belgique*, 23 (Bulletin des séances): 10-13.
Malaise C. (1890) - Sur les graptolithes de Belgique. *Bulletin de l'Académie royale des Sciences, des Lettres et des Beaux-Arts de Belgique*, 3e série, 20: 440-452.
Malaise C. (1894a) - Sur l'aspect llandeilien du massif d'Oxhe. *Annales de la Société géologique de Belgique*, 21 (Bulletin): 108-110.
Malaise C. (1894b) - Sur la découverte de *Beyrichia* dans le Silurien belge. *Annales de la Société géologique de Belgique*, 21 (Bulletin): 95.
Malaise C. (1899) - Espèces nouvelles de la bande silurienne de Sambre-et-Meuse. *Annales de la Société géologique de Belgique*, 24 (pro 1897) (Mémoires): 257-261.
Malaise C. (1900a) - Etat actuel de nos connaissances sur le Silurien de la Belgique (à continuer). *Annales de la Société géologique de Belgique*, 25bis: 179-216.
Malaise C. (1900b) - A propos du massif silurien du Fond d'Oxhe. *Annales de la Société géologique de Belgique*, 27 (Bulletin): 167-168.
Malaise C. (1901a) - Etat actuel de nos connaissances sur le Silurien de la Belgique (fin). *Annales de la Société géologique de Belgique*, 25bis: 217-221.
Malaise C. (1901b) - Sur le Silurien de Belgique. In: Congrès géologique international. Comptes rendus de la 8e session en France, tenu à Paris du 16 au 20 août 1900. Premier fascicule: pp. 561-571. Le Bigot Frères, Paris.

Malaise C. (1911) - Sur l'évolution de l'Echelle stratigraphique du Siluro-cambrien de Belgique. *Annales de la Société géologique de Belgique*, 38: BB7-BB28.

Martin F. (1969) - Les Acritraches de l'Ordovicien et du Silurien Belge. Détermination et valeur stratigraphique. *Mémoires de l'Institut royal des Sciences naturelles de Belgique*, 160 (pro 1968): 1-175.

M'Coy F. (1846) - A synopsis of the Silurian fossils of Ireland collected from the several districts by Richard Griffith F.G.S. Privately published, Dublin, 72 pp.

Menke C.T. (1828) - Synopsis methodica molluscorum generum omnium et specierum earum quae in Museo Menkeano adservantur. G. Uslar, Pyrmonti, 91 pp.

Mergl M. (2002) - Linguliformean and craniiformean brachiopods of the Ordovician (Třenice to Dobrotiva Formations) of the Barrandian, Bohemia. *Acta Musei Nationalis Pragae, Series B, Natural History*, 58(1-2): 1-82.

Michot P. (1934) - Le massif ordovicien du Fond d'Oxhe. *Annales de la Société géologique de Belgique*, 57(4): B59-B79.

Michot P. (1954) - Le Silurien. In: Fourmarier, P. (Ed.) - Prodrome d'une description géologique de la Belgique: 39-82. Société géologique de Belgique, Liège.

Michot P. (1957) - Assise d'Oxhe (ou Fond d'Oxhe). In: Waterlot G. (Ed.) - Fascicule 4a: France, Belgique, Pays-Bas, Luxembourg. Fascicule 4a1: Antécambrien et Paléozoïque inférieur. In: Pruvost P. (Ed.) - Lexique Stratigraphique International. Volume 1 (Europe): 316-317. C.N.R.S, Paris.

Michot P. (1969) - La faille d'Ombret. *Annales de la Société géologique de Belgique*, 92(2): 243-254.

Moore R.C. (1952) - Brachiopoda. In: Moore R.C., Lalicker C.G. & Fischer A.G. - Invertebrate Fossils: 197-267. McGraw-Hill, New York.

Mortier J., Vanmeirhaeghe J., Harper D.A.T., Štorch P., Zalasiewicz J., Van Den Haute P., Deckers J., Mestdagh T., Pille T. & Verniers J. (2024) - Stratigraphy, biostratigraphy, and chitinozoans of the uppermost Ordovician and Silurian of the Condroz Inlier. *Memoirs of the Geological Survey of Belgium,* 65: 1-239.

Mottequin B. (2021) - Earth science collections of the Centre Grégoire Fournier (Maredsous) with comments on Middle Devonian–Carboniferous brachiopods and trilobites from southern Belgium. *Geologica Belgica*, 24(1-2): 33-68.

Mottequin B., Marion J.-M. & Delcambre B. (2021) - Carte géologique de Wallonie: Huy – Nandrin 48/3-4. 1/25 000. Service public de Wallonie, Agriculture, Ressources naturelles et Environnement, Namur, avec une notice explicative de 115 p.

