

The Ordovician of the Condroz Inlier, Belgium: Trilobites from the southeastern margin of Avalonia

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Abstract

During the Early Palaeozoic, Belgium was located in the eastern part of the microcontinent of Avalonia, which moved from high to low latitudes during the course of the Ordovician. In the Belgian Condroz Inlier (“Bande de Sambre-et-Meuse”), Ordovician trilobites have been reported from four formations: the early Llanvirn Huy Formation, the Caradoc Sart-Bernard and Oxhe formations, and the Ashgill Fosses Formation. These assemblages are some of the easternmost occurrences of trilobites in Avalonia, and they include aspects that are particularly interesting from a palaeobiogeographical standpoint.

The trilobite faunas of the Huy and Sart-Bernard formations are revised in detail, while the others are discussed more briefly, having been redescribed in recent years. The Huy Formation belongs to a biofacies characteristic of the outer shelf/upper slope, and its faunas are typically Avalonian, almost identical to those recorded from the Skiddaw Group of northern England, and from the Ebbe and Remscheid anticlines in the Rhenish Massif, Germany. *Pricyclopyge binodosa*, which is inferred to be mesopelagic, is common to all these areas, and also occurs in Bohemia and Armorica. *Placoparia cambriensis* has a remarkably wide distribution in the early Llanvirn, and has been recorded from a range of biofacies across Avalonia, Armorica, Morocco and Bohemia. It is suggested that this species may have been epipelagic. Re-examination of the trilobites from the Sart-Bernard Formation has confirmed that all are conspecific with, or compare closely with Bohemian taxa. The trilobite assemblages of the Oxhe Formation are typical eastern Avalonian faunas, while the Ashgill Fosses Formation assemblage has much in common with those of other parts of Armorica, as well as with Baltica and Bohemia, attesting to the increasing proximity of Avalonia, Baltica and the Prague Basin during the latest Ordovician.

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1. Introduction

The Condroz Inlier (“Bande de Sambre-et-Meuse”), along with the Brabant Massif and the Ardenne inliers, is

one of the areas of outcrop of Lower Palaeozoic rocks in Belgium. While trilobites have not been reported from the Ordovician of the Ardennes, and only from the uppermost Ordovician (Ashgill) of the Brabant Massif, several assemblages have been recorded from the Condroz Inlier, from four formations: the early Llanvirn (early Abereiddian) Huy Formation, the Sart-Bernard Formation (attributed herein to the middle Caradoc,

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broadly equivalent to the British Burrellian Stage), the middle Caradoc (late Burrellian, Longvillian Substage) Oxhe Formation and the early to middle Ashgill (Pusgillian to Rawtheyan) Fosses Formation.

It is today widely accepted that the Belgian Ordovician sediments were deposited on the southeastern border of the microcontinent of Avalonia (Cocks et al., 1997; Servais and Fatka, 1997; Verniers et al., 2002). The trilobites of the Condroz Inlier should therefore palaeogeographically reflect the rifting from Gondwana during the early Ordovician and the migration of Avalonia northwards towards collision with Baltica during the late Ordovician. The Ordovician palynomorphs (acritarchs and Chitinozoa) of Belgium clearly indicate a shift from peri-Gondwanan (cold-water) assemblages in the early and early middle Ordovician towards (temperate to warm water) Baltic assemblages in the late Ordovician (Servais and Maletz, 1992; Samuelsson and Verniers, 2000; Servais et al., 2003; Vanmeirhaeghe and Verniers, 2004).

The objective of this paper is to discuss the affinities, in terms of taxonomy, palaeobiogeography and palaeoecology, of the trilobite faunas of the Ordovician of the Condroz Inlier. The assemblages from the Huy, Sart-Bernard, Oxhe and Fosses Formations are compared with those from England and Wales, and also with those described from western Germany (Ebbe Anticline, Rhenish Massif), the Prague Basin and from Armorica. The assemblages are integrated into a model of trilobite biofacies and are plotted on a palaeogeographic reconstruction.

2. Geological setting

2.1. The Condroz Inlier (“Bande de Sambre-et-Meuse”)

Cambrian to Silurian sediments in Belgium crop out in three different areas: in the northern part in the Brabant Massif; in the southeastern part in the Ardenne inliers, traditionally called “massifs” (from west to east: the Rocroi, Givonne, Serpont and Stavelot Inliers), and in the central part, south of the Sambre and Meuse rivers, in the Condroz Inlier, that is also named “Bande condrusienne” or “Bande de Sambre-et-Meuse”.

All these massifs or inliers are overlain unconformably by Upper Palaeozoic sediments. Belgian geologists have focused most of their studies on these world-famous Devonian and Carboniferous sequences, that have provided many names for internationally used geological series and stages. In contrast, the Lower Palaeozoic has been investigated to a lesser extent, and detailed reinvestigations started only during the 1980s.

The stratigraphical succession of the Cambrian to Silurian sediments, traditionally named the Caledonian

rocks in Belgian literature, was summarized by Verniers et al. (2001), who listed all the lithostratigraphical units. While the investigations on the Brabant Massif and the Ardenne inliers provided a detailed knowledge of the litho- and biostratigraphy of these areas (Verniers et al., 2001; Herbosch and Verniers, 2002), the Condroz Inlier has remained poorly known, and the lithological succession is still partly unresolved. This area of outcrop is currently in the progress of being restudied and remapped. Detailed definitions and descriptions of its constituent formations, with precise biostratigraphical dating should therefore be available in the coming years.

The Condroz Inlier is a long and narrow band of outcrops, directed WSW–ENE, parallel to and south of the Sambre and Meuse Rivers (Fig. 1). It is about 65 km long, but only 0.5 km to 4 km wide. The westernmost outcrops are to the east of Charleroi; eastwards, it extends almost as far as Liège. The outcrops consist of sedimentary rocks ranging from early Ordovician to late Silurian age, predominantly siliciclastics, generally not turbiditic and partially calcareous in the uppermost Ordovician (Ashgill). Mostly deposited in a deeper shelf setting, the sediments were attributed to the Condroz Shelf (Verniers et al., 2001, 2002).

The various components of the Condroz Inlier are brought together as at least four inliers along the Midi Overthrust that separates the Namur and Dinant synclinoria, which are composed of Devonian–Carboniferous sediments. They all result from Variscan deformation, and together comprise the Condroz Inlier. They are (Fig. 1):

- (1) a small northern inlier at Ombret (the Ombret Inlier);

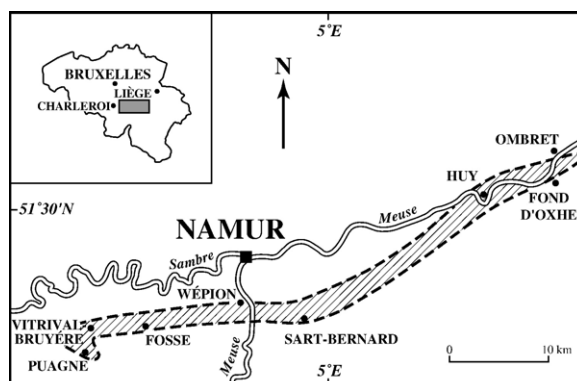


Fig. 1. Location of the Condroz Inlier, Belgium. The shaded area represents the ‘Bande de Sambre-et-Meuse’, and includes the main Ordovician inlier, extending approximately from Vitruval-Bruyère to the east of Huy, together with the smaller subsidiary inliers at Ombret, Oxhe and Puagne.

- (2) a major central inlier (the Condroz Inlier *sensu stricto*);
- (3) a small southeastern inlier between Huy and Liège: the Oxhe Inlier (also named the Fond d'Oxhe Window);
- (4) a small inlier in the southwestern part near Charleroi: the Puagne Inlier.

The original research on the numerous discontinuous outcrops during the 19th century was followed by more detailed investigations towards its end and during the earlier part of the 20th century. A stratigraphical succession and a first general overview was published by Malaise (1910). Subsequently, after studying additional outcrops, Maillieux (e.g. 1926, 1938, 1939) modified the stratigraphical scheme by adding some new formation names. Michot (1928, 1932a,b, 1934) mapped the area in detail and provided a further stratigraphical scheme and a tectonic scenario. By redating the complete Ordovician–Silurian succession with acritarchs, Martin (1969) introduced further lithological units, subdividing the Ordovician sequence into six formations (“assises”), from base to top, the units of Wépion, Huy, Sart-Bernard, Vitrival-Bruyère, Oxhe and Fosses (for a summary of the concept of the Ordovician stratigraphy, see Servais and Maletz, 1992). Four additional formation names were used subsequently: the Tier d’Olné Formation and the Ombret Formation were described from the Ombret Inlier (Martin et al., 1970; Vanmeirhaeghe and Verniers, 2002); the Basse-aux-Canes Formation was considered a part of the Vitrival-Bruyère Formation by Michot (1934) and Martin (1969), but has recently been mapped as an independent unit in the Puagne Inlier (Delcambre and Pingot, 2004); and the Génicot Formation has recently been described from the westernmost extension of the Condroz Inlier (Delcambre and Pingot, 2004; Vanmeirhaeghe and Verniers, 2004).

Because the outcrop conditions are poor, as continuous sections are rare, and because, in addition, contrasting lithological units occur in different inliers, it remains difficult to correlate some of the formations. Except for the youngest Ordovician formations (Fosses and Génicot) that can easily be distinguished, most of the lithological units consist of grey to black siliciclastics which are poorly fossiliferous. The thickness of most formations can be estimated only roughly (Verniers et al., 2001). Macrofossils are usually rare and sometimes completely absent. Organic-walled microfossils (acritarchs and Chitinozoa) have been described from most units (for a summary of the biostratigraphical data, see Verniers et al., 2001). Because the age of many of the units remains unclear, the succession and correlation of

some of them is not yet fully understood; acritarchs and Chitinozoa give the best prospects for a refined stratigraphy and correlation.

2.2. The Ordovician sequence of the Condroz Inlier (Fig. 2)

The British regional series and stages have traditionally been used in the Belgian Lower Palaeozoic. Fig. 2 shows the correlation of the different formations of the Condroz Inlier with them, and also with the Global Series and Stages and with the time-slices of Webby et al. (2004). Taking into account that the lithological units occur in four different inliers and that the formation names can change from one inlier to another, the stratigraphy of the different units of the Condroz Inlier can be summarized as follows.

Most of the Ordovician formations have been described from central part of the Condroz inlier, which is over 60 km long. The oldest, dated by graptolites and acritarchs, is the Chevlipont Formation (formerly the “assise de Wépion”) of early Tremadoc age (Graulich, 1961; Martin, 1969), equivalent to the Ordovician time-slice 1a of Webby et al. (2004). It is present only in the Wépion borehole, where it is overlain unconformably by the Huy Formation (Graulich, 1961; Verniers et al., 2001). No Cambrian sediments have been recorded in the Condroz Inlier.

The Huy Formation was reinvestigated by Servais and Maletz (1992) from a number of localities in the Condroz Inlier. These authors confirmed its early Llanvirn *Didymograptus artus* graptolite Biozone age, based on graptolites and acritarchs, equivalent to the time-slice 4b of Webby et al. (2004), i.e. corresponding to the Middle Darriwilian (see below).

The nature of the contact with the overlying Sart-Bernard Formation is obscure. The age of this latter formation, first described by Maillieux (1939), remained uncertain, and until recently it was attributed to the Llanvirn (e.g. Verniers et al., 2001). There is now no doubt, however, that it is of early to middle Caradoc age (see below). The Sart-Bernard Formation was described (Maillieux, 1939) from the railway cutting at Sart-Bernard, in the central part of the Condroz Inlier, and its relation to the Vitrival-Bruyère Formation, found in the western and central parts of the same inlier is not fully understood. The Sart-Bernard Formation was recently mapped in the Puagne Inlier where it underlies the Basse-aux-Canes Formation (Delcambre and Pingot, 2004).

