Reassignment of Pentamerus davyi Oehlert to Zdimir robustus (Barrande) (Brachiopoda, Devonian): Stratigraphic and palaeogeographic implications

Michel Ballevre, Denise Brice, Hubert Lardeux, Pierre Morzadec, Bernard Mottequin

Reassignment of *Pentamerus davyi* Oehlert to *Zdimir robustus* (Barrande) (Brachiopoda, Devonian): stratigraphic and palaeogeographic implications.

Attribution de Pentamerus davyi Oehlert à Zdimir robustus Barrande (Brachiopoda, Dévonien): implications stratigraphiques et paléogéographiques.

Michel Ballèvre[a,*], Denise Brice[b], Hubert Lardeux[c], Pierre Morzadec[d] & Bernard Mottequin[e]

[a] *Equipe Tectonique-Terre-Temps-Traçage, Géosciences Rennes (UMR-CNRS 6118), Université de Rennes 1, F-35042 Rennes Cedex, France.* michel.ballevre@univ-rennes1.fr

[b] *Laboratoire de paléontologie stratigraphique, Faculté libre des sciences et Technologies, 41 rue du Port et Groupe ISA 48 boulevard Vauban, 59046 Lille Cedex, France*

[c] *Le Verger-Beaucé, 35520 Mélesse, France*

[d] *17 rue du Hyl, 35510 Cesson-Sévigné, France*

[e] *Royal Belgian Institute for Natural Sciences, Q.D. Earth and History of Life, Vautier Street 29, 3-1000 Brussels, Belgique*

ABSTRACT

The brachiopod fauna of the Chalonnes Limestone (Armorican Massif, France) is famous because of the presence of large, thick-shelled species first described by Oehlert (1881). One of these species originally assigned to *Pentamerus davyi* Oehlert, 1881 is here revised. External as well as internal characters of the shell allow its attribution to *Zdimir robustus* (Barrande, 1879), a species from the Trebotov Limestone in the Prague area. This reassignment is consistent with an Upper Emsian age for the Chalonnes Limestone.

Keywords: brachiopoda, *Zdimir*, Devonian, Chalonnes Limestone

RESUME

La faune de brachiopodes du Calcaire de Chalonnes (Massif armoricain, France) est célèbre en raison de la présence d'espèces de grande taille à coquille épaisse, décrites pour la première fois par Oehlert (1881). L'une de ces espèces (originellement désignée sous le nom

de *Pentamerus davyi* Oehlert, 1881) est révisée dans ce travail. Ses caractères externes et internes permettent son attribution à *Zdimir robustus* (Barrande, 1879), une espèce décrite par Barrande dans la région de Prague. Cette attribution est compatible avec un âge Emsien supérieur pour le Calcaire de Chalonnes, et renforce les affinités biogéographiques bohémiennes des faunes de l'unité de Châteaupanne.
Mots clés : brachiopodes, *Zdimir*, Dévonien, Calcaire de Chalonnes

1. Introduction

The Devonian reefal limestones of Chalonnes, in the southern Armorican Massif (western France), display an abundant fauna (Le Maître, 1934) essentially consisting of stromatoporoids, tabulate and rugose corals as well as a few brachiopods. The latter were first described by Oehlert (1881), who recognized three large-sized species, namely *Uncites galloisi* Oehlert, 1881 (up to 7 cm long), *Pentamerus davyi* Oehlert, 1881 (max. 6 cm long) and the giant *Amphigenia? bureaui* Oehlert, 1881, which can reach 17 cm in length.

Despite a revision by Le Maître (1932, 1934), who was conservative in keeping the same nomenclature as Oehlert (1881), the brachiopods have not been re-investigated since their first description. This poses major problems when putting them in a larger-scale context, i.e. the Early to Middle Devonian faunas of western Europe. The three large-sized species described in the Chalonnes Limestone have not been found in any other place, except perhaps in the Palaeozoic from the Graz area in Austria (Heritsch, 1915, 1935). This might be due to the description of the same species under different names in other places, or to endemism of the Chalonnes species. A taxonomic revision should help solve this issue, as well as the exact age of the fauna, because the Chalonnes Limestone is considered to be either Emsian, or Eifelian or even Givetian.

The aim of this paper is to revise one of three large-sized brachiopod species from the Chalonnes Limestone, namely *Pentamerus davyi*. Because we will show that it is a junior synonym of *Zdimir robustus* Barrande, 1879, this enables to suggest an Upper Emsian age for the Chalonnes Limestone based on its brachiopod fauna, and once again points its biogeographic links with the classic Barrandian area in central Bohemia.

2. Geological setting

The stratigraphy of the Palaeozoic sediments in the Ancenis to Chalonnes area has recently been revised by Ducassou et al. (2011). Two well-preserved (i.e. faulted and tilted but not folded or cleaved) Palaeozoic successions are distinguishable, in the Châteaupanne and the Tombeau Leclerc units (Fig. 1). We are only concerned with the former succession, which rests unconformably over a Proterozoic basement (Mauges micaschists). Ordovician sediments (dated from the Floian to the Katian) are unconformably covered by Devonian sediments. The latter are composed of the Chalonnes Limestone succeeded by the Sainte-Anne Sandstone (Fig. 2).