Öpik A.A. (1930) - Brachiopoda Protremata der Estländischen Ordovizischen Kukruse-Stufe. *Universitatis Tartuensis (Dorpatensis) Acta et Commentationes, series A*, 17: 1-262.

Öpik A.A. (1934) - Über die Klitamboniten. *Tartu Ulikooli Geoloogia-Instituudi Toimestuesed Acta et Commentationes Universitatis Tartuensis*, 39: 1-239.

Owens R.M. & Servais T. (2007) - The Ordovician of the Condroz Inlier, Belgium: Trilobites from the southeastern margin of Avalonia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 245: 272-294.

Parkes M.A. (1994) - The brachiopods of the Duncannon Group (Middle-Upper Ordovician) of southeast Ireland. *Bulletin of the Natural History Museum (Geology)* 50(2): 105-174.

Paškevičius J. (1994) - Baltijos Respublikų Geologija [=The Geology of the Baltic Republics]. Vastybinis leidybos centras, Vilnius, 447 pp. [in Lithuanian].

Pickerill R.K. & Brenchley P.J. (1979) - Caradoc marine benthic communities of the South Berwyn Hills, North Wales. *Palaeontology*, 22(1): 229-264.

Pohl A., Nardin E., Vandenbroucke T.R.A. & Donnadieu Y. (2016) - High dependence of Ordovician ocean surface circulation on atmospheric CO2 levels. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 458: 39-51.

Popov L.E., Bassett M.G., Holmer L.E. & Laurie J.R. (1993) - Phylogenetic analysis of higher taxa of Brachiopoda. *Lethaia*, 26: 1-5.

Popov L.E. & Pushkin V.I. (1986) – Ordovikskie bezzamkovye brahiopody ûžnoj Pribaltiki [Ордовикские беззамковые брахиоподы южной Прибалтики]. *Novyie i maloizvestnye vidy iskopaemykh životnyh i rastenij Belorussii*: 11-22. Nauka i Tekhnika, Minsk.

Potter A.W. & Boucot A.J. (1992) - Middle and late Ordovician brachiopod benthic assemblages of North America. In: Webby B.D. & Laurie J.R. (Eds) - Global perspectives on Ordovician Geology: 307-323. Balkema, Rotterdam.

Rasmussen C.M.Ø. (2011) - Final destination, first discovered: the tale of *Oanduporella* Hints, 1975. In: Gutiérrez-Marco J.C., Rábano I. & García-Bellido D. (Eds) - Ordovician of the World: 447-454. Cuadernos del Museo Geominero, 14. Instituto Geológico y Minero de España, Madrid.

Rasmussen C.M.Ø., Harper D.A.T. & Blodgett R.B. (2012) - Late Ordovician brachiopods from west-central Alaska: systematics, ecology and palaeobiogeography. *Fossils and Strata,* 58:1-103

Reed F.R.C. (1910) - New fossils from the Dufton Shales. *Geological Magazine*, 7(5): 211-220, 294-299.

Rong J.-y. & Cocks L.R.M. (1994) - True *Strophomena* and a revision of the classification and evolution of strophomenoid and 'strophodontid' brachiopods. *Palaeontology*, 37(3): 651-694.

Salter J.W. (1852) - A systematic description of Palaeozoic fossils in the Geological Museum of the University of Cambridge. Appendix A. Description of a few species from Wales and Westmoreland referred to in the foregoing work [Appendix to Sedgwick A. & McCoy F. 1851], i-viii.

Salter J.W. & Aveline W.T. (1854) - On the "Caradoc Sandstone" of Shropshire. *Quarterly Journal of the Geological Society, London,* 10: 62-75.

Schallreuter R., Verniers J. & De Geest P. (2000) - An Ordovician ostracod from Belgium. *Neues Jahrbuch für Geologie und Paläontologie*, *Monatshefte*, 2000(9): 570-576.

Schuchert C. (1893) - Classification of the Brachiopoda. *American Geologist*, 11: 141-167.

Schuchert C. (1913) - Class 2. Brachiopoda. In: von Zittel K. A. (Ed.) - Text-book of Palaeontology, vol. 1, part 1, 2nd edition, translated and edited by C. R. Eastman: 355-420. MacMillan and Co. Ltd., London.

Schuchert C. & Cooper G.A. (1932) - Brachiopod genera of the suborders Orthoidea and Pentameroidea. *Memoirs of the Peabody Museum of Natural History*, 4(1): 1-270.