The Vitrival-Bruyère Formation, described originally by Maillieux (1926) and Michot (1928) from the western part of the Condroz Inlier, provided a few graptolites attributed to the *Climacograptus peltifer* (i.e. *Diplograptus*

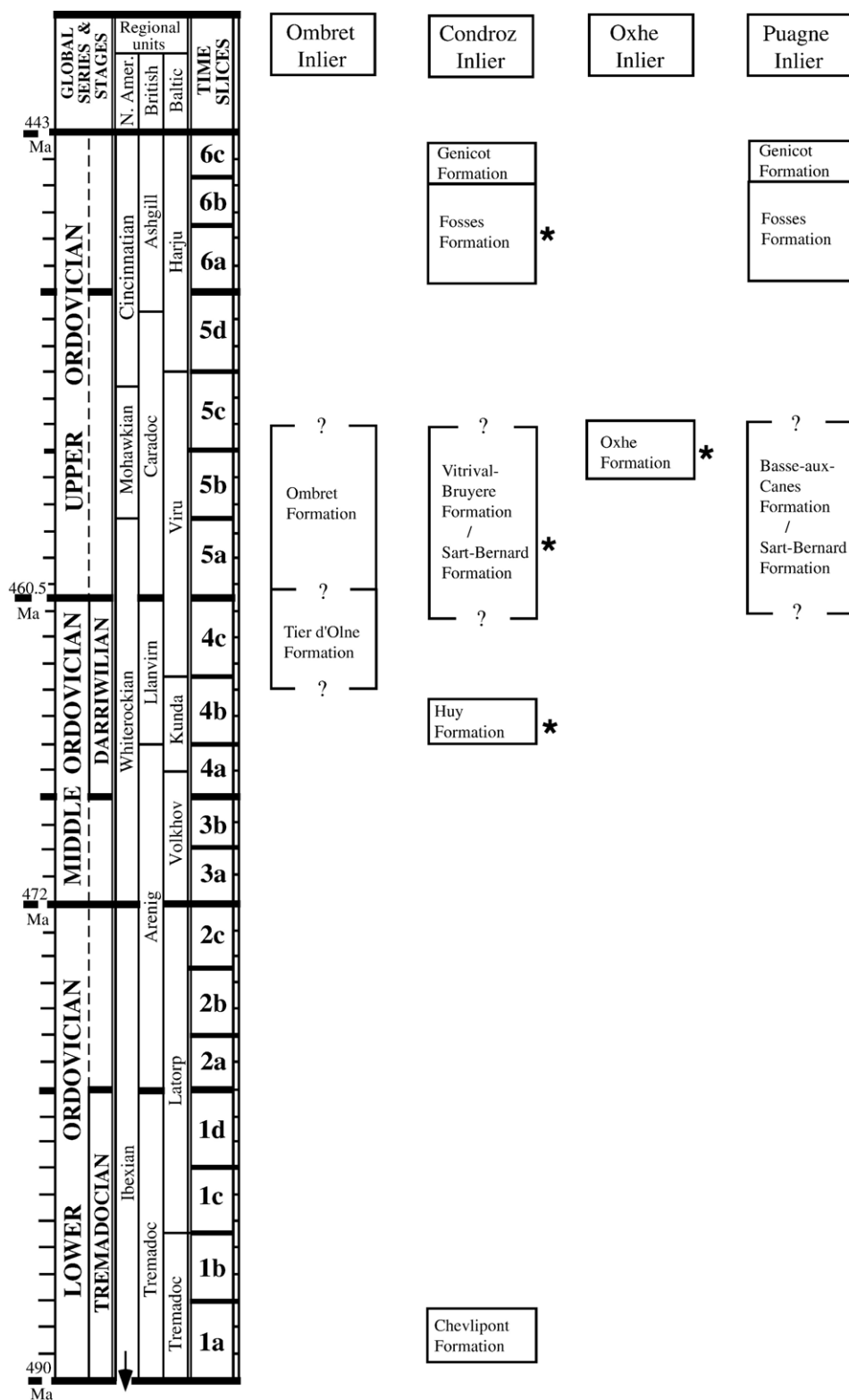


Fig. 2. Stratigraphical correlation table of Ordovician formations in the Condroz Inlier, Belgium. Left hand column after Webby et al. (2004). Asterisks indicate the formations that contain trilobites.

foliaceus) Biozone by Bulman (1950). These graptolites indicate an early (but not earliest) to middle Caradoc age, equivalent to the time-slice 5b and the lower part of time-slice 5c of Webby et al. (2004). Graptolites have not been recovered subsequently, but recent investigations of Chitinozoa from this formation (Billiaert, 2000; Herbosch and Verniers, 2002) provided a broad late Llanvirn to early Caradoc age. The presence of *Cyathochitina calix* and *Laufeldochitina stentor* indicates a correlation with time-slice 4c and/or time-slice 5a of Webby et al. (2004).

Two additional formations have been described from the westernmost part of the central Condroz Inlier (and from the Puagne Inlier, located in the same area). The Fosses Formation is highly fossiliferous and has been recognized since the mid-19th century. The brachiopods and trilobites were described by Sheehan (1988) and Lespérance and Sheehan (1988), the crinoids, bryozoans, echinoderm debris, cystoids, molluscs and algae by Tourneur et al. (1993), the corals (rugose and tabulate) by Servais et al. (1997), and the Chitinozoa by Vanmeirhaeghe and Verniers (2004). This formation, which includes clayey limestones and calcareous shales, that are most probably related to the Boda Event (Fortey and Cocks, 2005), can be attributed to a pre-Hirnantian Ashgill age by different fossil groups. The Chitinozoa assemblages indicate the presence of the Baltoscandian *Tanuchitina bergstroemi* Biozone in the lower part of the formation and the *Conochitina rugata* Biozone in the upper half (Billiaert, 2000; Herbosch and Verniers, 2002; Vanmeirhaeghe and Verniers, 2004). The Fosses Formation thus correlates with the time-slices 6a and 6b of Webby et al. (2004). A detailed biostratigraphical revision, based on Chitinozoa, is currently in progress (Vanmeirhaeghe, pers. comm., 2006).

The Génicot Formation, previously included partly in the Fosses Formation as the Faulx-les-Tombes Member by Martin (1969), has recently been described and mapped by Delcambre and Pingot (2004) as a separate unit. Chitinozoa indicate a late Ashgill age (Vanmeirhaeghe and Verniers, 2004), because the formation was deposited above the regional P4 Chitinozoa Biozone, which is correlated with the upper part of the Rawtheyan. The formation can thus be correlated with the late Ashgill time-slice 6c of Webby et al. (2004). The Génicot Formation includes conglomeratic levels that have been interpreted as being possibly the sedimentological expression of the sea level drop associated with the Hirnantian glaciation (Herbosch and Verniers, 2002; Vanmeirhaeghe and Verniers, 2004).

Four other formations have been described from the three smaller inliers (Fig. 2). The Oxhe Inlier is constituted almost entirely by the Oxhe Formation,

except for small outcrops at its extremities that were attributed to an unnamed unit (now known to belong to the Huy Formation, see below) and to the lower Silurian (Dean, 1991). The Oxhe Formation has so far not been reported elsewhere. It was demonstrated by Dean (1991), on the basis of trilobites, to belong to the Longvillian Substage of the Burrellian Stage based on Chitinozoa assemblages (De Geest, 1998; Verniers et al., 2001). The formation should thus correspond to the upper part of time-slice 5b and/or to the lower part of time-slice 5c of Webby et al. (2004).

The small Ombret Inlier to the north of the central part of the Condroz Inlier comprises the Ombret Formation, dated by palynomorphs (acritarchs and Chitinozoa) as Caradoc (Martin et al., 1970), and the recently described Tier d'Ogne Formation, that was provisionally attributed to an interval spanning the early Llanvirn to the early–middle Caradoc (Vanmeirhaeghe and Verniers, 2002). The Ombret Formation comprises a sandstone-slate unit that shows greatest similarities with the Ittre Formation in the Brabant Massif. This latter formation has been attributed to the early to middle Caradoc (Servais et al., 1993; Samuelsson and Verniers, 2000). The Ombret Formation can thus possibly be correlated with time-slice 5a of Webby et al. (2004), but further detailed biostratigraphical investigations based on Chitinozoa are needed. A biostratigraphical investigation of the Tier d'Ogne Formation is currently in progress (Vanmeirhaeghe, pers. comm., 2006). It apparently underlies the Ombret Formation and is possibly a lateral equivalent of the Sart-Bernard Formation (and perhaps also the Huy Formation).

In the Puagne Inlier, in the southwestern part of the Condroz Inlier, Delcambre and Pingot (2004) mapped and named the Basse-aux-Canes Formation, which overlies the Sart-Bernard Formation. According to Herbosch and Verniers (2002), this unit resembles the Vitruval-Bruyère Formation, which crops out farther to the east, but it does not contain the sandstone beds of the latter. The Basse-aux-Canes Formation is unfossiliferous and, according to several authors (Michot, 1934; Martin, 1969), is a part of the Vitruval-Bruyère Formation. Verniers et al. (2001) considered it to be a possible lateral facies change of (and thus part of) the Vitruval-Bruyère Formation. Only limited biostratigraphical data are available so far. Based on two samples yielding Chitinozoa, Herbosch and Verniers (2002) indicated that the age could range from late Llanvirn to middle Caradoc.

In summary, between the Huy Formation, that can be attributed firmly to the early Llanvirn (time-slice 4b of Webby et al., 2004) and the Fosses Formation, that is of

Ashgill age (time-slices 6a–b), different outcrops with similar lithologies and poor fossil content have been attributed to six formations: Sart-Bernard, Tier d’Olne, Ombret, Vitruval-Bruyère, Oxhe and Basse-aux-Canes. The stratigraphical relationships between these remain unclear. Trilobite assemblages have been found in two of them: the Sart-Bernard and Oxhe Formations, and one specimen from the Vitruval-Bruyère Formation.

2.3. The Huy Formation

The Huy Formation was described originally from the town of Huy, from the cuttings east and west of the tunnel between its two railway stations (Huy-Nord and Huy-Statte). It can be recognized easily in the Condroz Inlier, because it consists of grey to black, silty, finely micaceous, commonly graptolitic mudstones. The formation is present, always with numerous graptolites, at Huy, in the railway cutting at Sart-Bernard and in the Wépion borehole. The ‘unnamed formation’ of Dean (1991) in the Oxhe Inlier, for which he suggested a possible Llandeilian age, subsequently yielded graptolites to TS and Maletz that confirm that it belongs to the *D. artus* Biozone. It is identical lithologically to the Huy Formation, to which it is here attributed.

Servais and Maletz (1992) reviewed the stratigraphical concept of this unit. They revised the graptolites on the basis of existing collections in the Institut Royal des Sciences Naturelles de Belgique, Brussels (IRScNB), and new material collected from the Huy and Sart-Bernard outcrops. All recorded graptolite taxa indicate firmly an early *D. artus* graptolite Biozone age (early Abereiddian, early Llanvirn; corresponding to the time-slice 4b of Webby et al., 2004, i.e. to the Middle Darriwilian).

Besides the graptolites, Servais and Maletz (1992) illustrated crinoid and brachiopod fragments, and specimens of *Tomaculum problematicum* Groom, which is found in great numbers in this formation, and considered to represent faecal pellets of an unknown epibenthic animal (Eiserhardt et al., 2001a). Among the macrofossils, they also illustrated a few trilobites and these are discussed in detail in the present work. The Huy Formation has also yielded numerous phyllocarids, attributed to *Caryocaris* sp. by Vannier et al. (2003).