The basal member of the Chalonnes Limestone is made of coarse- to fine-grained quartz sandstones with interbedded shales (up to 1 m thick). These siliciclastic sediments, dated as late Pragian to early Emsian by spores (Strullu-Derrien et al., 2010), have provided a unique flora, including one of the oldest wood-bearing plant (Gerrienne et al., 2011; Strullu-Derrien et al., 2014; Gerrienne & Gensel, 2016). Above the basal member, bedded then massive limestones develop to a thickness of 100 to 200 m. Some beds display abundant stromatoporoid and coral associations, while others record rich populations of large, thick-shelled but poorly diversified brachiopods. The age of this fauna is still largely disputed. According to Le Maître (1934), the Chalonnes Limestone is Coblenzian (Emsian) in age. Dubreuil & Vachard (1979) described foraminifera and algae and suggested a Givetian age. Coen-Aubert (2011) partially revised the coral fauna, and suggested a late Eifelian-early Givetian age, although pointing out that a larger time interval could be potentially present in the whole thickness of the Chalonnes Limestone.

Above the Chalonnes Formation, the sandstones rich in volcanic fragments of the Sainte-Anne Formation (c. 100m) contain abundant plants (hence their former name of “Grès à Psilophytes”) (Ducassou et al., 2009) and rarely, disarticulated brachiopods and crinoids. A revision of the most common brachiopod species, *Dalejodiscus minor* (Roemer, 1850), indicates that the sandstones cannot be younger than the early Eifelian (Ballèvre et al. 2010).

3. The brachiopod *Pentamerus davyi* Oehlert, 1881.

The distribution of *Pentamerus davyi* in the Chalonnes Formation has been reported by Le Maître (1934), who mention its occurrence in two localities, namely Saint-Charles quarry in Chaudefonds-sur-Layon (about 150m thick) and Châteaupanne quarry in Chalonnes-sur-Loire (about 120-130m thick). In both quarries, brachiopods are unevenly distributed within the limestone sequence. In the Châteaupanne quarry, *Pentamerus davyi* has

been found in the northernmost (i.e. uppermost) layers, where it is associated to other large, thick-shelled, brachiopods (*Amphigenia? bureaui*). These carbonate layers with shell pavements have attracted a lot of attention (Bureau et al., 1910; Couffon, 1910; Le Maître, 1934), but are unfortunately no more visible today, due to the progress of the quarrying. *Pentamerus davyi* has also been reported from the base and the middle of the succession in the Châteaupanne quarry (Le Maître, 1934). It is therefore present in the entire succession of the Chalonnes Limestone.

Our revision relies on the material available in the collections from the Musée des Sciences de Laval (where the Oehlert collection is now housed), the Faculté Catholique de l'Ouest (Angers), the Natural History Museums of Angers and Nantes and the Université Catholique de Lille where Le Maître's collection is housed.

Systematic palaeontology

Order Pentamerida Schuchert & Cooper, 1931

Superfamily Gypiduloidea Schuchert & LeVene, 1929

Family Gypidulidae Schuchert & LeVene, 1929

Subfamily Conchidiellinae Rzhonsnitskaia, 1961

Genus ***Zdimir*** Barrande, 1881

Type species. - *Porambonites* ? *robustus* Barrande 1879 (= *Zdimir solus* Barrande 1881)

***Zdimir robustus* (Barrande 1879)**

Figures 3, 4 and 5

1879 *Porambonites* ? *robustus* - Barrande, vol. V, pl. 80, fig. IIa and b, pl. 94, fig. VII.

1881 *Zdimir solus* - Barrande, vol. VI, p. 171-172, pl. 292, figs. 17-20.

1881 *Pentamerus davyi* - Oehlert, vol. 12, p. 7, pl. V, fig. 10-13.

1886 *Pentamerus davyi* Oehlert – Barrois, p. 190-191, pl. V, fig. 4.

1888 *Pentamerus (Zdimir) solus* Barrande - Novak, p. 588-590, figs. 1-4.

1898 *Conchidium hassiacum* Frank, p. 71, pl. I fig. 1-4

1900 *Pentamerus davyi* Oehl. – Bureau, p. 248 fig. 50

1900 *Conchidium hassiacum* Frank - Lotz, p. 231-233, pl. IV fig. 1-3

1927 *Uncites gryphus* Schl. – Ganichaud, p. 6

1934 *Pentamerus davyi* Oehlert – Couffon, p.71 fig. 49

1934 *Pentamerus davyi* Oehlert - Le Maître, p. 59, pl. II, fig. 7-10.

1934 *Conchidium (Pentamerus) davyi* Oehlert – Péneau, p. 119.

1938 ? *Conchidium davyi* Oehlert – Comte, p. 56.

1953 *Conchidium hassiacum* Frank = *Pentamerus rhenanus* F. Roem. - Kegel, p. 25

1955 *Zdimir solus* Barrande 1881- Havlicek, p. 546-548 (Czech text) and p. 653 (English text), pl. XII figs. 6, 8.

1959? *Conchidium davyi* Oehlert – Comte, p. 171, 177, 187, and 393.

1962 *Zdimir robustus* (Barrande 1879) - Boucot & Siehl, p. 123-125, pl. 18, figs.1-7.

