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Biostratigraphic significance of brachiopods near the Devonian–Carboniferous boundary

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Abstract – The biostratigraphic significance of selected uppermost Famennian (Upper Devonian) and lower Tournaisian (Mississippian) brachiopod genera, belonging to the orders Rhynchonellida (e.g. *Araratella*), Spiriferida (e.g. *Sphenospira*, *Prospira*), Spiriferinida (*Syringothyris*) and Productida (except Chonetidina), is discussed. Owing to the difficulties of identifying productidine and strophalosiidine genera, in contrast to rhynchonellides and spiriferides, the biostratigraphic potential of the former has generally been overlooked. Brachiopods flourished in neritic environments that were unfavourable for conodonts and ammonoids. In the absence of the latter traditional marker fossils, they are potentially important for locating the Devonian–Carboniferous boundary in shallow water depositional settings in conjunction with rugose corals and foraminifers. On a worldwide scale, further work is required to reach a better assessment of the aftermath of the Hangenberg biological Crisis on brachiopods, notably in revising the faunas from the classical areas of the Famennian and Tournaisian stages in Western Europe.

Keywords: Productida, Rhynchonellida, Spiriferida, Spiriferinida, Famennian, Tournaisian, Hangenberg Crisis.

1. Introduction

Palaeodiversity was strongly affected at the Devonian–Carboniferous (D–C) boundary, as a consequence of the Hangenberg Crisis interval (Fig. 1), which extended from the end of the Famennian (from the base of the middle *Siphonodella praesulcata* conodont Zone) to the base of the Tournaisian (entry of the ammonoid *Gattendorfia*) (Kaiser *et al.* 2011). On a global scale, the stratigraphic interval under consideration is marked by significant lithological changes such as the development of black shales and sandstones in marine carbonate environments and hiatuses (Kaiser *et al.* 2011), whose causes are still hotly disputed (Caplan & Bustin, 1999; Streel *et al.* 2000; Kaiser *et al.* 2011) but are probably related to major sea-level changes (Becker, 1996).

In terms of biostratigraphy, the D–C boundary corresponds to the first occurrence of the conodont *Siphonodella sulcata* (Fig. 1) in the current GSSP of La Serre (southern France), but recent research has shown that the evolutionary lineage from *S. praesulcata* to *S. sulcata* is inadequate to define this boundary (Corradini & Kaiser, 2009; Kaiser, 2009; Corradini *et al.* 2011).

Judging from the stratigraphical record of brachiopods, the Hangenberg Crisis seems to have been less severe than the end Frasnian Crisis as no extinction of brachiopod orders occurs at the D–C boundary. Significant post-crisis recovery took place during the Tournaisian (Sun & Baliński, 2011), especially within the spiriferides and the productidines, and similar recoveries have been documented in other fossil groups, notably goniatites (Kullmann, 2002) and trilobites (Brauckmann, Chlupáč & Feist, 1993).

The purpose of this paper is to refine the biostratigraphic potential of some rhynchonellides, spiriferides, spiriferinides, productidines and strophalosiidines (Brachiopoda) known around the D–C boundary that were previously discussed by Nicollin & Brice (2004). The history of the brachiopods in the aftermath of the Hangenberg Crisis is discussed briefly.

2. Brachiopod genera with stratigraphic value at the Devonian–Carboniferous boundary

Although the current GSSP of the base of the Carboniferous is under review as a result of recent studies on conodonts (see Section 1), it is worth remembering that selected brachiopod genera are valuable biostratigraphic tools in neritic facies, which were unfavourable for ammonoids and conodonts, owing to their short stratigraphical range and their extensive geographical distribution (Brice, Legrand-Blain & Nicollin, 2007).

During the last decades, our knowledge of the brachiopod faunas from the uppermost

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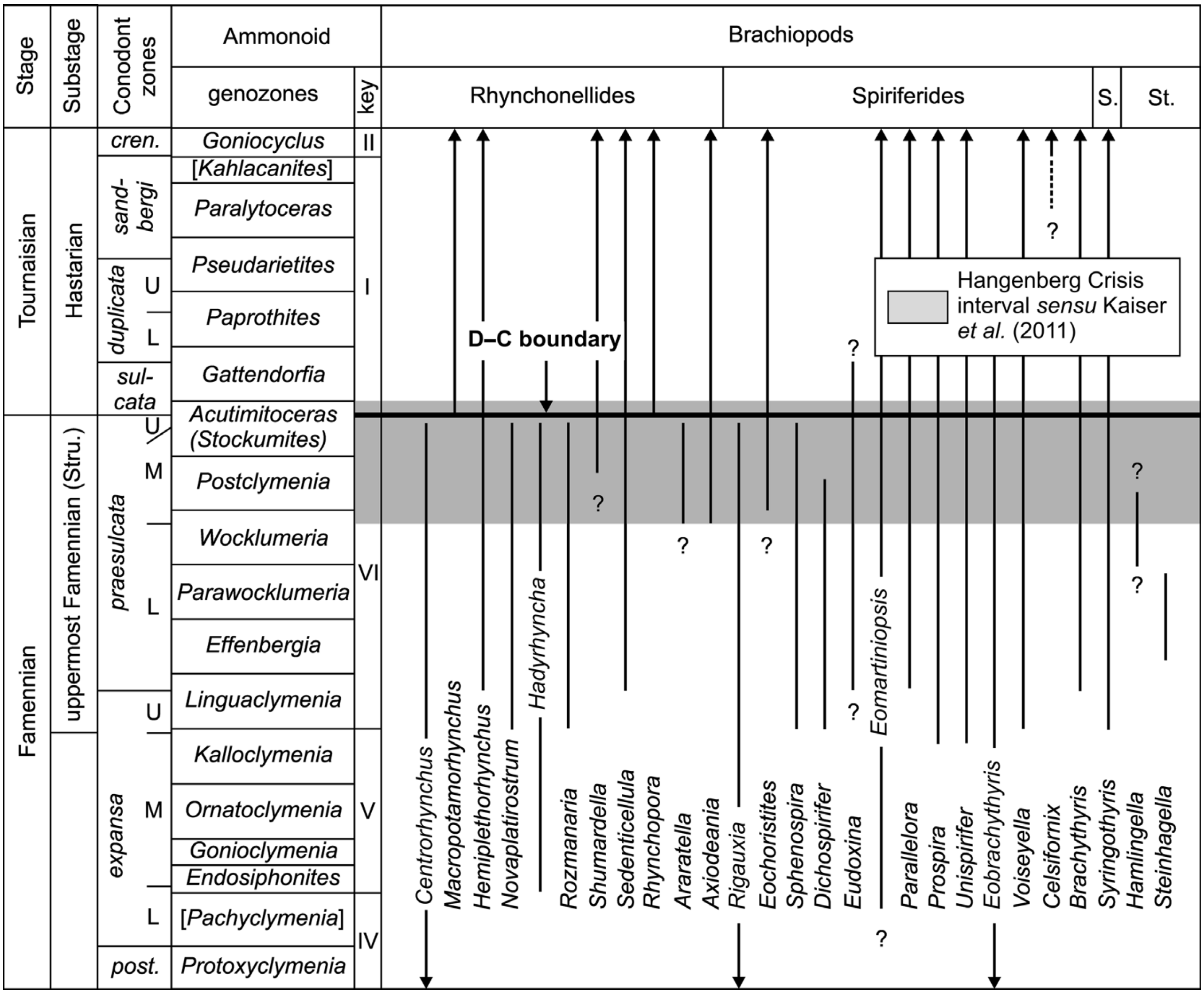