Servais and Maletz (1992) also listed the taxa recorded from the rich, but poorly preserved acritarch assemblages of the Huy Formation from which they illustrated a selection of specimens. These assemblages are typical for the late Arenig to early Llanvirn interval and clearly of peri-Gondwanan (not Baltic) affinity (Servais et al., 2003). Recent studies on Chitinozoa also

confirm the early Llanvirn age, as a characteristic assemblage with *Siphonochitina tenuicollis*, almost identical to the basal Llanvirn assemblage of Jenkins (1967) from the Hope Shale Formation (Shropshire, England), has been recovered from the Huy Formation at Sart-Bernard (J. Vanmeirhaeghe, pers. comm., 2005).

2.4. The Sart-Bernard Formation

The Sart-Bernard Formation was described originally by Maillieux (1939), who listed and illustrated the fossils in a monograph. All his specimens were collected from the railway cutting at the type locality of Sart-Bernard. The formation consists of micaceous and sandy shales, clearly coarser grained than the graptolitic shales of the Huy Formation. Graptolites are present, but very rare, while other fossil groups, such as trilobites, brachiopods, bivalves and phyllocarids can be found in greater, but always limited numbers. Maillieux (1939) attributed the formation to the “Llandeilo”. Michot (1954), however, considered the Huy and Sart-Bernard Formations to comprise a single unit, under the latter name. He attributed it to the ‘Llanvirn’, following Bulman (1950), who demonstrated a “*Didymograptus bifidus*” Biozone age for the graptolite-bearing horizons of the Huy Formation. Although Martin (1969) again used both formation names, most subsequent authors followed Michot in using only one (for a review, see Servais and Maletz, 1992; Verniers et al., 2001).

Until recently, the Sart-Bernard Formation was still considered to be of Llanvirn age (Vanmeirhaeghe and Verniers, 2004) and it was believed to overlie the Huy Formation directly (Verniers et al., 2001; Herbosch and Verniers, 2002). However, new biostratigraphical investigation demonstrates that it is younger, most probably of early to middle Caradoc age.

The reinvestigation of the trilobite assemblages in this study clearly indicates a mid-Caradoc age for the faunas. The *Dalmanitina* specimens that are common in the Sart-Bernard Formation belong to *D. proaeva* cf. *elfrida*, which occurs in the Vinice Formation in Bohemia. According to Fortey et al. (2000), the latter equates broadly with the British Cheneyan Stage. This suggests that parts at least of the Sart-Bernard Formation are slightly younger than the Oxhe Formation, of which the trilobites were investigated by Dean (1991) and attributed to the Longvillian Substage of the underlying Burrellian Stage.

Additional biostratigraphic information has been provided by the restudy of graptolites and Chitinozoa. A newly collected graptolite (IRScNB a12202) from the Sart-Bernard Formation exposed in the eastern railway

cutting at Sart-Bernard belongs to *Glyptograptus*, possibly *G. euglyphus* (J. Maletz, 2005, pers. comm.). This species occurs in the upper *teretiusculus* and *gracilis* biozones, which would imply a late Llanvirn (Llandeilian) to early Caradoc (Aurelucian) age. Preliminary results from current investigations on the Chitinozoa indicate the presence in the Sart-Bernard Formation of an assemblage including *D. juglandiformis* (J. Vanmeirhaeghe, 2005, pers. comm.). This species is indicative of the Baltoscandian Jõhvi to Middle Oandu (middle Caradoc) *S. cervicornis* Biozone.

Although the biostratigraphical data need to be confirmed (Chitinozoa investigations are currently in progress), the different fossil groups indicate clearly that the Sart-Bernard Formation is distinct from and younger than the Huy Formation. While the possible presence of the graptolite species *G. euglyphus* would indicate an age near the Llanvirn/Caradoc boundary (upper part of time-slice 4c or time-slice 5a of Webby et al., 2004), the genus ranges higher, and therefore a younger age is not precluded. The preliminary Chitinozoa data suggest an age in time-slice 5b or in the lower part of time-slice 5c. The trilobites seem to confirm a Middle Caradoc age, as the fauna recorded in the Sart-Bernard Formation has elements common to the Vinice Formation in Bohemia, of probable Cheneyan (time-slice 5c) age.

The Sart-Bernard Formation is thus of comparable lithology and of similar age to the Vitruvial-Bruyère, Oxhe, Tier d'Ogne, Ombret and Basse-aux-Canes Formations. These six lithological units possibly represent lateral facies changes within a single stratigraphical complex that in different outcrop areas shows contrasting lithologies and fossil content. Therefore, a stratigraphical gap, including at least the middle Llanvirn, but probably also parts of the late Llanvirn and earliest Caradoc, seems to be present in the succession of the Condroz Inlier.

3. Palaeogeography of the Condroz Inlier: the southeastern margin of Avalonia

It is today widely accepted that during the Lower Palaeozoic, Belgium was a part of the eastern extremity of the microcontinent of Avalonia. According to Cocks et al. (1997), Avalonia comprised not only England and Wales, but also the various parts of Belgium, and the microcontinent extended eastwards into western Germany. Cocks et al. (1997) placed the northeastern margin of Avalonia at the Elbe line in central Germany. However, eastern Avalonian sediments certainly extend at least to Rügen, northeastern Germany (Servais, 1994; Servais and Fatka, 1997; Verniers et al., 2002) and probably even farther east into the Polish part of Pomerania, where

Ordovician sediments of Rügen type have been described from boreholes (Bednarczyk, 1974; Wrona et al., 2001; Samuelsson et al., 2002a). According to the most recent reconstructions (e.g. Cocks and Torsvik, 2002), the Condroz Inlier and the Ardenne inliers are located in the southeastern part of Avalonia.

Hence, the Lower Palaeozoic history of Belgium is related to the rifting and migration history of Avalonia (e.g. Verniers et al., 2001, 2002). During a period of sedimentation up to the early Tremadoc (Chevripont Formation), Belgium was attached (or near) to the Gondwanan supercontinent. The middle Tremadoc to middle/late Arenig stratigraphical hiatus, observed in all successions in Belgium, most probably corresponds to the rifting event of the microcontinent Avalonia away from Gondwana. This rifting from Gondwana is believed to have taken place in the early–early middle Ordovician (Fortey and Cocks, 2003), but this has been challenged by Landing (2005). During the northward drift of Avalonia away from Gondwana and in the direction of Baltica, between the mid/late Arenig and the middle Ashgill, sedimentation took place mostly on a shelf. In the Condroz Inlier, predominantly siliciclastic sediments were deposited between the early Llanvirn (Huy Formation) and the Caradoc, with some carbonate input in the Ashgill (Fosses Formation). The palaeobiogeographical affinities of the faunas from the Condroz Inlier, and in particular of the trilobites of the Huy, Sart-Bernard, Oxhe and Fosses Formations, should thus be closely related to those from southern England and Wales, with a rapid change from Gondwanan affinities in the early Ordovician towards Baltic affinities in the late Ordovician.

Due to its position in the southeastern part of Avalonia, it is particularly interesting to compare the affinities of the Belgian faunas with those from farther east, i.e. those from western Germany (Rhenish Massif), which also belongs to the easternmost part of Avalonia, and also with those from Bohemia, which is considered by several workers to belong to a separate microcontinent, Perunica (Havlíček et al., 1994). The succession of Ordovician sediments in the Condroz Inlier can be compared readily with the succession in the Ebbe and Remscheid anticlines in the Rhenish Massif, as many analogies exist. The Ordovician units of the Ebbe Anticline also have grey to black shales with integrated silt layers as the dominant lithologies. These rocks were named “Herscheider Schichten”, and four Ordovician units were recognised. These are, from base to top, the Plettenberger Bänderschiefer (early Abereiddian, earliest Llanvirn), the Unterer (Kiesberger) Tonschiefer (early to mid-Abereiddian, early Llanvirn), the (Rahlenberger) Grauwackenschiefer (Aurelucian,

earliest Caradoc) and the Oberer (Solinger) Tonschiefer (late Caradoc). The biostratigraphy of the succession is based, as in the Condrosz Inlier, on data from graptolites, acritarchs (Maletz and Servais, 1993) and Chitinozoa (Samuelsson et al., 2002b). The succession is lithologically and biostratigraphically very similar to that of the Condrosz Inlier, with sediments from the early Llanvirn up to the late Caradoc. Interestingly, the same stratigraphical hiatus in the middle to late Llanvirn is observed. The fossil content of the succession of the Ebbe Anticline also closely resembles that of the Condrosz Inlier. The graptolites, trilobites and acritarchs of the Huy Formation are very similar to those from the Plettenberger Bänderschiefer and the Unterer (Kiesberger) Tonschiefer (Eiserhardt et al., 2001b), with the same, very characteristic occurrence of *Tomaculum problematicum* in the graptolitic shales, suggesting, at least for this period, a common sedimentary basin. It is probable that the basin in which the Ordovician sediments of the Condrosz Inlier and of the Ebbe Anticline were deposited extended into northern Germany and northwestern Poland, as lithological similarities exist in the subsurface sediments from these areas.

The Rügen Ordovician was described and dated by Jaeger (1967), using graptolites. These were reviewed in detail by Maletz (1998), who confirmed the presence of graptolitic shales attributed to the Llanvirn *artus*, *murchisoni* and *teretiusculus* biozones, and to the early Caradoc *gracilis* Biozone. In addition, late Tremadocian sediments were recognised from palynological investigations (acritarchs and Chitinozoa), which also confirmed the ages provided by the graptolites (Samuelsson et al., 2000; Servais et al., 2001). Because of their palaeobiogeographical affinities with peri-Gondwanan taxa (Servais, 1994; Katzung et al., 1995; Samuelsson et al., 2000), the acritarchs and Chitinozoa indicate clearly that the sediments belong to Avalonia. Trilobites have not so far been recovered from Rügen.

The Ordovician of the subsurface of north-western Poland is very similar to that of Rügen. Over 20 boreholes encountered Ordovician strata in the Koszalin-Chojnice area. The grey to black mud-silt deposits have been attributed to the late Llanvirn (Llandeilian) *teretiusculus* and the early to middle Caradoc *gracilis*, *multidens* and base of *clingani* graptolite biozones (Bednarczyk, 1974). The age of the sediments has recently been confirmed by Chitinozoa (Wrona et al., 2001; Samuelsson et al., 2002a), which also indicate Avalonian palaeobiogeographical affinities. Benthic faunas are very rare, and trilobites have not so far been described from northwestern Poland.

The trilobite assemblages of the Condrosz Inlier, ranging from the early Llanvirn (Huy Formation) through

the Caradoc (Sart-Bernard, Oxhe Formations) into the early–mid Ashgill (Fosses Formation) are therefore some of the easternmost occurrences in Avalonia, which is particularly interesting for palaeobiogeographical considerations.

4. Material

For the present study, the trilobite collections of the Huy and Sart-Bernard Formations have been re-examined in detail. Those from the middle Caradoc (Longvillian) Oxhe Formation and from the Ashgill Fosses Formation are discussed in the context of their palaeogeographical affinities; they were described fully by Dean (1991) and Lespérance in Lespérance and Sheehan (1988), respectively.

Existing collections from the Huy Formation, all housed in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRScNB), originate from the outcrops at Huy (cuttings along the Namur-Liège railway near Huy-Nord station, see Servais and Maletz, 1992, fig. 3) and Sart-Bernard (cuttings along the Namur-Luxembourg railway, near Sart-Bernard station, see Servais and Maletz, 1992, fig. 4), and from the Wépion borehole. These are complemented by new collections made from the western railway cuttings at Sart-Bernard, which are now housed in the Institut Royal des Sciences Naturelles de Belgique.