1976 *Conchidium hassiacum* Frank = *Pentamerus rhenanus* F. Roem - Kegel, p. 27

1989 *Zdimir hassiacus* (Frank, 1898) - Struve, p. 138, fig. 25-27

Material. 45 more or less complete samples have been examined, including Oehlert's collection housed in the Musée des Sciences de Laval, Université Catholique de l'Ouest (4 complete samples and 5 dorsal valves), Museum of Angers (3 complete samples and 1 dorsal valve), Museum of Nantes (20 samples, including 3 complete samples and 1 section in plane of bilateral symmetry, 16 pedicle valves), and Le Maître's collection housed in the Faculté Libre des Sciences et Technologies (Université Catholique de Lille).

Types. The material originally used for the description of *Pentamerus davyi* is preserved in the Musée des Sciences de Laval under the numbers ML-PAL-01793 (a transverse section, ML-PAL-29295 (an entire specimen corresponding exactly to the one drawn by Oehlert (1881) in his original figures 10-11-12) and ML-PAL-29300 (an other transverse section, similar to figure 13 of the original publication).

Description. Usually large, biconvex and strongly unequivalve, outline subtriangular to longitudinally elongate, without ventral sulcus and dorsal fold (Fig. 4). The greatest width is near of the midlength. The pedicle valve is always larger than the brachial one, slightly longer than wide, displaying an interarea slightly concave with an open delthyrium. The prominent beak is incurved over the brachial valve, which is gently convex and subcircular in outline. Both valves are covered by fine ribs which increase in number by bifurcations at different distances from the beaks (intercalations are not observed). Some external characters are quite variable. Specifically, the delthyrium is not always apparent, because it can be masked by the beak of the brachial valve. In such cases, the interarea may be difficult to be seen. Most samples are nearly symmetrical, although some slight distortions from the bilateral symmetry are also clearly seen, especially on the pedicle valve.

The internal characters are shown after serial transverse sections of one specimen (Fig. 5). The shell of the pedicle valve is thick, composed of an outer lamellar layer and an inner prismatic layer. The prismatic layer is thinner than the lamellar layer, and the calcite prims are oriented perpendicular to the boundary with the lamellar layer. The thin dental plates converge to form a spondylium with an angle of about 80 degrees. The ventral septum supporting the spondylium is very short. The shell of the brachial valve is not as thick as the one of the pedicle valve and is made, like the cardinalia, by a very thin lamellar layer only. The outer plates diverge, the brachial process are short and almost vertical while the inner plates are slightly concave separated at their extremities. The length of the brachial lamellae is about half the size of shell (Fig. 4-6).

Remarks. The studied specimens display typical pentameride internal structures, and are assigned to the genus *Zdimir* on the basis of their strongly biconvex shells, which display interareas, contrary to *Conchidium* and allied genera, external surface covered by fine to large ribs that bifurcate irregularly (Rzhonsnistkaia, 1961; Boucot & Siehl, 1962; Carlson et al., 2002). Other distinctive features of *Conchidium* are its high ventral septum supporting the spondylium almost along the full length of the shell and the dorsally inclined flanges joining the bases of the brachial process (e.g. Amsden et al., 1967; Carlson et al., 2002).

As explained by Boucot & Siehl (1962), several large-sized and costate pentameride species, from strata previously included in the Middle Devonian, were assigned to the Silurian genus *Conchidium* Oehlert 1887 for a long time only on the basis of external features, without taking their internal morphology and the presence of well-developed dorsal and ventral interareas into account. This issue was partly resolved by Khodalevich (1939), who erected the genus *Conchidiella* Khodalevich, 1939 in order to include large, strongly costate pentamerides of “Middle” Devonian age, but still considering the new genus as closely related to that of Oehlert. The revision of *Zdimir* Barrande 1881 by Boucot & Siehl (1962) clearly showed that *Conchidiella* is a junior synonym of Barrande’s genus (see these authors for more details). The internal characters (e.g. the very short median septum) of the specimen from Châteaupanne here illustrated (Fig. 4-6 and 5) are very similar to those of the specimens from Hlubočepy, as illustrated by Boucot and Siehl (1962, plate 18, figs. 1-7).

It is remarkable that Barrande (1879) and Oehlert (1881) published at about the same time the description of the same species, under the different names of *Pentamerus davyi* and *?Porambonites robustus* (= the type species of *Zdimir* Barrande, 1881) respectively. The first description of *Z. robustus* by Barrande (1879) was based on a single dorsal valve. Later on, Barrande (1881) described and figured *Zdimir solus* as a bivalve, although stressing some of

its morphological characteristics as similar to the pentamerides. Following the death of Barrande in 1883, Novak (1888) was able to identify it conclusively as a pentameride brachiopod. It follows that Oehlert, even if he knew Barrande's work at the time he published his *Pentamerus davyi*, was not in a good position for establishing the synonymy. The proposal that *"?Porambonites" robustus* was in fact a dorsal valve of *Zdimir solus* has been made by Boucot & Siehl (1962), with the consequence that *Zdimir solus* is a junior synonym of *Zdimir robustus*.

Amongst the species assigned to the genus *Zdimir*, two main groups are to be distinguished.

The **first group** (*Zdimir* gr. *hercynicus* Halfar, 1879) is characterized by species which present rather large ribs and a slightly plicate commissure (*P. hercynicus, Z. languedocianus* de Trommelin & de Grasset in Barrois, 1886a, *P. oehlerti* Barrois, 1882). Our specimens differ from *Z. hercynicus* by their subtriangular outline and unequivalve profile while it is variable and almost equivalve in the latter, but internal characters are similar. *Z. languedocianus* differs from *Z. robustus* by its subrounded outline, the presence of a significant ventral fold and a dorsal sulcus, which are developed near the anterior commissure.