Figure 1. Distribution of significant brachiopod genera present in the uppermost Famennian–Hastarian interval. The regional Kinderhookian Substage (not illustrated here) is essentially equivalent to the Western European Hastarian Substage (Heckel & Work *in* Menning *et al*. 2006). Conodont and ammonoid zonations are adapted from Kaiser *et al*. (2011). Abbreviations: *cren*. – *crenulata*; D–C – Devonian–Carboniferous; L – lower; M – middle; *post*. – *postera*; S. – spiriferinides; St. – stropalosiinides; Stru. – 'Strunian'; U – upper.

Famennian–Hastarian interval has increased significantly in various parts of the world (see references herein) but despite all these efforts, it still remains incomplete. For example, brachiopods from the Franco-Belgian Basin, i.e. the type area of the 'Strunian' (Streel, Brice & Mistiaen, 2006) and the Hastarian (Hance & Poty, 2006), remain imperfectly known despite several recent studies (Legrand-Blain, 1991, 1995*a*; Brice, 1997).

We focus here mainly on the genera that occur with certainty within the uppermost Famennian on the basis of conodont and goniatite data (Fig. 1). In spite of the problems inherent in the present definition of the D–C boundary (see above), we accept the level recently proposed by Kaiser (2009) for the D–C boundary in the current GSSP (La Serre), which is now placed within bed 84, whereas it was previously placed at the base of the bed 89 (Paproth, Feist & Flajs, 1991). This modification has some consequences for the age of the brachiopod faunas reported from La Serre by Legrand-Blain & Martínez Chacón (1988). For the references to the authors who erected the genera listed below, their description and their classification, see Brunton *et al*. (2000), Savage *et al*. (2002), Carter & Johnson (2006) and Carter *et al*. (2006).

2.a. Rhynchonellides

Rhynchonellides have been used for the biostratigraphy of the Famennian Stage on a worldwide scale. Among the genera listed below and included in Figure 1, five (*Araratella*, *Centrorhynchus*, *Hadyrhyncha*, *Novaplatirostrum* and *Rozmanaria*) disappeared at the end of the Devonian, whereas four survived into the Tournaisian (*Axiodeaneia*, *Hemiplethorhynchus*, *Sedenticellula* and *Shumardella*), and two occur for the first time in the basal Tournaisian (*Macropotamorhynchus* and *Rhynchopora*). Other rhynchonellide genera that may have biostratigraphic potential are also briefly discussed.

2.a.1. Superfamily Rhynchotrematoidea

The Rhynchotrematoidea comprises genera that are characterized internally by dental plates that are sometimes fused to the valve walls, a usually long dorsal median septum (rarely absent) and a variably developed septalium. Within this superfamily, only two genera, *Nekhoroshevia* (Trigonirhynchiinae) and *Hemiplethorhynchus* (Ripidiorhynchinae), both belonging to the Family Trigonirhynchiidae, crossed the D–C boundary. No new genera appeared during the Tournaisian and the whole superfamily became extinct during the Viséan.

Three representatives of the Family Trigonirhynchiidae (characterized by the presence of dental plates and a median septum, septalium covered or uncovered) are selected here. *Centrorhynchus* (Trigonirhynchiinae according to Nicollin & Brice, 2004) includes medium- to large-sized shells, subpentagonal in outline, with a prominent fold and sulcus, ventral flanks sometimes slightly concave and strong, subtriangular ribs arising at the beaks, and a posteriorly covered septalium. The genus first occurs within the middle Famennian and disappears close to the D–C boundary. It has a worldwide distribution: Europe (Rozman, 1962; Conil *et al.* 1986; Halamski & Baliński, 2009), North Africa (Brice, Legrand-Blain & Nicollin, 2005), Asia (e.g. Abramian, 1957; Martynova, 1961; Brice, 1971), North America (Sartenaer, 1970; Carter & Kammer, 1990) and Australia (Veevers, 1959). *Centrorhynchus* has in some cases been misidentified as *Ptychomaletoechia,* which is externally very similar (Sartenaer, 1970). The latter was reported in the Tournaisian of China (e.g. Tan, 1987; Chen & Shi, 1999) but, according to Sun & Baliński (2011), the Tournaisian species included in this genus, namely '*Ptychomaletoechia*' *kinlingensis* (Grabau *in* Chu, 1933), needs to be revised as it is externally quite different from typical *Ptychomaletoechia* species. The cosmopolitan genus *Macropotamorhynchus* (Trigonirhynchiinae) is characterized by small shells with a weak fold and sulcus, covered by strong, angular ribs arising at the umbones and a posteriorly covered septalium. It is diagnostic of the Tournaisian, notably in Europe (Sartenaer, 1970), North America (Carter, 1987, 1991; Carter & Kammer, 1990), China (Sun & Baliński, 2011) and North Africa (Brice, Legrand-Blain & Nicollin, 2005, 2007). *Hemiplethorhynchus* (Ripidiorhynchinae) has a rather weak fold and sulcus and numerous fine to medium, angular ribs originating at the beaks and an uncovered septalium. It is generally considered as a Tournaisian genus with a wide geographic distribution (see Brice, Legrand-Blain & Nicollin, 2005), but it is known from the latest Famennian of southern China (Tan, 1987).