5. Trilobites of the Huy Formation

5.1. Faunal elements

Trilobites are sparse, with a total of some 40 specimens known. About 75% of these are cyclopygids, of which the majority belong to *Pricyclopyge binodosa*; *Cyclopyge kossleri* and *Ellipsotaphrus monophthalmus* occur in smaller numbers. The remainder of the fauna comprises four specimens of *Placoparia cambriensis* and individual ones each of *Colpocoryphe* aff. *bullata*, *Dionidella* aff. *siegfriedi*, *Dionide* aff. *jubata*, *Corrugatagnostus morea* and an asaphid meraspis. This association is typical of the cyclopygid biofacies, with benthic atheloptic elements, and is consistent with the inferred depositional environment of the Huy Formation on an ocean-facing outer shelf and slope. Remarks on individual taxa are given below.

5.1.1. *Pricyclopyge*

P. binodosa is the commonest trilobite in the Huy Formation, represented by well-preserved specimens. It has been recorded from Sart-Bernard, Huy station cutting,

and from the Wépion borehole (Servais and Maletz, 1992). In all those specimens in which the glabella is preserved, the position at which it achieves its maximum width (tr) is consistent with its attribution to *P. binodosa* (Fortey and Owens, 1987, p. 181). It can

reasonably be assumed that other less complete material (e.g. Servais and Maletz, 1992, p. 272) should be attributed to this subspecies.

There has been considerable discussion on the significance of the presence or absence of a spinose sixth

Trilobite Species	Area Formation	Shelve Inlier	S W Wales	Cumbria	Condroz Inlier	Ebbe and Remscheid anticlines	Prague Basin
		Hope Shale Fm	Llanfallteg & Aber Mawr Fms	Skiddaw Group Tarn Moor, Kirk Stile & Kirkland Fms	Huy Fm	Herscheider Schichten	Šárka Fm
<i>Corrugatagnostus morea</i>		+	+	+	+	g	
<i>Ectillaenus perovalis</i>		+	+			g	g
<i>Ogygiocaris seavilli</i>			+			cf.	
<i>Barrandia homfrayi</i>		+	+			?	
<i>Iliaenopsis thomsoni</i>		+	+				
<i>Girvanopyge occipitalis</i>		+	+	+		g	g
<i>Cyclopyge kossleri</i>			+		+	g	+
<i>Cyclopyge</i> aff. <i>grandis</i>				+			
<i>Degamella nuda</i>			+			g	g
<i>Ellipsotaphrus monophthalmus</i>		+	+		+	+	
<i>Gastropolus obtusicaudatus</i>		+	+				
<i>Microparia porrecta</i>			+			g	g
<i>Microparia shelvensis</i>		+	+				
<i>Microparia teretis</i>			+				
<i>Novakella copei</i>			+				g
<i>Novakella incisa</i>			+				
<i>Priscyclopyge binodosa</i>		+	+	+	+	+	+
<i>Eoharpes primus</i>			cf.			+	+
<i>Protolloydolithus neintianus</i>			+				
<i>Stapeleyella murchisonii</i>		+	+	+			
<i>Dionide</i> aff. <i>jubata</i>		+	+		+	+	g
<i>Dionide levigena</i>			+				
<i>Dionide turnbulli</i>			+				
<i>Dionidella siegfriedi</i>		g			aff.	+	
<i>Ampyx linleyensis</i>		+	+				
<i>Seleneceme acuticaudata</i>			+				
<i>Placoparina shelvensis</i>			+				
<i>Placoparia cambriensis</i>		+	+	+	+	+	+
<i>Colpocoryphe bullata</i>		+		aff.	aff.		g
<i>Platycalymene tasgarensis</i>			+				
<i>Ormathops llanvirnensis</i>			+				g
<i>Selenopeltis macrophthalma</i>		+	+			+	+

Fig. 3. Occurrence of trilobite species in Lower Llanvirn formations (Aberiddian Stage, *D. artus* Biozone) in Avalonia and Bohemia. Based on data from: Fortey and Owens (1987), Fortey et al. (1989), Havlíček in Chlupáč et al. (1998), Koch (1999a,b), Rushton in Cooper et al. (2005) and Whittard (1955–1967). Crosses indicate the presence of a species, 'g' the genus only. In the Hope Shale Formation, the left hand column refers to occurrences in the lowest part, below the Hyssington Volcanic Member, and the right hand column to this member and higher parts of the formation.

thoracic segment, following Marek's (1961, p. 32) assertion that this was a matter of preservation. Fortey and Owens (1987, p. 181) agreed with Whittard (1966, p. 287) that two subspecies, *P. binodosa binodosa* and *P. binodosa prisca*, were represented, but (op. cit., p. 181) did not follow Hörbinger and Vaněk (1985) in according subgeneric significance to the presence or absence of thoracic pleural spines. Some authors (e.g. Chlupáč et al., 1998, pl. 15, fig. 8; Bruthansová, 2003, pl. 3, fig. 4), however, continued to attribute specimens with spinose sixth thoracic segments to *P. binodosa*. As well as the presence or absence of these, the shapes of the thoraces of *P. prisca* and *P. binodosa* are distinctive: in the former the pleurae widen (tr.) consistently towards the posterior, achieving their greatest width at the sixth segment (e.g. Marek, 1961, pl. 1, fig. 20), while in the latter they are widest (tr.) at the third or fourth segments (herein Fig. 4c; Rushton and Hughes, 1981, pl. 2, fig. 21). These thoracic characters are here considered to be of specific significance, and *P. prisca* and *P. binodosa* are treated as separate species. Gradualistic changes in the glabellar width and eye identified by Fortey (1985) and by Fortey and Owens (1987, 1990) are appropriately accorded subspecific status, and these are paralleled in lineages of *P. binodosa* (*P. b. eurycephala* and *P. b. binodosa*) and of *P. prisca* (*P. p. prisca* and *P. p. longicephala*).

P. binodosa binodosa is characteristic of deeper water facies in the lower Llanvirn of *D. artus* Biozone age in the Skiddaw Group, northern England (Fortey et al., 1989; Rushton in Cooper et al., 2005); the lowest part of the Hope Shale Formation, Shropshire (Owens in Rushton et al., 2000), and the Herscheider Schichten, Ebbe Anticline (Koch, 1999a). In Armorica, such facies in the Llanvirn are limited to the Pierre-Melière Formation in the Ancenis Syncline (Henry, 1989; Henry et al., 1997), the only district in this region from which *P. binodosa* has been recorded (described as *P. synophthalma*? by Henry (1980, pp. 38–39) but subsequently (Henry et al., 1997, p. 376) transferred to this species). As in the Huy Formation, *P. binodosa* is the most abundant trilobite in the Skiddaw Group, Hope Shale Formation, Herscheider Schichten and in the Pierre-Melière Formation. In Bohemia, both *P. binodosa binodosa* and *P. prisca* occur in the Šárka Formation, and Bruthansová (2003, pl. 3, figs. 4, 7) illustrated thoraces respectively with and without spines as the former; she noted (Bruthansová, 2003, p. 304) that *P. binodosa* (i.e. inclusive of *P. prisca* as interpreted here) is the most common cyclopygid in the Šárka Formation.

Pricyclopyge is now known from much farther afield than indicated by Fortey et al. (1989, p. 14), for

example from the Arenig-Llanvirn Volcancito Formation, Famatina, Argentina (Esteban, 1996, 1999) from the late Llanvirn–early Caradoc Middle Pagoda Formation, Hunan, south China (Zhou et al., 2001) and the mid-Caradoc Modaoxi and Shuangjiakou formations, Hunan (Zhou et al., 1999). It is thus proving to have a wide peri-Gondwanan distribution, and its likely mesopelagic habitat is now widely accepted (Fortey, 1985; Fortey and Owens, 1987; McCormick and Fortey, 1998).

5.1.2. *Cyclopyge*

Two cranidia (Servais and Maletz, 1992, pl. 2, fig. 9; herein Fig. 4d) have prominent, transverse crescentic S1 and an elongated, forward-tapering glabella, characters which are consistent with *C. kossleri* which is known from the Šárka Formation of Bohemia and Llanfallteg Formation of South Wales (see respectively Marek, 1961, pl. 1, figs. 14–17; Fortey and Owens, 1987, fig. 37a). A pygidium figured by Servais and Maletz (1992, pl. 2, fig. 10) as *Novakella* sp. has a tapering axis which is like that of *C. kossleri* (Marek, 1961, pl. 1, figs. 15–17; Fortey and Owens, 1987, figs. 37a–b), and is possibly more appropriately referred to the latter. A degree four(?) meraspis (Fig. 4j) from Sart-Bernard is attributed to this species on the basis of the presence of deep, forwardly convex S1, while a disarranged moult and an incomplete glabella (not figured) probably belong to *C. kossleri*.

5.1.3. *Ellipsotaphrus*

An incomplete cranidium from Le Petit Fond d'Oxhe from Dean's 'unnamed formation' was attributed by him (Dean, 1991, p. 124, pl. 1, fig. 3) to *E. monophthalmus* and is the only known specimen of this widespread species from the Huy Formation. It is long-ranging, being recorded elsewhere from the late Arenig (Fennian Stage) of SW Wales (Fortey and Owens, 1987), the early Llanvirn (Abereiddian Stage) of SW Wales, south Shropshire and the Ebbe Anticline (Whittard, 1961; Koch, 1999a) and the late Llanvirn (Dobrotivá Formation) of Bohemia (Marek, 1961).

5.1.4. *Placoparia*

Three specimens of *Placoparia* have been collected from the Huy Formation at the Sart-Bernard cutting. Servais and Maletz (1992) illustrated a moult arrangement; a thorax plus part of a pygidium, and a small, poorly preserved axial shield are figured here (Fig. 4e,f). In none of these specimens is the glabella well preserved, but in that figured by Servais and Maletz (1992, pl. 2, fig. 7) the librigena shows coarse pitting and four pygidial

axial rings, and all three specimens have 12 thoracic segments. These characters are diagnostic of *P. cambriensis* (see Hammann, 1971, p. 58), and there can be little doubt that all belong to this species, the only *Placoparia* known from the *D. artus* Biozone.

P. cambriensis has a remarkably wide distribution in the *D. artus* Biozone of England and Wales (Skiddaw Group, Cumbria—Cooper et al., 1995, 2005; Fortey et al., 1989; Aber Mawr and Llanfallteg formations, S. Wales—Fortey and Owens, 1987; Kennedy, 1989; Nant Ffrancon Subgroup, N. Wales—Dean and Martin in Young et al., 2002; Hope Shale Formation, Shelve Inlier—Whittard, 1958), Ebbe Anticline (Herscheider Schichten—Hammann, 1971; Koch and Lemke, 2000: specimens described as *P. aff. zippei*, although badly preserved, conform morphologically to *P. cambriensis*), Bohemia (Šárka Formation—Havlíček in Chlupáč et al., 1998; Bruthansová, 2003), Armorica (Traveusot and Pierre-Melière Formations—Henry and Clarkson, 1975; Henry, 1980, 1989), central Spain (*cambriensis* Biozone—Rabano, 1990), Portugal (Valongo Formation—Romano, 1976) and Morocco (Tachilla Formation—Destombes, 1971). Šnajdr (1990, p. 204) reverted to placing specimens from the Šárka Formation in *P. barrandeii*, long considered to be a junior subjective synonym of *P. cambriensis*, because he considered the type specimens of the latter too poorly preserved to uphold this. He was followed in using *P. barrandeii*, but with reservation, by Henry et al. (1997, p. 380) in their discussion of *Placoparia* specimens from the Pierre-Melière Formation. Better specimens of *P. cambriensis* are now available from the type area (Fortey and Owens, 1987), and these confirm the synonymy of *P. barrandeii*.