The **second group** (*Zdimir* gr. *robustus*) contains species with numerous thin ribs and a rectimarginate commissure (*Pentamerus rhenanus* Roemer 1856, *Porambonites robustus* Barrande 1879 = *Zdimir solus* Barrande 1881, *Conchidium hassiacum* Frank 1898). Our specimens clearly belong to this second group, and closely resemble *Z. robustus*, which includes large-sized shell subtriangular in outline and covered by relatively thin ribs. So, the specimens from the Chalonnes Formation previously identified as *Pentamerus davyi* Oehlert, 1881 cannot be distinguished from Barrande's species and are herein considered as conspecific with the latter.

Conchidium hassiacum has been recognized since its original description (Frank 1898; Lotz 1900) as a species closely related to *Pentamerus davyi*. Distinguishing criteria, based on the single specimen published by Oehlert, were a larger size and a larger number of ribs. However, the herein established intraspecific variability of *P. davyi* does not allow to maintain this distinction between the two species. The number of ribs cannot be taken as a specific character, because they increase irregularly during the growth of each individual. For example, the specimen illustrated by Oehlert (1881) has a length of 27 mm and 25 ribs, whereas the specimen herein illustrated (Fig. 4) has a length of 37 mm and 45 ribs along the

margin. Based on this criterion, the difference between *Pentamerys davyi* and *Conchidium hassiacum* vanishes.

The slight distortions from the bilateral symmetry observed in our specimens are also reported in *Zdimir robustus* from Hlubočepy (Barrande, 1881; Novak, 1888; Boucot and Siehl, 1962) and *Z. hassiacum* from Lindener Mark (Lotz, 1900, fig. 2b; Struve, 1989, fig. 25). Taking into account the close similarity between *Conchidium hassiacum* and *Pentamerus davyi*, we may consider that only one species is present in these three localities (Hlubočepy, Montjean, and Lindener Mark), and that it should be referred to *Zdimir robustus*.

4. Stratigraphic distribution of *Zdimir* in western and central Europe

Previous syntheses have pointed out that *Zdimir* is known from Europe to China (Chen & Liao, 2006; Lu et al., 2017) and Japan (Tazawa, 1988), and that its stratigraphical range is limited to the Upper Emsian (*serotinus* and *patulus* conodont Biozones) and Early Eifelian (*partitus* Biozone) (Godefroid in Brice et al., 2000).

4.1 Data

A summary of the geographical and stratigraphical distribution of the genus *Zdimir* in Europe is shown on figures 6 and 7. To clarify the uncertainties that are associated with the construction of these figures, we would like to make the following comments.

4.1.1. Zdimir gr. *hercynicus*

In the **Rheno-Hercynian zone**, several localities are known from the Ardennes to the Harz. In the **Ardennes** (northern France and southern Belgium) (Fig. 6-1 and 2), *Zdimir hercynicus* is quite abundant, being a characteristic element of the "*cultrijugatus* fauna". In northern France, Le Maître (1929) listed this species in the Fourmies area. In southern Belgium (southern and south-eastern borders of the Dinant synclinorium), *Z. hercynicus* is known only from the late to latest Emsian and occurs within the Hierges, Saint Joseph and Eau Noire Formations (Maillieux, 1938, 1941; Lecompte, 1962, 1967, 1970; Godefroid, 1968, 1971; Bultynk, 1970; Vandenven, 1975; Lessuisse et al., 1979; Godefroid et al., 1994; Zapalski et al., 2007). According to Godefroid (1968) and Bultynck (1970), the acme and disappearance of *Z. hercynicus* are recorded in the Eau Noire Formation, and more

particularly in the upper half of the disused chronostratigraphic unit Co1b, which is of latest Emsian age and located well below the Emsian-Eifelian boundary (see also Bultynck & Dejonghe, 2001).

In the **Eifel** (Fig. 6-2), the uppermost occurrence of *Z.* cf. *hercynicus* is found close to the boundary between the Heisdorf and Lauch formations, i.e. the Emsian-Eifelian boundary (Struve, 1982, fig. 6). However, a single occurrence has been reported from the Lauch Formation (as *Conchidium* cf. *hercynicum*) by Krömmelbein et al. (1955, p. 23).

In the eastern Rheinische Schiefergebirge (**Latrop anticline)** (Fig. 6-3), *Z. hercynicus* is reported in the Orthocrinus Formation, the latest formation of the Upper Emsian (Langenstrassen, 1972; Langenstrassen & Müller, 1982).

In the **Harz Massif** (Fig. 6-4), *Zdimir* occurences are known in the Oberharz, i.e. in the Kahleberg Group (e.g. Beushausen, 1900), now divided into several formations (e.g. Dahmer, 1946; Zcheked in Hinze, 1971; Mohr, 1993; Buchholz et al., 2008). Halfar (1879) described and illustrated *Z. hercynicus* from the layers ("Obere *speciosus*-Schichten") located just below the "*Calceola*-Schiefer", the basal member of the Goslar Formation (Buchholz & Luppold, 2008). The age of this formation was considered until recently as early Eifelian, the boundary between the Lower and the Middle Devonian being located into this formation, and locally defined by the "*corbis*-Bank" (Simon et Dahmer, 1954). It is now accepted that it most probably belongs to the uppermost Emsian (see discussion in Buchholz et al., 2008, p. 535).