2.a.2. Superfamily Camarotoechioidea

The Camarotoechioidea, characterized internally by strong dental plates, a long dorsal median septum and a short, generally uncovered septalium, disappeared in the Tournaisian, in which only some genera belonging to the Leiorhynchinae (Leiorhynchidae) subsisted.

Rossirhynchus (= *Septemirostellum* according to Savage, 2002*a*; Leiorhynchidae), which includes dorsibiconvex shells, subpentagonal in outline, with steeply rounded flanks and strong, angular ribs, is known from the Tournaisian of Iran (e.g. Gaetani, 1964; Bahrammanesh *et al.* 2011) and Australia (Roberts, 1971). However, further investigations are needed to establish its precise stratigraphic extension and, thus, it is not included in Figure 1. *Rossirhynchus* was previously reported from the Tournaisian of South America (Argentina, Chile), but the species assigned to it was recently transferred to the endemic genus *Azurduya* by Cisterna & Isaacson (2003).

2.a.3. Superfamily Pugnacoidea

Representatives of the Family Rozmanariidae, of which *Novaplatirostrum*, *Hadyrhyncha* and *Rozmanaria* are selected here, are characterized by shells that are smooth or only bear low ribs and lack or have a low dorsal median septum; this family vanished at the end of the Famennian.

Novaplatirostrum includes medium-sized, flattened, equibiconvex shells with a large, low fold and shallow sulcus arising at about the three-quarter point of the shell length, and few, low simple ribs restricted to the anterior median part of the valves. Until now, it has only been reported from the uppermost Famennian of Germany (Sartenaer, 1997) and Poland (Halamski & Baliński, 2009). *Hadyrhyncha* has a medium-sized, ovate shell with a dorsal sulcus and ventral fold arising at the mid-length, and weak, rounded ribs; it occurs in the upper to uppermost Famennian of the Czech Republic (Havlíček, 1979), in the uppermost Famennian of Poland (Halamski & Baliński, 2009) and in the upper Famennian of Morocco (Sartenaer, 1998). *Rozmanaria* includes small-sized, smooth shells transversely ovate in outline, with a dorsal sulcus and ventral fold that are very strong anteriorly. It is known from the upper Famennian of Russia (Rozman, 1962) and in the uppermost Famennian (UD V–VI) of Germany (Weyer, 1972) and Poland (Halamski & Baliński, 2009). *Shumardella* (Petasmariidae) is characterized by a small-sized, dorsibiconvex, subtrigonal shell with a strong fold and sulcus, which bear a few strong ribs arising at the umbones. It is a typical Tournaisian genus, although it was reported within the 'Etroeungt Zone' in the southern Ural Mountains by Krestovnikov & Karpyshev (1948). It is well known within the Kinderhookian of North America (Carter, 1987, 1988, 1991) and in the basal Tournaisian of North Africa (Brice, Legrand-Blain & Nicollin, 2005).

2.a.4. Superfamily Stenoscismatoidea

The Stenoscismatoidea, which appeared in the Pragian, flourished mainly during the Carboniferous and the Permian.

Sedenticellula (Stenoscismatidae, Stenoscismatinae) includes medium-sized shells covered by simple, bifurcating or intercalating, low, narrow ribs arising at or very near the umbones; as in the other members of the Stenoscismatoidea, it possesses particular internal features such as a dorsal camarophorium and a ventral spondylium. Its oldest occurrence is reported within the uppermost Famennian (Lower to Middle *praesulcata* zones) of southern France (Legrand-Blain & Martínez Chacón, 1988) but, during the Tournaisian, it seems to be restricted to the Kinderhookian (or possibly the early Osagean) of the USA (Carter, 1988, 1991).

2.a.5. *Superfamily Lambdarinoidea*

The oldest record of these micromorphic rhynchonellides with a usually bilobed or cordiform outline is from the lower Famennian of Poland (Baliński, 1982). The Family Lambdarinidae shows a distinctive radiation that seems to have taken place just after the D–C boundary with the appearance of the genera *Lambdarina* and *Dacryrina* (see Baliński & Sun, 2008 for more details). The latter could be valuable index fossils but in order to extract them from limestones and marls they need to be silicified (Baliński & Sun, 2008) and thus, their biostratigraphic utility is probably reduced.

2.a.6. *Superfamily Rhynchoporoidea*

Members of the Rhynchoporoidea typically have an endopunctate shell, which is quite exceptional among rhynchonellide brachiopods. *Rhynchopora* (Rhynchoporidae, Rhynchoporinae) has a transversely subpentagonal outline, with a fold and sulcus that become prominent anteriorly, a rectangular tongue and numerous ribs. This genus occurs at the base of the Tournaisian (*sulcata* Zone) of southern France (Legrand-Blain & Martínez Chacón, 1988) and in the Kinderhookian of the USA (e.g. Carter, 1988, 1991), but extends to the Permian (Savage, 2002*b*). *Araratella* (Araratellidae according to Sartenaer & Plodowski, 2003) is very useful for recognizing the D–C boundary owing to its short stratigraphical range (uppermost Famennian) and its wide geographical distribution (see Sartenaer & Plodowski, 2003 for more details).