Not only is *P. cambriensis* widespread geographically, it is found also in a variety of biofacies. It occurs in sediments of deeper water origin in the Huy Formation, Skiddaw Group, Herscheider Schichten, Šárka Formation and the Pierre-Melière Formation, where it is associated with cyclopygids and atheloptic forms; in sediments of outer shelf origin in the mid Hope Shale, Llanfallteg and Aber Mawr Formations with raphiophorid biofacies species; and in shallower water inner shelf sediments in the Traveusot, Valongo and Tachilla Formations, and the Spanish *cambriensis* Biozone, where it is associated with, among others, *Neseuretus* species. *P. cambriensis* is blind, and has been considered to be a member of the atheloptic association, yet its wide distribution finds closer parallels with pelagic taxa, and this satisfies the geological evidence given by Fortey (1985, p. 222) of its association with shallow and deep water biofacies, and by its not being constrained by the disposition of palaeocontinents. Associated benthic species from the formations listed above

show close relationships to the environments in which they are inferred to have lived. For instance, *Colpocoryphe* from deeper water sediments have either minute eyes or are blind (e.g. *C. inopinata*: Henry, 1980, pl. 8, figs. 4, 6; *C. bohémica*: Henry et al., 1997, figs. 2.1–2.7), while those from shallower water in Armorica have larger, ‘normal-sized’ eyes (e.g. *C. thoralis conjugens*: Hammann, 1983, pl. 12, figs. 112, 116, 117; Rabano, 1990, fig. 6). The water depth over most of Armorica, with the exception of the Ancenis Syncline, was too shallow to permit the ingress of the mesopelagic *P. binodosa*, which suggests that in spite of being blind, *P. cambriensis* might have been epipelagic. If it was symbiotic or commensal, this could account for its lacking hypertrophied eyes which are a hallmark of pelagic forms. Alternatively, it may have been tolerant of a wide range of benthic habitats, and perhaps had long-lived larval stages that permitted wide distribution in Avalonian and circum-Gondwanan (Armorica, Perunica) terranes. Younger species of *Placoparia*, from the later Llanvirn (Llandeilian/Dobrotiván) do not have such wide distribution: *P. borni* and *P. tournemini* are restricted to Armorica (Henry, 1980; Romano, 1976; Rabano, 1990), while *P. zippei* has not been found outside Bohemia (Hammann, 1971). These restricted distributions might be accounted for by the various terranes in which it occurs being farther apart than they were in the early Llanvirn, while the absence of *Placoparia* from Avalonia after this time could perhaps be explained by this microcontinent having moved northwards into lower, warmer latitudes.

5.1.5. *Colpocoryphe*

A cranidium with attached thoracic segments from Huy is the only representative of this genus from the Huy Formation. The facial sutures are adaxially concave, and there is no palpebral lobe, indicating that this is a blind, atheloptic species. Comparison with coeval forms suggests that it is most similar to and probably conspecific with *C. bullata* from the Hope Shale Formation (see below).

Colpocoryphe is also represented by rare specimens from the Hope Shale, Kirkland and Pierre-Melière Formations. Whittard (1960, p. 150, pl. 18, figs. 10–11) figured a cranidium from the Hope Shale Formation as *Neseuretus bullatus*, and admitted (op. cit., p. 151) that this species in many respects (including the square-fronted glabella, disposition of glabellar furrows and nature of anterior border) is ‘nearer to *Colpocoryphe*’, but claimed that the dome-shaped anterior area, limited laterally by the anterior furrows is absent in *Colpocoryphe*. However, it is similar to that of *C. taylorum* Fortey and Owens (1987, fig. 100a,g) and to *C. inopinata*

(Novák in Perner, 1918) (see Henry, 1980, pl. 8, figs. 4, 6), far more so than to such *Neseuretus* species as those figured by Whittard (1960, pls. 19, 20). For these reasons, the Hope Shale species can firmly be assigned to *Colpocoryphe*. Whittard (1960, p. 151) described a small palpebral lobe, but we are doubtful if this is a really present. The specimen from the Huy Formation (Fig. 4h) shows clearly that no palpebral lobe is present, and the same applies to that from the Kirkland Formation, figured by Fortey et al. (1989, fig. 1s) as *Platycalymene* sp., where the “ghosted” left hand facial suture takes an adaxially concave path like that of the Huy Formation specimen; this character, together with the square-fronted glabella indicates attribution to *Colpocoryphe* rather than to *Platycalymene*. A similar concave path appears to be present in *C. bullata*, especially on the right hand side (Whittard, 1960, pl. 18, fig. 9). The likelihood is that these three specimens are conspecific, but on account of poor preservation those from the Huy and Kirkland Formations are referred to *C. aff. bullata*.

5.1.6. *Dionidella*

One small dionidid trilobite from the Huy Formation at Sart-Bernard (Fig. 4g) has the genae pitted across their entire width, with the exception of a triangular alar region adjacent to the posterolateral part of the glabella, and the margin of the cranidium is concave. The pygidium has the anterior pleural bands extending close to the margin, but the posterior terminate at the paradosubulral line. In these characters, this specimen has a close resemblance to *Dionidella incisa* Prantl and Přibyl (see Horný and Bastl, 1970, pl. 13, fig. 1) from the Dobrotivá Formation, Bohemia, indicating assignment to *Dionidella*. *D. siegfriedi* Koch and Lemke (1998b, figs. 3, 4) from the Unterer Tonschiefer of the Ebbe Anticline is similar to the Huy Formation specimen, and is characterised by having two sagittal spines on the glabella; the latter is not sufficiently well preserved to show whether these are present. A specimen from the Plettenberger Bänderschiefer figured by Siegfried (1969, pl. 19, fig. 4) and by Koch and Lemke (1998b, fig. 1d) as *Dionide jubata* differs from this species, but is like *D. siegfriedi* in having a concave cranial margin, a triangular alar region adjacent to the glabella, and appears to possess a pair of glabellar spines; this specimen is likely, therefore, to belong to *D. siegfriedi*. The holotype (and only specimen) of *Dionide rotundata* Whittard 1940b (Whittard 1958, pl. 14, fig. 1) from the Hope Shale Formation, Shelve Inlier, later synonymised with *D. jubata* by Whittard (1958, p. 98) has a concave cranial margin, and small, triangular alar regions, like the *Dionidella* specimens from the Huy Formation and

Herscheider Schichten. The other specimens attributed to *D. jubata* by Whittard (1958, pl. 14, figs. 2–5) all have a narrow cranial border and lack smooth alar regions, and are probably not conspecific (see also below). It is likely that *D. rotundata*, *D. siegfriedi*, ‘*D. jubata*’ (*pars*, of Siegfried, 1969 and Koch and Lemke, 1998b) and the dionidid from Sart-Bernard all belong to one species of *Dionidella*, but the available material is insufficiently preserved for this to be confirmed.

5.1.7. *Dionide*

Dean (1991, p. 141, pl. 1, fig. 2) described an incomplete dionidid pygidium from the Huy Formation (his ‘unnamed formation’) of the Oxhe Inlier as *D. jubata*. Specimens attributed to this species were figured from the Hope Shale Formation by Whittard (1958, pl. 14, figs. 2–5) and from the Herscheider Schichten by Koch and Lemke (1998b, p. 616, fig. 1a–c). The type stratum for *D. jubata* is the Dobrotivá Formation (Llandeilian) of the Prague district, and Šnajdr (1981, p. 282, pl. 3, figs. 7, 8; pl. 4, figs. 1–7) selected a lectotype and included figures (op. cit., pl. 4, figs. 2, 3) of latex casts of the cephalon. These show that this species has a distinctly wider cranial border and (on the dorsal surface) a straighter lateral glabellar margin than do external moulds of Hope Shale Formation specimens (Whittard, 1958, pl. 14, fig. 3), which may not, therefore, be conspecific; the same presumably applies to the other Llanvirm occurrences from the Condroz Inlier and the Ebbe Anticline. Because of these distinctions, the Llanvirm *Dionide* specimens are here referred to *D. aff. jubata*.

5.1.8. *Asaphid*

A degree one meraspis from Sart-Bernard is the only representative of this family from the Huy Formation. It differs from a meraspis from the Herscheider Schichten attributed to *Nobiliasaphus?* sp. by Koch and Lemke (2000, p. 516, fig. 1) in lacking deep S1, and from meraspides of *Ogygiocaris macrops* Rushton and Hughes (1981, pl. 4, figs. 12, 13) from the Llanvirm of the Great Paxton Borehole, eastern England, in having a wider pygidial border and narrower pleural fields. The width of the border is most closely matched in small pygidia of *Merlinia anxia*, also from Great Paxton (Rushton and Hughes, 1981, pl. 5, figs. 5, 6), but these have wider pleural fields.

5.1.9. *Corrugatagnostus*

A pygidium from the ‘unnamed formation’ (i.e. Huy Formation) in the Oxhe Inlier was figured by Dean (1991, pl. 1, fig. 1) as *C. morea*, which as he noted compares closely with British and Bohemian material of