In the **Armorican Massif**, *Zdimir* has been reported in the Central Armorican Domain, from the Crozon peninsula to the Laval area (Barrois, 1886c; Collin, 1912; Renaud, 1942, 1953, 1955). However, these reports are not precise enough in order to check the range of Barrande's genus in the Early to Middle Devonian strata. Precise data on its stratigraphical range are from the beds 48 to 55 of the Fret Formation, in the classic locality of Reun ar C'hrank (Morzadec, 1983) (Fig. 6-5). The conodont zonation of this section indicates an upper Emsian age (*serotinus* Zone) for the *Zdimir* occurrences. Another well-located occurrence of *Zdimir?* sp. (*Zdimir* confirmed in this paper) has been found further east, in the lower part of the Marettes Formation, dated as Upper Emsian (Brice, 1981) (Fig. 6-6).

Zdimir occurrences in the **Cantabrian Zone** (northwestern Spain) (Fig. 6-13 and 14) were first reported by Barrois (1882) as *Pentamerus oehlerti*, later considered as a synonym of *Pentamerus hercyniae*. The detailed vertical distribution of *Zdimir hercynicus* by Arbizu *et al.* (1979) has showed its presence in the Middle and Upper Members of the Moniello Formation. The latter dates from the Upper Emsian to early Eifelian (Garcia-Alcalde et al., 2000; García Alcalde, 2015). *Zdimir* is also reported in the León Province, in the Santa Lucia

Formation (Comte, 1936), where it is restricted to the *patulus* Biozone (García-López and Sanz-López, 2002). Further east, in the **Central Iberian chains**, *Zdimir* occurrences are located in the Ramblar Formation, also of Upper Emsian age (Carls, 1988; Garcia-Alcalde et al., 2000).

The Devonian succession of the **Montagne Noire** (Feist, 1985) (Fig. 6-15) also yielded representatives of *Zdimir* (*Pentamerus languedocianus* de Trommelin & de Grasset 1877 in Barrois, 1886a; Bergeron, 1889, 1900) in the Cabrières area. The pentamerides come from the "Calcaires à polypiers siliceux", now the Izarne Formation, whose conodont content indicates an Emsian to Early Eifelian age (Feist et al., 1985). The rich fauna of the Izarne Formation consists of trilobites (Feist, 1977), ostracods (Feist & Groos-Uffenorde, 1979) and rugosa (Pedder & Feist, 1998). Unfortunately, the brachiopods have not been revised, and the exact location of the pentameride-bearing layers within the Izarne Formation is not known.

4.1.2. Zdimir gr. *robustus*

Zdimir robustus is found in the Trebotov Limestone, in the **Prague area** (Fig. 6-12) with the type locality Hlubočepy (Barrande, 1879, 1881; Novak, 1888; Hall, 1893; Havlíček, 1955). This formation is well dated from the upper Upper Emsian and basal Eifelian, the *patulus-partitus* boundary being located in the uppermost part of the Formation (Chlupáč et al., 1979, 1998).

Two occurrences of *Zdimir* gr. *robustus* are known in the south-eastern part of the **Rhenish Massif** (Fig. 6-10 and 11). Firstly, the classic occurrence of *Z. rhenanus* in the so-called "*Pentamerus Quartzite*" (Roemer, 1874; Lotz, 1901; Boucot and Siehl, 1962; Bender, 2008) is located close to Wetzlar, in the Hörre Unit. The stratigraphical position of the Pentamerus Quartzite is difficult to ascertain, because its structural setting is poorly understood, and because it does not contain conodonts and/or tentaculites (Bender, 2008). If the proposal that the Pentamerus Quartzite results from a secondary silicification of a "*Greifensteiner Kalk*" is followed (Lotz 1901), a latest Emsian-earliest Eifelian age based on tentaculites (Alberti, 1985) and trilobites (Kim, 1997) may be assigned to the Pentamerus Quartzite.

Secondly, two isolated occurrences (Kleinlinden and Cleeberg) of *Z. hassiacus* have been reported from the Giessen area (Frank, 1898; Lotz, 1900; Struve, 1989). Their stratigraphical position is also difficult to establish. Although the massive limestones from this area have been attributed to the Givetian because they were compared to the

"*Stringocephalen-Kalk*", there is no decisive argument for that, the occurrence of *Stringocephalus* Defrance in Blainville, 1827 in these limestones being doubtful.

In the **Armorican Massif** (Fig. 6-8 and 9), close to the studied area, *Pentamerus davyi* has been reported by Barrois (1886b) from the Valet Limestone (Davy, 1884), which belongs to the Tombeau Leclerc Unit. This Formation is dated on the basis of tentaculites and conodonts from the Upper Emsian (Lardeux & Weyant, 1993).