2.a.7. *Superfamily Rhynchotetradoidea*

The Rhynchotetradoidea include shells characterized internally by a variably developed spondylium, a strong dorsal median septum and an uncovered septalium. This superfamily originated in the Famennian and had a long evolutionary history, becoming extinct in the Middle Jurassic. Their first radiation took place in the Tournaisian with the origination of several new genera among the rhynchotetradid subfamilies Rhynchotetradinae and Axiodeaneiinae, as well as among the Tetracameridae. On the basis of Savage's (2002*c*) data, cosmopolitan genera such as *Rhynchotetra* (Rhynchotetradinae) and the tetracamerids *Tetracamera*, *Rotaia* and *Yanishewskiella* first occurred in the lower part of the Tournaisian, but further investigations are needed to establish their stratigraphic extension in various parts of the world. Carter (1991) provided information related to the stratigraphic range of the three first genera in North America, and of those only *Rhynchotetra* has its first occurrence close to the D–C boundary (Kinderhookian).

Both genera of the Subfamily Axiodeaneiinae (Rhynchotetradidae), which share an elongate outline and a sessile spondylium, are of some interest for recognizing the D–C boundary interval. *Axiodeaneia*, characterized by a narrowly elongate outline, a biconvex profile, low, very coarse angular ribs covered by thin radial striae and a low tridentate tongue, spans the interval from the base of the Kinderhookian to that of the Osagean in North America (Carter, 1987, 1988, 1991). The genus is also reported at the top of the Famennian and at the base of the Tournaisian in South China (Guangxi) by Li *et al.* (2011) and in basal Tournaisian strata of Central Europe (Havlíček, 1979). *Paraphorhynchus*, which differs from *Axiodeaneia* in having a high serrate tongue, rounded ribs and a shorter dorsal median septum, is known from the latest Famennian to the Kinderhookian in North America (Carter, 1991). Savage (2002*c*) reported the genus in Europe, the Urals, Novaya Zemlya and Kazakhstan, but without stratigraphic information, while Bahrammanesh *et al.* (2011) recorded its presence in the Tournaisian of North Iran. However, the stratigraphic range of the genus in the areas listed above needs to be clarified.

2.b. Spiriferides

Members of this order (Fig. 1) are generally predominant within the brachiopod associations of the Famennian–Tournaisian interval and are particularly diverse. The end of the Famennian marked the extinction of two typically Devonian superfamilies (Adolfioidea, Cyrtospiriferoidea), but also the development of the first spiriferide prismatic shell layer among the ulbospiriferids (Theodossioidea), which is a characteristic feature of the Carboniferous–Permian Spiriferoidea, Paeckelmannelloidea and Brachythyroidea (Carter & Gourvennec, 2006*a*). The Mississippian is characterized by important radiations among the spiriferide superfamilies Martinioidea, Spiriferoidea and Paeckelmannelloidea (see fig. 1102 in Carter & Gourvennec, 2006*a*). No genera of the superfamilies Delthyridoidea and Reticularioidea are selected here. The Delthyridoidea underwent a long decline after their acme in the Lower Devonian and became extinct in the Mississippian (Viséan); besides the long-ranging genus *Tylothyris* (see Nicollin & Brice, 2004), only one new genus (*Texathyris*; presently known only from Texas) appeared during the Tournaisian (top of the Kinderhookian, see Carter, 1991). The evolutionary history of the Reticularioidea is quite similar to that of the Delthyridoidea. They also had their acme in the Lower Devonian and almost disappeared during the Pennsylvanian but underwent a last radiation in the early Permian before becoming extinct at the end of this period (Carter & Gourvennec, 2006*a*). Some elythid genera (*Kitakamithyris*, *Toryniferella*) have already been discussed by Nicollin & Brice (2004).

2.b.1. *Superfamily Adolfioidea*

This superfamily, known from the Wenlock (Johnson, 2006*a*), became extinct at the end of the Famennian. It includes several genera that seem to be restricted to the upper Famennian such as the adolfiid *Volgospirifer* from the Russian Platform (Tsyganko, 2008) and the echinopiriferids *Enchondrospirifer* (Afghanistan; Brice, 1971) and *Sergunkovia* from the Urals and Central Asia (Nalivkin, 1979), but to our knowledge, only *Rigauxia* (Echinospiriferidae), which first occurred in the Frasnian, has been reported in the uppermost Famennian of the Middle East (Brice, 1971, 1999; Kebria-ee & Taghvaei, 2010) and Western Europe (García-Alcalde & Menéndez-Álvarez, 1988). This genus includes small- to medium-sized shells covered by simple ribs on the flanks and the fold and in the sulcus, with subradial and tuberculate capillae.

2.b.2. *Superfamily Theodossioidea*

The Theodossioidea, which include shells devoid of a fold and sulcus (or with these features only poorly developed) and without a delthyrial plate, had their acme in the Upper Devonian, but became extinct during the Tournaisian, in which the only representatives are in the Family Palaeochoristitidae that originated during the upper Famennian.

Eochoristites (Palaeochoristitidae), including moderately biconvex shells with usually simple ribs on the flanks and strong simple or divided ribs in the sulcus, is known from the uppermost Famennian of China (Xu & Yao, 1988), but is an especially valuable guide for the lower part of the Tournaisian in North Africa (Havlíček, 1984; Legrand-Blain, 1995*a*; Brice, Legrand-Blain & Nicollin, 2005). In southeastern China, the genus also occurs in the Hastarian (Chen & Shi, 1999; Chen, 2004; Sun & Baliński, 2011), but is mainly a guide for the Ivorian (Y. Sun, pers. com.).