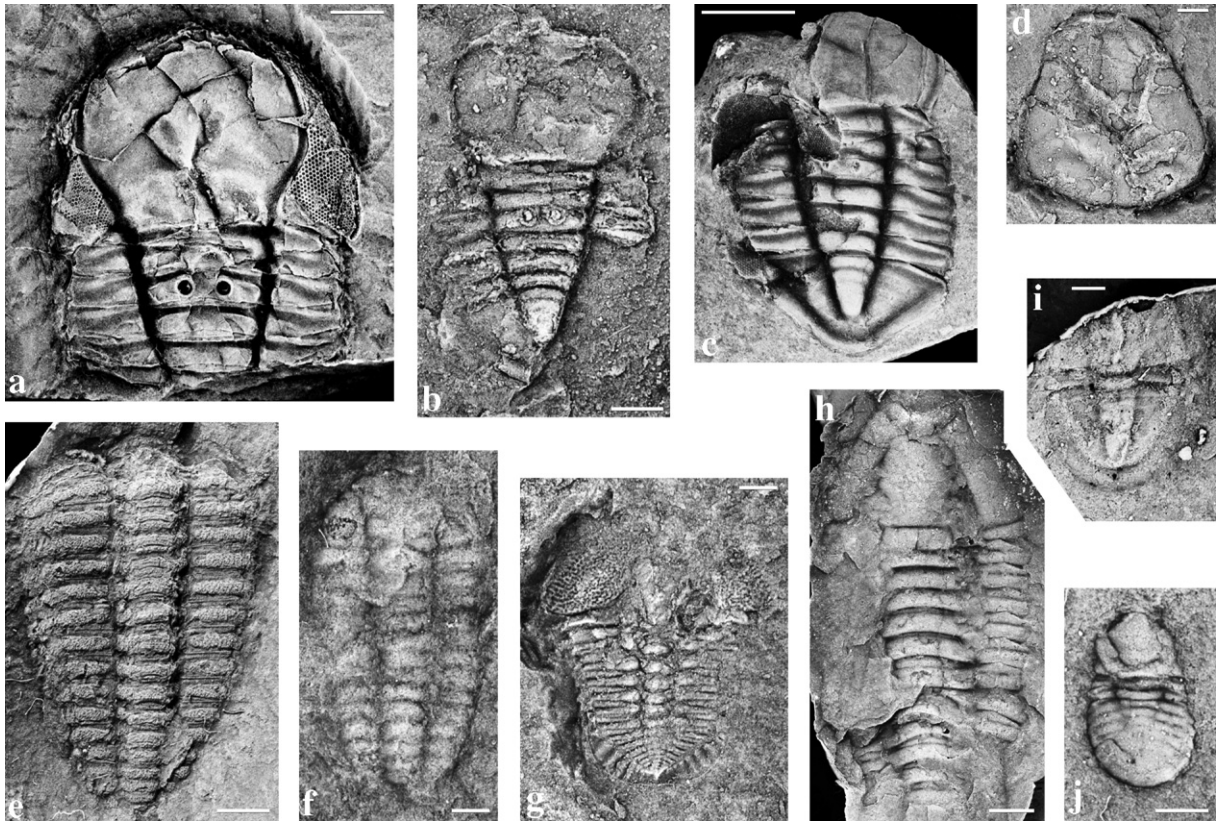


Fig. 4. Selected trilobites from the Huy Formation: (a–c) *Pricyclopyge binodosa binodosa* (Salter): (a) IRScNB a6887, cephalon with parts of five thoracic segments, (b) IRScNB a6887, small, incomplete axial shield, (c) IRScNB a9760, moult arrangement (orig. Maillieux, 1939, pl. 1, fig. 13). (d, j) *Cyclopyge kossleri* (Klouček): (d) IRScNB a12198, cranidium, (j) IRScNB a12201, meraspis, latex cast from external mould. (e, f) *Placoparia cambriensis* Hicks: (e) IRScNB a9430, thorax with parts of cephalon and pygidium, latex cast from external mould, (f) IRScNB a12199, small holaspis. (g) *Dionidella* aff. *siegfriedi* Koch and Lemke, IRScNB a12200, small axial shield. (h) *Colpocoryphe* aff. *bullata* (Whittard), IRScNB a9340, incomplete axial shield, latex cast from external mould. (i) Asaphid meraspis, IRScNB a9340, latex cast from external mould. (a–g, i) From railway cutting at Sart-Bernard; (h) from Huy railway tunnel. Scale bars represent: 1 mm (b, d, f, g, i, j), 2 mm (a, e) and 5 mm (c, h).

this species. It is long-ranging and has been recorded also from the *D. artus* Biozone of the Hope Shale Formation, the Skiddaw Group, and the Llanfallteg Formation in Britain, and from the Šárka, Dobrotivá and Libeň Formations of Bohemia (Nielsen, 1999).

5.2. Comparison of the trilobites of the Huy Formation with coeval faunas (Fig. 3)

As the Condroz Inlier occupies a position at the southeastern margin of the microcontinent Avalonia, it is particularly interesting to compare the faunal composition of the Huy Formation with the trilobite assemblages from England and Wales, the nearby Ebbe and Remscheid anticlines in western Germany, the assemblages described from the Prague Basin, Bohemia (Fig. 3), and from Armorica.

5.2.1. Northern England

Llanvirm strata within the Skiddaw Group crop out in the English Lake District and in the nearby Cross Fell Inlier. Trilobites occur throughout the Skiddaw Group, but are scarce (Fortey et al., 1989; Rushton in Cooper et al., 2005), and the generic composition is much like that of the Huy Formation, being a cyclopygid biofacies with benthic atheloptic forms. The Kirk Stile Formation of the Skiddaw Inlier has yielded *P. cambriensis* at Outerside, and the Tarn Moor Formation of the Ullswater and Bampton inliers has yielded in the former *P. cambriensis* and in the latter *P. binodosa*, *Cyclopyge* aff. *grandis*, *Girvanopyge* sp. and *Stapeleyella munchisonii*. In the Cross Fell Inlier, *P. binodosa*, *P. cambriensis*, *C. morea* and *S. munchisonii* have been recorded from the Kirkland Formation. Many of these were figured by Fortey et al. (1989, fig. 1: b, d, e, j, k, m, n, q, s) and by Rushton in

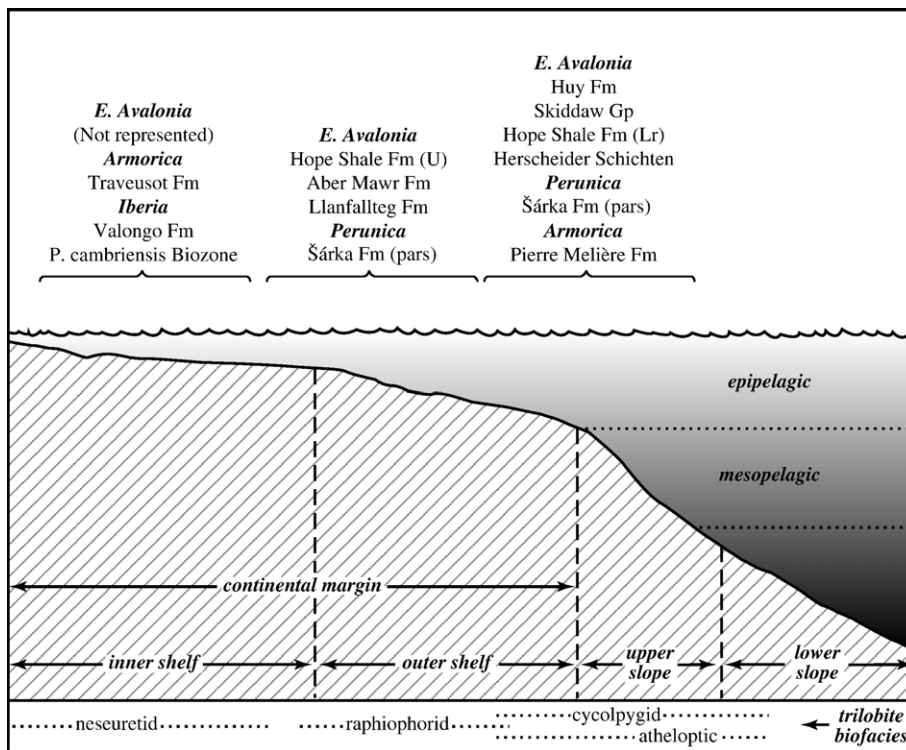


Fig. 5. Interpretation of various early Llanvirn (*D. artus* Biozone) trilobite biofacies in East Avalonia, the Armorican Massif, Iberia and Perunica.

Cooper et al. (2005, fig. 3: b, c, g). The Skiddaw Group is interpreted (Cooper et al., 1995, 2005) as having been deposited in comparatively deep water on an ocean facing outer shelf and slope (Fig. 5).

5.2.2. The Shelve Inlier, Shropshire

Over 40 species of trilobite have been recorded from the Hope Shale Formation (Whittard, 1955–67), which as currently defined (Lynas in Cave and Hains, 2001) encompasses what Whittard described as the Hope Shales, Stapeley Volcanic Group and Stapeley Shales. Two (Hyssington and Stapeley) volcanic members are present within in the sequence. Rushton in Cave and Hains (2001, p. 26) noted that the trilobite fauna of the Hope Shale Formation in total has similarities to raphiophorid communities, but remarked that there is also some resemblance to the atheloptic community. Further analysis of the fauna, based on Whittard's (1940a,b, 1955–1967) data indicates that the lowest part of the Hope Shale Formation is dominated by *P. binodosa*, described by Whittard (1940b, p. 123, 1961, p. 175) as 'very common' and 'an exceedingly common and characteristic trilobite' at these levels, where it is accompanied by other cyclopygids including *Microparia shelveensis*, *Gastropolus obtusicaudatus*, *Ellipso-*

taphrus monophthalmus and *Girvanopyge occipitalis*, together with *P. cambriensis* and such benthic forms as *Ectillaenus perovalis*, *Colpocoryphe bullata* and *Barrandia homfrayi*. On this basis, Owens in Rushton et al. (2000, p. 236) described this fauna as belonging to the cyclopygid biofacies, with atheloptic elements present. Younger faunas of the Hope Shale Formation (see Fig. 3), especially those associated with the volcanic members all appear to lack abundant cyclopygids and do not have a dominance of atheloptic species, and represent the raphiophorid communities recognised by Rushton. From this, we infer that only the lowest part of the Hope Shale Formation contains the atheloptic fauna and cyclopygid biofacies, and in these respects closely resembles that of the Huy Formation (Fig. 5). It is this part that might have been affected by major subsidence along the Pontesford-Linley Fault, on the southeastern margin of the Welsh Basin (Prigmore et al., 1997).

5.2.3. Southwest Wales

The Llanfallteg and Aber Mawr formations have faunas very similar in composition to those of the Hope Shale Formation from the Hyssington Volcanic Member upwards (Fig. 3), with common *E. perovalis*, *B. homfrayi*, *S. murchisonii*, *Ampyx linleyensis*, *P. cambriensis* and

Ormathops llanvirnensis (Fortey and Owens, 1987; Kennedy, 1989); cyclopygids are present, but are not a dominant element of the fauna. Like the upper parts of the Hope Shale Formation, the *D. artus* Biozone sediments of this region are interpreted as having been deposited on the outer shelf, supporting a raphiophorid community (Fig. 5).

5.2.4. Ebbe Anticline

As in the Huy Formation and Skiddaw Group, trilobites are scarce, and Richter and Richter (1954) described a small number of specimens. Sustained collecting by Koch and Lemke since the early 1980s has produced some 70 specimens from localities in the vicinity of Plettenberg and Kiesbert (Koch, 1999a,b; Koch and Lemke, 1995, 1996, 1997, 1998a,b, 2000). From the quantities of specimens enumerated by Koch (1999a, pp. 378–379), it is evident that these faunas are dominated by cyclopygids, and represent the cyclopygid biofacies. They comprise between 62% and 85% of the trilobites present, and of identifiable specimens *P. binodosa* is the most widespread species (e.g. Koch, 1999a, figs. 9a–c, 10a–b, 11a–c), and *Waldminia spinigera*, similar to, and perhaps congeneric with *Girvanopyge*, is well represented at a locality near Kiesbert. Most of the other trilobites are blind forms representing an atheloptic fauna.

In the nearby Remscheid Anticline, the Herscheider Schichten here have yielded cyclopygid trilobites, attributed by Koch and Lemke (1997, 1998a) to *Degamella praecedens*, *Girvanopyge* sp. and *Microparia* aff. *zdenkoniki*. The Herscheider Schichten of the Ebbe and Remscheid inliers are lithologically like the Huy Formation and parts of the Skiddaw Group, and have comparable associations of trilobites, graptolites and acritarchs, indicating deposition in a similar palaeoenvironment.

5.2.5. Bohemia

The Šárka Formation has yielded a diverse trilobite fauna, comprising over 40 genera, listed by Havlíček et al. (1994) and by Havlíček in Chlupáč et al. (1998). It is evident that the trilobite biofacies are not homogeneous throughout this formation, and these are currently being investigated (Bruthansová, 2003); some parts at least contain the cyclopygid biofacies. From the formation as a whole, about 20% of the genera have been interpreted as pelagic, and there are numerous (about 40%) atheloptic elements (Havlíček in Chlupáč et al., 1998, p. 55). The remaining 40% of the genera have ‘normal’ eyes, and most of these are either endemic, or are common to Armorican terranes. Four species, *P. binodosa*, *P. cambriensis*, *E. monophthalmus* and *Selenopeltis macrophthalma* are widespread, the first three being common to the Huy Formation.

The genera *Colpocoryphe* and *Dionide*, common to the Huy and Šárka formations, are represented by different species in each.