4.1.3. Other occurrences

Further east, the well-known Devonian succession of the **Graz area** (Fig. 6–16), in the Eastern Alps (Heritsch, 1915, 1918, 1935; Solle, 1934; Flügel, 1975), have been compared to the Chalonnes Formation (Le Maître, 1934, 1935; Heritsch, 1935). Indeed, the reefal deposits of the *barrandei* limestones, now the Plabutsch Formation (Hubmann, 1993, 2003; Hubmann & Suttner, 2007), have in common with the Chalonnes Limestone horizons that are interpreted as brachiopod pavements. The *Zdimir* species from these horizons, originally named *Pentamerus petersi* (Hoernes, 1886), are now under revision (Suttner & Chen, 2009). The age of the Plabutsch Formation, which is generally considered Eifelian, is difficult to establish. However, the recent discovery of rare conodonts at the base of the Plabutsch Formation suggests an age ranging from the *serotinus* to the *costatus* biozones (Suttner & Berkyová, 2009), hence indicating a late Emsian-basal Eifelian age.

Z. cf *hercynicus* has also been reported in northern Morocco (Fig. 6-17), from the Chabat Jenanat conglomerates in the Immouzer du Kandar inlier, south of Fès (Brice et al., 1983; Charrière & Regnault, 1989). This formation is attributed, on the basis of its brachiopod fauna, to the Upper Emsian.

4.2 Stratigraphic implications

As shown in figure 7, *Zdimir* is restricted to the Upper Emsian, and possibly the basal Eifelian. However, in Eastern Europe (Ural Mountains), the Brachiopod Zone *Zdimir pseudobaschkiricus – Punctatrypa sibirica* characterizes the *patulus* and *partitus* conodont Biozones, i.e. the uppermost Emsian and the lowermost Eifelian (Sapelnikov et al., 1995; Feist et al., 1997). Boucot & Siehl (1962) pointed out that *Zdimir* was unknown in the early Devonian. However, the international convention on the boundary of the Early to Middle Devonian at the base of the *partitus* Biozone resulted in a transfer to the late Early Devonian

of most – if not all - of the "Middle" Devonian occurrences of *Zdimir*. For example, the Trebotov Limestone was considered Eifelian at the time of Boucot and Siehl (1962)'s work, but the Emsian-Eifelian boundary is today located in its uppermost part.

Many occurences of *Zdimir* are reported as brachiopod pavements in reefal environments, and it is highly probable that *Zdimir* was a reef dweller. Although this statement cannot be generalized (some of the *Zdimir* occurences are in sandstones or terrigenous rocks far away from reefs), its ecological preferences have some consequences for the biostratigraphical interpretation. Therefore, the temporal range of *Zdimir* may be bounded by the development of the reefs which he was inhabiting, thus lowering its biostratigraphical value. Altough we acknowledge that some *Zdimir* occurrences may occur outside its "normal" range (Upper Emsian to Early Eifelian, i.e. *serotinus* to *partitus* conodont biozones), it would be very unlikely that all over the world the occurrences would belong to this range, except in the studied area.

We thus conclude that the best age estimate for the Chalonnes Limestone is Upper Emsian, an age which is fully consistent with (i) that proposed by Le Maître (1934), (ii) the late Pragian-early Emsian age deduced from the spore content of the basal member of the Chalonnes Limestone (Strullu-Derrien et al. 2010), and (iii) the youngest possible age (Early Eifelian) for the overlying Sainte-Anne Formation (Ballèvre et al., 2010). However, a Late Emsian age is not consistent with the Givetian age proposed by Dubreuil & Vachard (1979) or the late Eifelian – early Givetian age deduced from a revision of the rugose corals by Coen-Aubert (2011). In the first case, the discrepancy could result from our imperfect knowledge of the stratigraphical extent of algae and foraminifera at the time of their publication. In the second case, the lack of stromatoporoid-coral reefs of Emsian age in the Ardenne area could prevent a full record of the constitutive species, with the consequence of a very low-diversity fauna for these groups (Zapalski et al., 2007). Comparing the coral fauna of Chalonnes with those of the Ardennes may therefore be misleading.

4.3 Palaeogeographic implications

As regards the palaeogeography of western and central Europe before the Variscan orogeny, the following remarks

1. The Palaeozoic sedimentary sequences of the Chalonnes area (Le Maître, 1934, 1960; Lardeux and Cavet, 1994; Ducassou et al., 2009, 2011; Ballèvre et al., 2010) are clearly distinct from those of the Central and Northern Armorican domains (e.g.

Robardet et al., 1994). Specifically, a major difference is recorded during the Silurian and Early Devonian. The marine sedimentation proceeds uninterrupted in the Northern and Central-Armorican Domains from the Silurian to the Emsian (e.g. Morzadec et al., 1988). On the contrary, the Chalonnes area records uplift and erosion of a land surface, colonized by the early plants (Strullu-Derrien et al., 2010), and then inundated by a shallow sea from the Pragian to early Emsian. The growth of the Emsian reefal carbonate platform ended suddenly with the arrival of a large amount of detrital terrigenous material from a nearby land, also colonized by early plants (Ducassou et al., 2009, 2014).

2. The Devonian faunas (like the earlier Ordovician faunas, out of scope of this paper) have Bohemian affinities (Le Maître, 1934, 1960). Revision of the brachiopod *Pentamerus davyi*, a key element of the Emsian fauna in the Chalonnes Limestone, and its attribution to *Zdimir robustus*, emphasizes once again this statement. The "Armorican" affinities of the exotic slices in the Wetzlar and Giessen area (Oczlon, 1994; Franke & Oncken, 1995; Plusquellec & Jahnke, 1999; Franke, 2000; Huckriede et al., 2004; Doublier et al., 2012) should be compared, not to the Central- and North Armorican successions, but to those from the Chalonnes area.