2.b.3. *Superfamily Cyrtospiriferoidea*

Cyrtospiriferoids, which generally have a well-developed delthyrial plate, are emblematic of the Emsian–Famennian interval. They became extinct at the end of the Famennian. Among the Family Cyrtospiriferidae, two genera are valuable for recognizing the upper part of the Famennian. *Sphenospira* (Cyrtospiriferinae) is known from the upper Famennian in North America (Cooper, 1954). *Sphenospira julii* (Dehée, 1929), an index species of the uppermost Famennian, is reported from Eurasia (e.g. Afanasjeva *et al.* 2003; Nicollin & Brice, 2004; Halamski & Baliński, 2009; Grechishnikova & Levitskii, 2011), and doubtfully in North Africa (Brice, Legrand-Blain & Nicollin, 2005). *Dichospirifer* (Cyrtiopsinae) is known from the upper and uppermost Famennian of Eurasia (Abramian, 1957; Brice, 1971; Plodowski & Kononova, 1994; Kebria-ee & Taghvaei, 2010; Grechishnikova and Levitskii, 2011), western North America (Johnson, 2006*b*) and North Africa (Nicollin & Brice, 2001; Brice, Legrand-Blain & Nicollin, 2005).

2.b.4. *Superfamily Ambocoelioidea*

Among the ambocoelioids, the upper Famennian is marked by the origination of a new family, the Eudoxinidae, which groups together small to very large forms that are notably devoid of dental adminicula. Nevertheless, the ambocoelioids were not particularly diverse during the Mississippian and comprise some long-ranging genera such as *Crurithyris* (Ambocoeliinae), which is generally considered as an opportunistic eurytopic taxon characteristic of stressful and/or dysaerobic environments (Campi & Shi, 2007), and *Verneuilia* (Verneuiliidae).

Eudoxina (Eudoxinidae) includes medium to large shells, thinly to very thinly ribbed, rounded in outline, with a poorly to moderately developed fold and sulcus containing fine to very fine ribs. It is restricted to the base of the Kinderhookian in the USA (Illinois, Iowa) (Carter, 1988, 1991) and to the same stratigraphic level in Russia (Kalashnikov, 1974; Fotieva, 1985) and the Ukraine (Poletaev, 1975). In China, the genus is tentatively reported at the top of the Famennian (Sun & Baliński, 2011).

2.b.5. *Superfamily Martinioidea*

In contrast to the ambocoelioids, in which diversity scarcely changed between the Upper Devonian and the Mississippian, martinioids had a significant radiation during the Mississippian with the appearance of large forms.

Only *Eomartiniopsis* is selected here; it includes shells that are characterized by a rounded outline, a fold and sulcus weakly rounded to moderately developed, and are devoid of ribs or have only a few ones on the flanks. It is doubtfully reported in the upper to uppermost Famennian of Poland by Halamski & Baliński (2009), but is known from the base of the Kinderhookian to the Osagean in North America (Carter, 1988, 1991), in the Tournaisian succession of North Africa (Brice, Legrand-Blain & Nicollin, 2005; Mottequin & Legrand-Blain, 2010), Russia (e.g. Fotieva, 1985) and Australia (Roberts, 1971).

2.b.6. *Superfamily Spiriferoidea*

Representatives of the Superfamily Spiriferoidea, which are characterized by a denticulate hinge line, appeared in the course of the upper Famennian, during which they were associated with the last members of the cyrtospiriferoids (e.g. *Sphenospira*).

Among the Family Spiriferidae, we have selected three genera of the Subfamily Prospirinae, namely *Parallelora, Prospira* and *Unispirifer*, which represent valuable guides for the D–C boundary. *Parallelora* includes medium-sized shells with flanks covered by rounded, simple or bifurcating ribs and with a few sulcal ribs, usually simple, and a rectangular ventral interarea. This genus first occurs in the upper Famennian and crosses the D–C boundary. During uppermost Famennian times, *Parallelora* is known from the Middle East (Plodowski, 1970), China (Xu & Yao, 1988), Russia (Nalivkin, 1979), North Africa (Legrand-Blain, 1995*a*; Brice, Legrand-Blain & Nicollin, 2005) and North America (Carter, 1974, 1991). *Prospira* is characterized by small- to medium-sized shells, subquadrate to subpentagonal in outline, with simple ribs on the flanks and a narrow fold and sulcus, with usually simple lateral ribs (except the median one) originating by bifurcation of the sulcus-bounding ribs. It spans the interval ranging from the uppermost Famennian to the Tournaisian. During the uppermost Famennian, the genus occurs in Western Europe (García-Alcalde *et al.* 1985; Conil *et al.* 1986; Legrand-Blain, 1995*a*; Brice, 1997), the Middle East (Brice, 1971, 1999; Kebria-ee & Taghvaei, 2010) and North Africa (Brice, Legrand-Blain & Nicollin, 2005). In North America (Carter, 1991) and Australia (Roberts, 1971), *Prospira* is a characteristic Tournaisian form. *Unispirifer* includes medium- to large-sized shells with numerous usually simple ribs on the flanks and with a sulcus bearing median ribs that may bifurcate (other sulcal ribs are usually simple). It is known from the uppermost Famennian, notably in Afghanistan (Brice, 1971, 1999) and Western Europe (Conil *et al.* 1986; Legrand-Blain & Martínez Chacón, 1988). It became cosmopolitan during the Tournaisian: North America (e.g. Carter 1988, 1991), North Africa (Havlíček, 1984; Mergl & Massa, 1992; Legrand-Blain, 1995*a*; Brice, Legrand-Blain & Nicollin, 2005), Europe (Sartenaer & Plodowski, 1996), South China (Sun & Baliński, 2011), Russia (Shilo *et al.* 1984; Poletaev, 2006; Afanasjeva, 2008) and Azerbaijan (Grechishnikova & Levitskii, 2011). *Eobrachythyris* (Sergospiriferinae), characterized by an equidimensional shell with a few simple lateral ribs and smooth sulcus or with a median rib, is known mainly from the upper and uppermost Famennian of Europe (D. Brice, unpub. data), the Middle East (Brice, 1971, 1999; Kebria-ee & Taghvaei, 2010) and North Africa (Brice & Nicollin, 2000), but also occurs in the Hastarian of Algeria (Brice & Nicollin, 2000).

2.b.7. Superfamily Paeckelmannelloidea

This superfamily originated in the course of the Famennian, as was the case for the Spiriferoidea, and its representatives share with representatives of the latter denticulate hinge lines and capillate microornament. These features may indicate that both superfamilies may derive from a common ancestor (Carter & Gourvennec, 2006*a*).