5.2.6. Armorica

Llanvirn faunas are mostly of shallow water, platform origin (Henry, 1980, 1989; Rabano, 1990), and dominated by Phacopida. The only species common to this area as a whole and to those discussed above is *P. cambriensis*, although certain genera, such as *Colpocoryphe*, are also widespread. Only in the Ancenis Syncline on the southeastern side of the Armorican Massif, are sediments of deeper water, offshore origin developed (Henry, 1980, 1989; Henry et al., 1997; Paris et al., 1999), represented by the Pierre-Melière Formation. Its trilobite fauna comprises species (*P. binodosa*, *P. cambriensis*) common to the Huy Formation, Skiddaw Group, Hope Shale Formation, Herscheider Schichten and Šárka Formation in addition to atheloptic forms (*Colpocoryphe bohémica*, *C. inopinata*, *Ormathops barroisi* and *O. ?atava*) that otherwise occur only in the last named (Henry et al., 1997).

5.3. Biofacies interpretation of the Huy Formation (Fig. 5)

The commonest and most widespread trilobite species in the Huy Formation, *P. binodosa*, is likely to have been mesopelagic (see references above), and as such probably penetrated shorewards only as far as the outer margins of the shelf. Fortey and Owens (1987, p. 106) used several lines of reasoning to suggest that the benthic atheloptic trilobite fauna, comprising species that were either blind or had atrophied eyes, lived at a water depth of 300 m or more. The presence of this association of trilobites is in accordance with the lithology and geological occurrence of the Huy Formation, suggesting that it accumulated on the shelf edge and upper slope. Such a location is supported by other faunal elements including caryocaridid arthropods (Vannier et al., 2003). The Skiddaw Group has been interpreted as being deposited in a similar environment (Cooper et al., 1995, 2005), and it carries a fauna closely similar to that of the Huy Formation, which includes mesopelagic and atheloptic trilobites (see above) and widespread caryocaridid arthropods (Vannier et al., 2003; Rushton in Cooper et al., 2005). On the basis of their lithology and faunas, the Herscheider Schichten are presumed to have accumulated in a similar palaeoenvironment. The lowermost Hope Shale Formation was deposited not on the margin of Avalonia, but in a deep part of the Welsh Basin associated with the Welsh Borderland Fault Complex (Prigmore et al., 1997).

Similar faunas occur in the Šárka Formation in Bohemia and in the Pierre-Melière Formation in Armorica,

both likely to have been deposited in the peri-Gondwanan area, and separated from eastern Avalonia by the Rheic Ocean. The mesopelagic *P. binodosa* presumably ranged across this, as did the epipelagic? *P. cambriensis*, but the accompanying benthic atheloptic trilobites are represented by different species to those from Avalonia, perhaps adapting independently to a similar environment to those in circum-Avalonian areas. Most of the coeval formations in Armorica accumulated in much shallower, inner shelf waters (Henry, 1980, p. 174, 1989; Rabano, 1990, p. 27) and lack cyclopygid trilobites, but some of the shallower water facies in the Welsh Basin region of eastern Avalonia (for example Aber Mawr and Llanfallteg formations, and the middle and upper parts of the Hope Shale Formation) contain Raphiophorid Community trilobite faunas which include some cyclopygids; these are likely to have been deposited on the outer shelf, in deeper waters than those of Armorica.

6. Trilobites of the Sart-Bernard Formation

6.1. Faunal elements

Trilobites are of fairly frequent occurrence at Sart-Bernard, and are dominated by *Dalmanitina proaeva* cf. *elfrida*, with smaller numbers of *Cyclopyge rediviva*, *Zeliszella* sp. and *Stenopareia* aff. *panderi*; a single specimen of *Prionocheilus* cf. *pulcher* has been recorded. Most specimens have suffered from some distortion, but otherwise preservation is good.

6.1.1. *Dalmanitina*

Cephalae, pygidia, hypostomata and some partially articulated specimens are present. Maillieux (1939, p. 41) determined them as *Dalmanitina atava* (Barrande), but this species, characteristic of the Šárka Formation, is now attributed to *Ormathops*; the present specimens are referable to *Dalmanitina*. P. Budil (pers. comm., 2005) has determined them as *D. proaeva* cf. *elfrida*, described by Šnajdr (1982) as a separate species, but considered by Budil to be a subspecies. Like *D. proaeva elfrida*, the Sart-Bernard specimens have on the genae fine, uniformly sized granules interspersed with shallow pits (Šnajdr, 1982, pl. 1, fig. 4; herein Fig. 6k), and this and other morphological features, including the straight axial furrows on the pygidium suggest that they are likely to belong to this subspecies, and there is no doubt that they can be referred to *D. proaeva* s.l. Besides Bohemia, *D. proaeva* has been recorded from the Bedinan Formation, southeastern Turkey (Dean, 1967, p. 112, pl. 6, figs. 1–9; pl. 7, figs. 4, 5; 1983, p. 98, pl. 12, figs. 2, 4, 9; pl. 13, fig. 3) and from the lower part of the Ktaoua Formation in the

Anti Atlas, Morocco (Destombes, 1972, p. 40, pl. 7, figs. 1–6) both of mid-Caradoc age.

6.1.2. *Zeliszella*

Maillieux (1939, p. 40, pl. 1, fig. 24) described three pygidia as *Dalmanitina hawlei* (Barrande), a species now included in *Zeliszella*. P. Budil (pers. comm., 2005) informed us that the type species, *Z. deshayesi* (Barrande) occurs together with *D. proaeva elfrida* in the Vinice Formation, but notes that one of the Sart-Bernard specimens (Fig. 6g) has the pleural ribs extending to the margin and is less elongated, although there is a similar number of pygidial axial rings (8) and pleural ribs (4–5); *Z. lapeyrei* (Bureau) from the Massif Armoricain is similar in these latter characters, as well as in its outline, but as in *Z. deshayesi*, the ribs do not extend to the margin. Budil notes that our specimen is like *Z. hawlei* in having prominent pleural bands reaching the pygidial margin, but that the pygidial outline is far more elongated. The Sart-Bernard specimens belong probably to an undescribed species, referred here to *Z. cf. deshayesi*.

6.1.3. *Cyclopyge*

Cyclopygids, comprising a poorly preserved disarranged exoskeleton (Fig. 6h), several pygidia (e.g. Fig. 6b–d) and an eye were described by Maillieux (1939, p. 35) as *C. rediviva* (Barrande). Allowing for distortion in the Sart-Bernard specimens, the pygidia are consistent with the description and figures of this species given by Marek (1961, p. 19, pl. 1, figs. 3, 4), which have a long postaxial area crossed by a weak, narrow sagittal ridge. In Bohemia, Marek (1961, p. 21) described *C. rediviva* as being relatively abundant in the Černín Beds (i.e. Vinice Formation). Maillieux (1939) also redetermined a single occurrence from the Vitřival-Bruyère Formation, originally described as '*Aeglina binodosa*' as *C. rediviva* (see Dean, 1991, p. 144).

6.1.4. *Stenopareia*

Three illaenid cephalae and five pygidia were attributed by Maillieux (1939, p. 37, pl. 3, fig. 6) to *Illaeus katzeri* (Barrande), but the pygidial outline, short pygidial axis and long postaxial area (see also Fig. 6e herein), suggest that these specimens belong to *Stenopareia*, and resemble *S. panderi* (Barrande) from the Zahořany Formation, Bohemia (Šnajdr, 1957, pl. 7, figs. 3–7). They are here referred to *S. cf. panderi*.

6.1.5. *Prionocheilus*

One laterally compressed cranidium (Maillieux, 1939, p. 38, pl. 3, figs. 7, 7a; herein Fig. 2a) is too badly preserved for it to be determined specifically, although it