6. Conclusions

Reassignment of *Pentamerus davyi* Oehlert, 1881 from the Chalonnes Formation (Armorican Massif) to *Zdimir robustus* (Barrande, 1879) has two major consequences. Firstly, it allows to propose an Upper Emsian age for the Chalonnes Limestone based on its brachiopod fauna, an age consistent with other estimates. Secondly, the occurrence of *Zdimir robustus* suggests close links between the Chalonnes area and central Bohemia, possibly also with the source of the "exotic slices" now found in the Wetzlar and Giessen area.

Acknowledgments

This work could not have been done without the painstaking efforts from our predecessors in collecting fossils (especially Edouard and Louis Bureau, Daniel and Pauline Oehlert, Joseph Péneau, Pierre Cavet), and in keeping them in the various collections at the Université Catholique de l'Ouest in Angers (Gérard Beaulieu), Musée des Sciences de Laval (Jérôme Tréguier), Muséum des sciences naturelles d'Angers (Benoît Mellier) and of the Muséum

d'histoire naturelle de Nantes (Serge Régnault). The specimen used for investigating the internal structure has been kindly provided by Benoît Mellier. The excellent photographs of *Zdimir* from the Châteaupanne quarry have been provided by Gérard Beaulieu. The owners of the Châteaupanne quarry (MM. Joël Binet, Jeremy Degryze and Renaud Jospin) are also acknowledged for allowing us to visit (more than once) the quarry. Many thanks are due to an anonymous reviewer on a previous version of this manuscript, and to M. Aretz (Toulouse) and J. García-Alcalde (Oviedo) for their pertinent reviews.

References

Alberti, G.K.B., 1985. Zur biostratigraphischen Untergliederung des Greifensteiner Kalkes und der Wissenbacher Schiefer (Unter- bis Mitteldevon, Rheinisches Schiefergebirges) mithilfe von Dacryoconarida (Tentaculiten). Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg 59, 51-56.

Amsden, T.W., Boucot, A.J., Johnson J.G., 1967. *Conchidium* and its separation from the subfamily Pentamerinae. Journal of Paleontology 41, 861-867.

Arbizu, M., Garcia-Alcalde, J.L., Garcia-Lopez, S, Mendez-Bedia, I., Sanchez de Posada, L.C., Soto, F.M., Truyols, M., Truyols, J., Alvarez F., Mendez, C., Menedez, J.R., 1979. Biostratigraphical study of the Moniello Formation (Cantabrian Mountains, Asturias, NW Spain). Geologica et Palaeontologica 13, 103-124.

Ballèvre, M., Ducassou, C., Lardeux, H., Régnault, S., 2010. A revised age (Emsian-Eifelian) for the Sainte-Anne Formation (Armorican Massif, France): implications for the onset of mountain building in the Variscan belt. Neues Jahrbuch für Geologie und Paläontologie 255, 237-254.

Barrande, J., 1879. Système silurien du centre de la Bohême. Vol. V, Ordre des Brachiopodes. Prague – Paris, chez l'auteur.

Barrande, J., 1881. Système silurien du centre de la Bohême. Vol. VI, Ordre des Acéphalés. Prague – Paris, chez l'auteur.

Barrois, C., 1882. Recherches sur les terrains anciens des Asturies et de la Galice. Mémoires de la Société Géologique du Nord 2(1), 1-630.

Barrois, C., 1886a. Sur le calcaire à polypiers de Cabrières (Hérault). Annales de la Société Géologique du Nord 13, 74-97.

Barrois, C., 1886b. Sur le calcaire dévonien de Chaudefonds (Maine-et-Loire). Annales de la Société Géologique du Nord 13 170-205.

Barrois, C., 1886c. Aperçu sur la constitution géologique de la rade de Brest. Bulletin de la Société Géologique de France (3) 14, 678-707.

Bender, P., 2008. Lahn- und Dill-Mulde. In : Deutsche stratigraphische Hommission (Hrsg.), Stratigraphie von Deutschland VIII. Devon, Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 52, 221-246.

Bergeron, J., 1889. Etude géologique du Massif ancien situé au sud du Plateau central. Paris, Masson, 361 p.

Bergeron, J., 1900. Livret-guide des excursions en France du VIII^{ème} Congrès Géologique International (Paris, 1900). XVIII- Massif de la Montagne-Noire. Lille, Le Bigot Frères Imprimeurs, 38 p.

Beushausen, L., 1900. Das Devon des nördlichen Oberharzes mit besonderer Berücksichtigung der Gegend zwischen Zellerfeld und Goslar. Abhandlungen der Königlisch Preussischen geologischen Landesanstalt, N.F. 30, 1-383.

Boucot, A.J., Siehl, A., 1962. *Zdimir* Barrande (Brachiopoda) redefined. Notizblatt des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 90, 117-131.

Brice, D., 1981. Les brachiopodes Pentamerida, Rhynchonellida et Terebratulia. In : Morzadec, P., Paris, F., Racheboeuf, P. (Coord.), « La tranchée de la Lézais, Emsien supérieur du Massif armoricain. Sédimentologie, paléontologie, stratigraphie. » Mémoires de la Société Géologique et Minéralogique de Bretagne 24, pp. 193-223.