Although Carter (2006) considered *Voiseyella* (Strophopleuridae, Strophopleurinae), which is characterized by small, strongly biconvex and transverse (mucronate) shells with a smooth, narrow fold and sulcus and bearing numerous simple lateral ribs, as only Tournaisian–Viséan in age, it was reported in the uppermost Famennian of Europe (Legrand-Blain & Martínez Chacón, 1988; Legrand-Blain, 1995*a*), Russia (see discussion in Legrand-Blain, 1995*a*), Afghanistan (Plodowski, 1968) and North Africa (Brice, Legrand-Blain & Nicollin, 2005).

Celsifornix (Strophopleuridae, Bashkiriinae) includes medium-sized, strongly transverse shells with a high ventral interarea, flanks covered by simple costae and a moderately developed fold and sulcus that bear some costae. This genus was first described in the Tournaisian (top of the Kinderhookian and base of the Osagean) of the USA (Illinois, Missouri) by Carter (1974) and reported in the Tournaisian of China, notably by Tan (1986) and Baliński & Sun (2010), where its first occurrence is very close to the D–C boundary (Sun & Baliński, 2011).

2.b.8. Superfamily Brachythyridoidea

The Brachythyridoidea group together shells with a narrow hinge line, and thus a typically ovate outline, that are devoid of internal plates in both valves (Carter & Gourvennec, 2006*a*). Like the Spiriferoidea and the Paeckelmannelloidea, they appeared during the Famennian. They underwent a radiation during the Tournaisian with the appearance of new genera within the Family Skelidorygmidae (*Phragmobrachythyris*, *Skelidorygma*).

The cosmopolitan genus *Brachythyris* (Brachythyrididae) is reported within the uppermost Famennian, notably in southern China (Xu & Yao, 1988) and the southern Ural Mountains (Krestovnikov & Karpychev, 1948), and crossed the D–C boundary. Several lower Tournaisian occurrences were reported in Western Europe (Legrand-Blain, 1995*a*), North America (Carter, 1988, 1991) and Kazakhstan and the Urals (Fotieva, 1985).

2.c. Spiriferinides

2.c.1. Superfamily Syringothyridoidea

Representatives of this superfamily are characterized by large shells generally transverse in outline, a high ventral interarea and, in some cases, the presence of a syrinx. Syringothyridoids first occurred during the upper Famennian but flourished in the Carboniferous and early Permian (Carter & Gourvennec, 2006*b*).

Only the cosmopolitan genus *Syringothyris* (Syringothyrididae, Syringothyridinae), which includes punctate shells with a smooth fold and sulcus, and a syrinx, is considered here. Although its representatives were particularly abundant during the Mississippian, several uppermost Famennian occurrences were reported in Europe (Legrand-Blain & Martínez Chacón, 1988), China (e.g. Xu & Yao, 1988; Ma, Zong & Sun, 2011), North America (Carter & Kammer, 1990; Carter, 1991) and North Africa (Brice, Legrand-Blain & Nicollin, 2005). *Syringothyris* was reported particularly in lower Tournaisian successions of Western Europe (Legrand-Blain & Martínez Chacón, 1988; Legrand-Blain, 1995*a*), the southern Urals (Nalivkin, 1975), China (Sun & Baliński, 2011) and North America (Carter, 1991).

2.d. Productidines and strophalosiidines

The suborders Productidina and Strophalosiidina are parts of the Order Productida. Representatives of the Suborder Chonetidina are not discussed here even though they are generally abundant near the D–C boundary (Legrand-Blain & Martínez Chacón, 1988; Afanasjeva, 2002). As stressed by Racheboeuf (*in* Brice *et al.* 2000), because of their particular morphological features and occurrences in various palaeoenvironments, chonetidines have real, potential biostratigraphic value, but those of the uppermost Famennian–Hastarian remain poorly known.

Teeth and dental sockets disappeared during the upper Famennian in the Productidina, but persisted in many taxa within the Strophalosiidina (Brunton *et al.* 1995). Dorsal spines, known from the Middle Devonian onwards within the Echinoconchoidea in which they are arranged as circular bands, independently appear in various families of the Productoidea during the Famennian and the Tournaisian (Poletaev & Lazarev, 1995). Among the ribbed Productidina, ribs tend to arise at the umbones from the Tournaisian onwards (Brunton & Lazarev, 1997).

In contrast to the rhynchonellides, spiriferides and spiriferinides, in which the internal features can be easily studied by serial sectioning, the identification of productidines and strophalosiidines requires perfectly preserved specimens showing the internal faces of the valves (e.g. details of the hinge line) and the details of the ornamentation (e.g. dorsal spines, etc). Their internal morphology can also be studied by transverse serial sectioning, but it is generally not sufficient for a precise description. Moreover, the generic identification can also vary from one author to another. For example, *Producta curtirostra* Winchell, 1865, from the Kinderhookian of the USA, was assigned to *Rugauris* by Muir-Wood & Cooper (1960), to *Sentosia*? by Nalivkin (1979) and to *Whidbornella* by Carter (1988). Owing to the difficulties in identifying productidines and strophalosiidines at the generic level, their biostratigraphical potential is commonly overlooked.

2.d.1. *Superfamily Productoidea*

Among the Family Productellidae, several cosmopolitan genera (e.g. *Productina*) appeared at the top of the Famennian (Brunton & Lazarev, 1997) but did not extend beyond the lower Tournaisian. *Orbinaria* and *Planoproductus* are probably present in the current GSSP of the D–C boundary, within the uppermost Famennian and at the base of the Hastarian, respectively (Legrand-Blain & Martínez Chacón, 1988). Some genera seem to be known exclusively from the Famennian, such as *Dorsirugatia* in Mongolia (Lazarev & Suur'suren, 1992; Lazarev *in* Brunton & Mundy, 1993; Brunton & Lazarev, 1997) and *Iniproductus* in Russia (Kuzbass) (Brunton & Lazarev, 1997). *Argentiproductus*, whose type species is of late Viséan age, spans the interval of the uppermost Famennian to the Serpukhovian (see Brunton & Mundy, 1993 for details). Brunton & Lazarev (1997) indicated that this genus first occurred around the D–C boundary. To our knowledge, its oldest occurrences are reported in the uppermost Famennian of the Urals by Nalivkin (1979) and within the lower part of the Kinderhookian in Illinois by Carter (1988). In South China, *Argentiproductus* is known from the middle part of the Tournaisian (Sun & Baliński, 2008, 2011), whereas in Western Europe, the genus, which is common during the Viséan, has been reported from the Ivorian of Ireland (Mottequin, 2010).