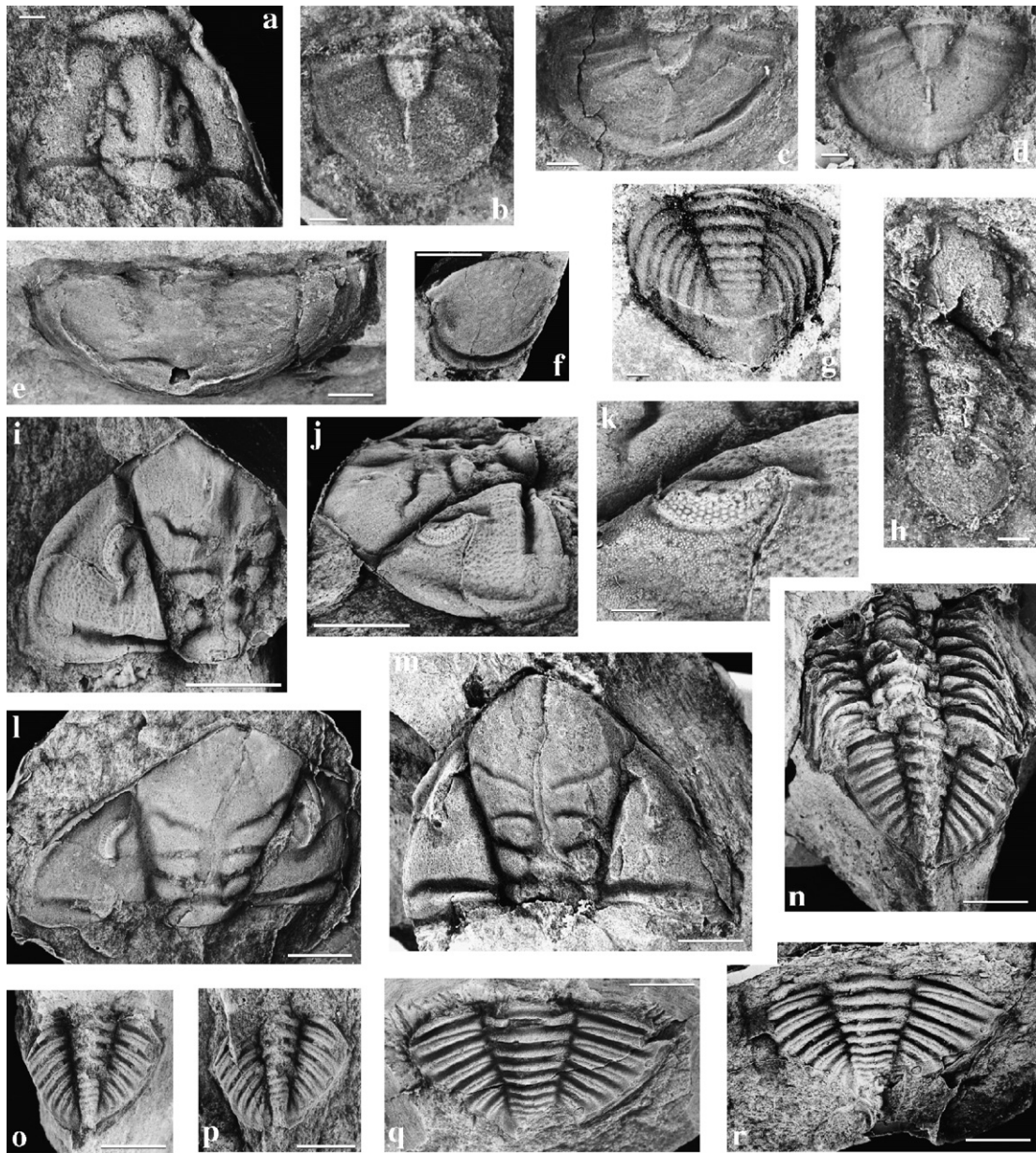


Fig. 6. Selected trilobites from the Sart-Bernard Formation: (a) *Prionocheilus* aff. *pulcher* (Barrande), IRScNB a9808, laterally compressed cranidium, latex cast (orig. Maillieux, 1939, pl. 3, fig. 7, 7a). (b–d, h) *Cyclopyge rediviva* (Barrande): (b) IRScNB a9806, pygidium, internal mould (orig. Maillieux, 1939, pl. 3, fig. 12), (c) IRScNB a9805, pygidium, internal mould, (d) IRScNB a9805, pygidium, latex cast of external mould, (h) IRScNB a9803, disarranged dorsal exoskeleton, internal mould (orig. Maillieux, 1939, pl. 3, fig. 9). (e) *Stenopareia* aff. *panderi* (Barrande), IRScNB 11280, antero-posteriorly compressed pygidium, internal mould. (g) *Zeliskella* cf. *deshayesi* (Barrande), IRScNB a9810, pygidium, internal mould (orig. Maillieux, 1939, pl. 1, fig. 24). (f, i–r) *Dalmanitina proaeva* cf. *elfrida* Šnajdr: (f) IRScNB a9817, hypostoma, internal mould (orig. Maillieux, 1939, pl. 3, fig. 19), (i–k) IRScNB a9814, cephalon, latex cast of incomplete external mould; (i) dorsal view, (j) lateral oblique view, (k) detail of eye and sculpture of gena (counterpart figd Maillieux, 1939, pl. 3, fig. 16). (l) IRScNB a9816, cephalon, latex cast of external mould (counterpart figd Maillieux, 1939, pl. 3, fig. 18). (m) IRScNB a9815, cephalon, internal mould (orig. Maillieux, 1939, pl. 3, fig. 17). (n) IRScNB a9812, thorax and pygidium, internal mould (part of moult arrangement figd Maillieux, 1939, pl. 3, fig. 14), (o, p) IRScNB a9821, small pygidium, internal mould and latex cast of counterpart external mould (orig. Maillieux, 1939, pl. 3, fig. 23). (q, r) IRScNB a9819, pygidium, internal mould and latex cast of counterpart external mould (orig. Maillieux, 1939, pl. 3, fig. 21). All from railway cutting at Sart-Bernard. Scale bars represent: 1 mm (a, b, c, d, g, h, k) and 5 mm (e, f, i, j, l–r).

generally resembles *P. pulcher* which occurs in the Letná, Vinice and Zahořany Formations in Bohemia. It is figured here as *P. cf. pulcher*.

6.2. Comparison of the trilobites of the Sart-Bernard Formation with coeval faunas

6.2.1. Bohemia

As recognised by Maillieux (1939), the Sart-Bernard fauna shows great similarity to that of Bohemia, to the extent that he considered several taxa to be conspecific with Bohemian ones. This connection is reaffirmed here, although revised specific determinations (see above) have shown that the fauna is somewhat younger than supposed by Maillieux, being of mid-Caradoc rather than Llandeilian age. However, it remains true that all the trilobite species present are either conspecific with, or compare closely to Bohemian taxa; preservation and quantity of specimens available of rarer forms does not permit definitive identification, and further material may yet show that these, too, are conspecific.

6.2.2. Morocco and Turkey

Although *D. proaeva* is present in the Caradoc of these areas of Gondwana (Dean, 1967, 1983; Destombes, 1972), the accompanying faunas are different, perhaps reflecting a slightly shallower-water origin. Dean (1983, p. 94) noted the wide distribution of *D. proaeva* and *Colpocoryphe grandis* in the Caradoc of southeastern Turkey, and the Anti-Atlas, Morocco; these taxa are accompanied at some levels by other Bohemian taxa such as *Kloucekia phillipsii* and *Nobiliasaphus cf. nobilis*.

6.2.3. Avalonia

None of the genera present in the Sart-Bernard Formation have been recorded from the Caradoc of southern Britain (see Dean, 1963; Thomas et al., 1984, for lists). *Dalmanitina mucronata matutina*, described by Dean (1962) from the higher levels in the Dufton Shale Formation (Pusgillian Stage, now included in the early Ashgill) of northern England was transferred subsequently to *Mucronaspis* by Destombes (1972, p. 51), and the same may apply to the '*Dalmanitina*' described by Reed (1904) from the Caradoc Mydrim Shale Formation of southwest Wales.

7. Trilobites of the Oxhe and Fosses Formations

7.1. The Oxhe Formation

The trilobite fauna was revised by Dean (1991) who established a Longvillian age (Burrellian Stage, Long-

villian Substage) on the basis of the presence of *Broeggerolithus nicholsoni* (Reed) and *Brongniartella minor minor* (Salter). These belong to an assemblage which is widespread in southern Britain (Dean, 1991, fig. 5), occurring in northern England (Lake District and Cross Fell Inlier), North Wales (Snowdonia, Bala, Oswestry and Meifod areas), south Shropshire (Caradoc area) and southeastern Ireland (Slieveroe, near Rathdrum). This is a typical eastern Avalonian fauna, contrasting with coeval ones from Bohemia. However, links with Baltica are indicated by the identification by Bowdler-Hicks et al. (2002) of *B. nicholsoni* in the 'upper Chasmops beds' of Jämtland, Sweden.

7.2. The Fosses Formation

The stratigraphy and age of this formation were reviewed by Lespérance and Sheehan (1988). They noted that the trilobite faunas are clearly of Ashgill age, but not sufficiently diagnostic to give a precise correlation with the type Ashgill, although they are definitely pre-Hirnantian. Lespérance in Lespérance and Sheehan (1988) described the trilobites, many of which he attributed to new species. The trinucleid *Tretaspis hadelandica* s.l. ranges throughout most of the pre-Hirnantian Ashgill (Owen, 1980), but further, better-preserved material may offer the possibility of determination to subspecies level, with the potential of closer stratigraphical resolution. *Autoxolichas laxatus* (M'Coy) ranges to the top of the Cautleyan in Britain (Thomas et al., 1984, fig. 17, p. 40), and its presence hints at an early Ashgill age. The balance of the fauna includes *Arthrorhachis cf. tarda* (Barrande), *Phillipsinella* sp., *Stenopareia cf. glabra* (Kjerulf), *Cybeloides* sp., '*Otarion*' sp., *Primaspis* sp., *Calyptaulax* sp., *Sphaerocoryphe aff. thomsoni* (Reed), *Sambreuseaspis fossesensis* Lespérance, *Stygina laevis* Lespérance, *Panderia australis* Lespérance, *Novaspis abbatialis* Lespérance, *Atractopyge belgica* Lespérance and *Toxochasmops cognitus* Lespérance. This assemblage, as remarked by Lespérance in Lespérance and Sheehan (1988), has affinities with faunas from Baltica, e.g. the Oslo district. Dean (1991, p. 144) redetermined *Homalonotus omaliusii* Malaise from the Assise de Gembloux (later incorporated in the Fosses Formation) as *Brongniartella platynotus* (Dalman), which occurs in the Dalmanitina Beds of Västergötland, Sweden, giving a further link to Baltica. The fauna is also like those from other parts of eastern Avalonia, and the assemblage has many genera in common with the Králův Dvůr Formation, Bohemia (Shaw, 2000), attesting to the more cosmopolitan nature of Ashgill faunas consequent upon the increasing proximity of Avalonia, Baltica and peri-Gondwanan terranes during the late Ordovician.

8. Palaeobiogeographical interpretation

Four of the Ordovician formations (Huy, Sart-Bernard, Oxhe and Fosses) of the Condroz Inlier have yielded trilobite assemblages which have been dated as early Llanvirn, mid-Caradoc and Ashgill. That of the Llanvirn Huy Formation has been shown to be of outer shelf and upper slope origin, comprising mesopelagic and deep water benthic assemblages. It can be matched closely with other similar associations from the margins of Avalonia—i.e. Skiddaw Group and Herscheider Schichten, and there can be little doubt that all belong to comparable palaeoenvironments. While the benthic species are restricted to Avalonia, mesopelagic cyclopygids, especially *P. binodosa*, are of wide distribution, and occur in similar facies where these are present in marginal Armorica (Massif Armoricain) and in the Prague Basin, Bohemia (see Fig. 7). These latter areas have similar associations of benthic genera, adapted to deeper water conditions, but represented by different species. The most widespread element of the Huy Formation trilobite fauna, both in terms of palaeogeographical extent, and range of facies is *P. cambriensis* (Fig. 7), for which a possible epipelagic habitat is suggested (see above).

Like that of the Huy Formation, the trilobite fauna of the Oxhe Formation is distinctively Avalonian, as demonstrated by Dean (1991) who identified within it *B. nicholsoni* (Reed) and *B. minor minor* (Salter), widely distributed in the mid-Caradoc Longvillian Substage in southern Britain and eastern Ireland, and now known also from a similar horizon in Baltica (see above).

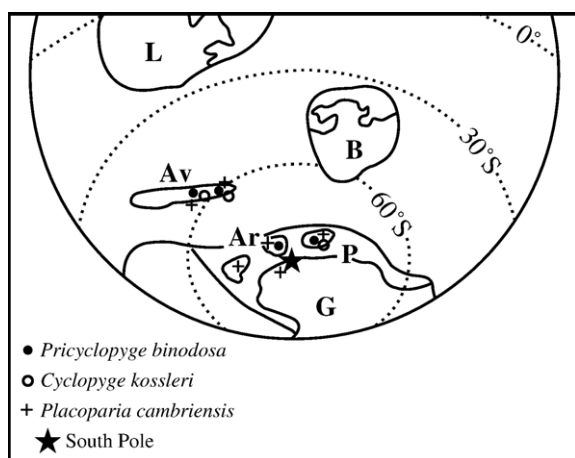


Fig. 7. Tilted Middle Ordovician (Llanvirn) palaeogeographical reconstruction, after Robardet (2003), placing Armorica (Ar) and Perunica (P) on the periphery of Gondwana. Other abbreviations: G: Gondwana, B: Baltica, L: Laurentia. The distribution of mesopelagic (*P. binodosa* and *C. kossleri*) and possible epipelagic (*P. cambriensis*) trilobite species is plotted.

The affinities of the trilobite fauna of the Sart-Bernard Formation, now known to be of mid-Caradoc age, are in complete contrast to those of the Huy and Oxhe Formations. Its relationships to the latter, of a similar age, are as yet unresolved (see above). The striking aspect of the Sart-Bernard trilobites is that they are referable to Bohemian taxa, and the fauna is dominated by *D. proaeva* cf. *elfrida* Šnajdr. This is the only fauna from Avalonia with such affinities, and its presence is difficult to explain in palaeogeographical terms, since most reconstructions show Avalonia well separated from Perunica (i.e. Bohemia) at this time. Elsewhere, *D. proaeva* (Emmrich) s.l. is known from the mid-Caradoc of Morocco and Turkey (see above), which along with Perunica and Armorica formed part of the margins of Gondwana, following Robardet's (2003) model. It is possible that the Rheic Ocean which separated these regions from Avalonia at this time was sufficiently narrow to allow these trilobites to migrate to eastern parts of the latter, or alternatively that the Perunican part of peri-Gondwana moved into slightly lower latitudes to form a 'bridge' between these areas and Armorica. There is no evidence that Bohemian trilobite faunas migrated farther onto Avalonia. The pelagic *C. rediviva* (Barrande) is known only from Bohemia and Sart-Bernard, and its distribution suggests that it was epipelagic, restricted apparently to the outer shelf and perhaps the slope; water temperature possibly also confined it to cooler, high-latitude regions. If this is so, such cooler waters could temporarily have prevailed in easternmost Avalonia, bringing with them 'Bohemian' trilobite faunas.

By the Ashgill, eastern Avalonia had moved close to Baltica and this is reflected in the trilobite fauna of the Fosses Formation. Although Lespérance in Lespérance and Sheehan (1988) identified a number of endemic species, it is possible, as noted above, that larger samples may reveal them to belong to species described from the British parts of Avalonia and from Baltica.

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