Sedgwick A. & M'Coy F. (1852) - A synopsis of the classification of the British Palaeozoic rocks, with a systematic description of the British Palaeozoic fossils in the geological Museum of the University of Cambridge. London and Cambridge, xcviii + 661 pp., 25 pls.

Servais T. & Maletz J. (1992) - Lower Llanvirn (Ordovician) graptolites and acritarchs from the 'Assise de Huy', Bande de Sambre-et-Meuse, Belgium. *Annales de la Société*

géologique de Belgique, 115(1): 265-285.
Sheehan P.M. (1987) - Late Ordovician (Ashgillian) brachiopods from the region of the Sambre and Meuse Rivers, Belgium. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 57: 5-81.
Sinclair G.W. (1946) - *Bancroftina*, a new brachiopod name. *Journal of Paleontology*, 20: 295.
Siveter D.J. (1984) - Ecology of Silurian ostracods. *Special Papers in Palaeontology*, 32: 71-85.
Siveter D.J. (2009) - Ordovician. In: Whittaker J.E. & Hart M.B. (Eds) - Ostracods in British Stratigraphy: 15-44. The Geological Society for the Micropalaeontological Society, Special Publications, London.
Sowerby J. de C. (1839) - Mollusca and Conchifers. In: Murchison R.I. - The Silurian System, Part 2. Organic remains: 577-768. J. Murray, London.
Suárez-Soruco R. (1992) - El Paleozoico Inferior de Bolivia y Perú. In: Gutiérrez-Marco J.C., Saavedra J. & Rábano I. (Eds.) - Paleozoico Inferior de Ibero-América: 225-239. Universidad de Extremadura, Mérida.
Vanmeirhaeghe J. (2006) - The evolution of the Condroz-Brabant Basin from Middle Ordovician to Llandovery: lithostratigraphical and chitinozoan biostratigraphical approach. Unpublished Ph.D. thesis, Ghent University, Belgium.
Vanmeirhaeghe J. (2007a) - Chitinozoans of the lower Llanvirn Huy and the middle Caradoc Sart-Bernard formations (Middle to Upper Ordovician): implications for the stratigraphy of the Condroz Inlier (Belgium). *Carnets de Géologie/Notebooks on Geology*, M01/10: 59-67.
Vanmeirhaeghe J. (2007b) - Review of the lithostratigraphy of the Middle Ordovician to Llandovery of the Condroz Inlier (Belgium) by chitinozoan biostratigraphy: does the sedimentary succession record the Ardennian deformation? *Geologica Belgica*, 10: 162-164.
Verniers J., Herbosch A., Vanguestaine M., Geukens F., Delcambre B., Pingot J.-L., Belanger I., Hennebert M., Debacker T., Sintubin M. & De Vos W. (2002) - Cambrian-Ordovician-Silurian lithostratigraphic units (Belgium). *Geologica Belgica*, 4 (pro 2001): 5-38.
Waagen W.H. (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.
Waagen W.H. (1885) - Salt Range fossils, vol. 1, part 4. Productus Limestone fossils, Brachiopoda. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, *series* 13, 5: 729-770.
Waisfeld B.G. & Henry J.L. (2003) - *Huemacaspis* (Trilobita, Kerfornellinae) from the Late Ordovician of the Argentine Cordillera Oriental. *Geobios*, 36: 491-499.
Whittington H.B. (1938) - New Caradocian brachiopods from the Berwyn Hills, North Wales. *Annals and Magazine of Natural History*, *series 11*, 2: 241-259.
Williams A. (1962) - The Barr and Lower Ardmillan Series (Caradoc) of the Girvan District, South-west Ayrshire, with descriptions of the Brachiopoda. *Geological Society of London Memoir*, 3: 1-267.
Williams A. (1963) - The Caradocian brachiopod faunas of the Bala District, Merionethshire. *Bulletin of the British Museum (Natural History), Geology*, 8(7): 327-471.
Williams A. (1974) - Ordovician Brachiopoda from the Shelve District, Shropshire. *Bulletin of the British Museum (Natural History), Geology, Supplement*, 11: 1-163.
Williams A., Carlson S.J., Brunton C.H.C., Holmer L.E. & Popov L.E. (1996) - A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London, series B*, 351: 1171-1193.
Williams A. & Wright A.D. (1963) - The classification of the "*Orthis testudinaria* Dalman" group of brachiopods. *Journal of Paleontology*, 37: 1-32.
Wright A.D. (1964) - The fauna of the Portrane Limestone II. *Bulletin of the British Museum (Natural History), Geology*, 9: 137-256.