Among the Family Productidae, the oldest genera (with ribbing usually absent or weak, and never developed at the umbo) are known from the Famennian. The disappearance of the articulation and the development of dorsal spines are progressive phenomena (Poletaev & Lazarev, 1995). However, the observation of such important generic features is not always possible and the generic identifications remain problematic, as is notably the case for the distinction between the genera *Nigerinoplica* (with teeth) and *Spinocarinifera* (without teeth). Representatives of *Spinocarinifera* from northern France and Belgium (Legrand-Blain, 1991), all devoid of teeth, occur in uppermost Famennian and lower Hastarian strata. The stratigraphic range of *Semiproductus* spans the interval of the uppermost Famennian to the top of the Tournaisian (Poletaev & Lazarev, 1995). Moreover, some genera with a particular external morphology (for example, a ventral median row of strong spines) are more easily identifiable and could be of the greatest interest in recognizing the D–C boundary. These are *Mesoplica*, *Leioproductus* (North America, Asia) and *Acanthoproductus* (Kazakhstan), which do not seem to cross the D–C boundary. *Mesoplica sensu stricto*, with low rounded costae not arising at the umbo, was cosmopolitan during the uppermost Famennian (Muir-Wood & Cooper, 1960). *Mesoplica sensu lato*, with different details of ornamentation, occurs within Hastarian beds in France (Brice, Legrand-Blain & Nicollin, 2005) and in the lower Kinderhookian of North America (Carter, 1991; Legrand-Blain, 1991).

2.d.2. *Superfamily Echinoconchoidea*

Among the Sentosiidae, *Sentosia* was cosmopolitan during the uppermost Famennian and locally persisted during the lower Hastarian (Legrand-Blain, 1995*a*; Poletaev & Lazarev, 1995). *Bagrasia* (probably a junior synonym of *Ericiatia*) was reported in the uppermost Famennian and the Hastarian of Russia (Lazarev, 1990) and North Africa (Legrand-Blain, 1995*a*, *b*).

2.d.3. *Superfamily Linoproductoidea*

Some species, previously assigned to *Ovatia* (Monticuliferidae), from the uppermost Famennian and Tournaisian of Russia (Poletaev & Lazarev, 1995), and possibly also from the Kinderhookian of North America (Carter, 1972) and the uppermost Famennian – Hastarian of northern France (Nicollin & Brice, 2004), were included in *Krekarpius* (Schrenkiellidae) on the basis of the spine distribution by Lazarev (2004) (see also Brunton, 2007). However, *Ovatia* has been recently reported in the uppermost Famennian of northwestern China by Zong, Ma & Sun (2012).

2.d.4. *Superfamily Strophalosioidea*

Among the Family Araksalosiidae, several genera are valuable index fossils of the Famennian (*Araksalosia*, *Hamlingella*, *Kahlella*) but most of them have a restricted geographical distribution. *Araksalosia* is known from the uppermost Famennian of Mongolia and Transcaucasia (Abramian, 1957; Lazarev, 1989). *Hamlingella* occurs within the uppermost Famennian of Western Europe (Goldring, 1970; Legrand-Blain, 1995*a*), North Africa (Legrand-Blain, 1995*a*; Brice, Legrand-Blain & Nicollin, 2005), Russia (Rzhonsnitskaya, 1988) and Transcaucasia (Abramian, 1974). Until now, *Kahlella* has only been reported in the upper(most) Famennian of the Algerian and Moroccan Sahara (Brice, Legrand-Blain & Nicollin, 2005, 2007). *Acanthatia* occurs in the upper(most) Famennian in Australia (McKellar, 1970), North America (Stainbrook, 1947), Russia (Bublichenko, 1971) and doubtfully in North Africa (Legrand-Blain, 1995*b*; Brice, Legrand-Blain & Nicollin, 2005). In North Africa, it was also reported in the lower Tournaisian by Mergl & Massa (1992) and, tentatively, by Brice, Legrand-Blain & Nicollin (2005). According to the latter, the assignment of North African species to *Acanthatia* remains tentative as they have apparently no cicatrix. The geographic and stratigraphic distribution of *Whidbornella* is quite similar to that of *Acanthatia*. *Whidbornella* is known from the uppermost Famennian in Western Europe (Legrand-Blain, 1995*a*) and North Africa (Legrand-Blain, 1995*a*, *b*; Brice, Legrand-Blain & Nicollin, 2005), and is also reported in the basal Kinderhookian of the USA by Carter (1988). *Steinhagella* is a valuable index genus for the upper(most) Famennian of Western Europe (Legrand-Blain, 1995*a*), North Africa (Brice, Legrand-Blain & Nicollin, 2005) and Russia (Lazarev, 1989).

Among the Family Chonopectidae, *Chonopectus* (chonetoid in appearance) is reported from the Russian Famennian and the Kinderhookian of the USA (see Brunton & Mundy, 1986 and Lazarev, 1989).

3. Brachiopod diversity at the D–C boundary

During the Late Devonian, brachiopod diversity was significantly affected at the end of the Frasnian by the extinction of the orders Pentamerida and Atrypida and by severe losses among the other more important orders (Baliński, 1996; Copper, 2002; Mottequin, 2008*a*). In contrast to other benthic macrofaunas such as the corals (Poty, Denayer & Mottequin, 2011), the post-extinction brachiopod recovery was rapid in the lower Famennian but, despite their great abundance, their diversity was quite low. New cosmopolitan genera appeared at this time particularly among the spire-bearers (athyridides, spiriferides) and the rhynchonellides concomitantly with new species of pre-existing and generally long-ranging orthide and orthotetide genera (Baliński, 2002; Mottequin, 2008*b*). Nevertheless, Devonian brachiopod diversity reached a nadir during the Famennian with 203 genera in comparison with 460 at the Emsian (Curry & Brunton, 2007), but spiriferides and non-chonetidine productides increased significantly during this stage. In broad terms, the Famennian is characterized by brachiopod faunas dominated by the Rhynchonellida, the Spiriferida and the Productida (including the Chonetidina as an important suborder at this time) (Curry & Brunton, 2007) (Fig. 2).

The uppermost Famennian ('Strunian') is characterized by radiations among several brachiopod orders such as the Productida, Spiriferida, Spiriferinida and Rhynchonellida, which developed morphological features heralding the early Mississippian brachiopod faunas (Gosselet, 1857; Cooper, 1954; Conil *et al.* 1986; Simakov, 1990). In common with major groups of invertebrates such as ammonoids (Kullmann, 2002), corals (Poty, 1999), stromatoporoids (Fagerstrom, 1994) and fishes (Friedman & Sallan, 2012), brachiopods suffered extinctions during the Hangenberg Crisis such as the disappearance of the last cyrtospiriferoids. It is clear that the development of euxinic conditions in basinal and shelf locations, which were responsible for the deposition of the Hangenberg Black Shale and its equivalents, followed rapidly by a major sea-level drop (Hangenberg Sandstone and its equivalents; see Kaiser *et al.* 2011), affected the brachiopod faunas at the D–C boundary. However, owing to hiatuses recorded on the platforms, the detailed timing of the brachiopod extinctions is difficult to locate precisely. However, the real impact of this crisis on the brachiopods is still in debate as, for example in South China, there would be no evident sign of brachiopod extinction related to the Hangenberg Crisis (Y. Sun, pers. com.).

Based on comprehensive studies, Sun *et al.* (2006) and Sun & Baliński (2011) have shown that the

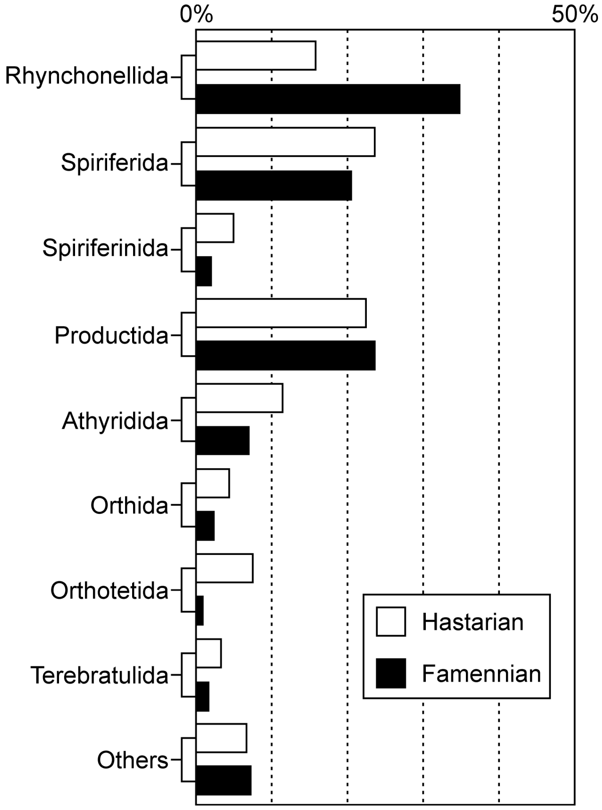

Figure 2. Relative proportions of different brachiopod orders recorded from the Famennian Stage (Upper Devonian) and the Hastarian Substage (Lower Carboniferous, base of the Tournaisian Stage) (modified from Curry & Brunton, 2007). The Order Productida includes the suborders Chonetidina, Productidina and Strophalosiidina.

brachiopod diversity, in South China, reached a nadir during the lower part of the Hastarian and a peak in the upper part of the Hastarian, although *c.* 60 % of the genera known from the uppermost Famennian survived into the lower Tournaisian, including mainly long-ranging genera (e.g. *Schizophoria*, *Leptagonia*) and some 'Strunian' elements (e.g. *Paralellora*, *Syringothyris*). In various parts of the world (e.g. North Africa, Armenia), the siliciclastic environments of the uppermost Famennian were colonized by large, multispinose araksalosiides (Strophalosiidina) (Lazarev, 1989; Legrand-Blain, 1995*a*, *b*), which became extinct at the end of the Devonian and were subsequently replaced by less spinose and smaller representatives of the Quadratiinae (Legrand-Blain, 1995*a*).

According to Curry & Brunton (2007), the Hastarian is marked by a severe decline of the rhynchonellides (16 % of the total brachiopod diversity) (Fig. 2), which subsequently declined further in the Carboniferous. The initial increase in brachiopod diversity during the Tournaisian can largely be attributed to the success of the Productida, in which the Chonetidina became less abundant leaving the morphologically diverse true productidines and strophalosiidines to flourish in various environments (Curry & Brunton, 2007).

4. Conclusions

Selected genera of the rhynchonellides, spiriferides, spiriferinides, productidines and strophalosiidines are very useful for correlations in neritic environments near the D–C boundary, in conjunction with foraminifers and rugose corals, where usual marker fossils (ammonoids and conodonts) are absent or rare. This is especially the case in mixed siliciclastic-carbonate depositional environments of Western Europe and North Africa. Further work is required to reach a better assessment of the aftermath of the Hangenberg Crisis on brachiopod diversity. A revision of the faunas from classical areas (e.g. the Franco-Belgian Basin, Germany, UK) is required because, owing to their rapid evolution and their large geographic distribution, brachiopods are prime tools for research dedicated to event palaeontology and palaeobiogeography.

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