Brice, D., Charrière, A., Drot, J., Regnault, S., 1983. Mise en évidence, par des faunes de Brachiopodes, de l'extension des formations dévoniennes dans la boutonnière d'Immouzer du Kandar (Sud de Fès, Maroc). Annales de la Société Géologique du Nord 103, 445-458.

Brice, D., Carls, P., Cocks, L.R.M., Copper, P., Garcia-Alcalde, J.L., Godefroid, J., Racheboeuf, P.R., 2000. Brachiopods. Courrier Forschungsinstitut Senckenberg 220, 65-86.

Buchholz, P., Luppold, F.W., 2008. Litho- und Biostratigrafie des älteren Mitteldevons im Oberharz. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 159, 263-281.

Buchholz, P., Trapp, E., Wachendorff, H., 2008. Nordwestlicher Oberharz und der Acker-Bruchberg-Zug. In "Deutsche Stratigraphische Kommission (Hrsg): Stratigraphie von Deutschland VIII. Devon. Schriftenreihe der Deutschen Gesellschaft für Geowissenschaften 52, 532-546.

Bultynck, P., 1970. Révision stratigraphique et paléontologique (brachiopodes et conodontes) de la coupe type du Couvinien. Mémoires de l'Institut Géologique de l'Université de Louvain 26, 1-152.

Bultynck, P., Dejonghe, L., 2001. Devonian lithostratigraphic units (Belgium). Geologica Belgica 4, 39-69.

Bureau, E., Bureau, L., Davy, L., Dumas, A., 1910. Compte-rendu de la réunion extraordinaire de la Société Géologique de France à Nantes et à Châteaubriant. Bulletin de la Société Géologique de France 8, 593-680.

Bureau, L.M. 1900. Notice sur la géologie de la Loire-Inférieure. In : Nantes et la Loire-Inférieure, III, Nantes, Imprimerie Grimaud, pp. 99-522.

Carls, P. 1988. The Devonian of Celtiberia and Devonian palaeogeography of SW Europe. In: Mc Millan, N.J., Embry, A.F., Glass, D.J. (Eds), Devonian of the world, Canadian Society of Petroleum Geologists 14(1), pp. 421-466.

Carlson, S.J., Boucot, A.J., Rong, J.-Y., Blodgett, R.A., 2002. Pentamerida In: Williams, A., Brunton, C.H.C., Carlson, J.J., et al. (Eds), Treatise on invertebrate paleontology. Part H (Brachiopoda, Revised), Geological society of America and University of Kansas, Boulder and Laurence 4, pp. 921-1026.

Charrière, A., Régnault, S., 1989. Stratigraphie du Dévonien de la boutonnière d'Immouzer du Kandar (sud de Fès, Maroc) : conséquences paléogéographiques. Notes et Mémoires du Service Géologique du Maroc 335, 25-35.

Chen, X.-Q., Liao, Z.-T., 2006. Discovery of the brachiopod Zdimir from the Devonian in the west of South Tianshan. Acta Palaeontologica Sinica 45, 351-358 (in Chinese with English summary).

Chlupáč, I., Lukes, P., Zirkmundova, J., 1979. The Lower/Middle Devonian boundary beds in the Barrandian area, Czechoslovakia. Geologica et Palaeontologica 13, 125-156.

Chlupáč, I., Havlicek, V., Kriz, J., Kukal, Z., Storch, P., 1998. Palaeozoic of the Barrandian (Cambrian to Devonian). Czech Geological Survey, Prague, 183 p.

Coen-Aubert, M., 2011. Reassignment to the Middle Devonian of some rugose corals investigated by Le Maître (1934) in the Chalonnes Formation from the southeatsern Armorican Massif (France). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre 81, 27-53.

Collin, L., 1912. Etude de la région dévonienne occidentale du Finistère. Thèse Doctorat, Univ. Paris, 470 p.

Comte, P., 1938. Brachiopodes dévoniens des gisements de Ferrones (Asturies) et de Sabero (Léon). Annales de Paléontologie 27, 41-88.

Comte, P., 1959. Recherches sur les terrains anciens de la Cordillère cantabrique. Memorias del Instituto Geológico y Minero de España 60, 440 p.

Couffon, O., 1910. Guide du géologue en Anjou. I – Chalonnes, Saint-Aubin-de-Luigné, Montjean, Saint-Pierre-Montlimart. Les Naturalistes Parisiens 5, 1-30

Couffon, O., 1934. Précis de géologie angevine. Angers, Imprimerie centrale, 194 p.

Dahmer, G., 1946. Revidiertes Verzeichnis der versteinerungen des Oberharzer Kahleberg-Sandsteins (Unter-Devon). Senckenbergiana Lethaea 27, 167-187.

Davy, L., 1884. A propos d'un nouveau gisement du terrain dévonien supérieur à Chaudefonds (Maine et Loire). Bulletin de la Société Géologique de France (3), 13, 2-8.

Doublier, M.P., Potel, S., Franke, W., Roache, T., 2012. Very low-grade metamorphism of Rheno-Hercynian allochthons (Variscides, Germany): facts and tectonic consequences. International Journal of Earth Sciences 101, 1229-1252.

Dubreuil, M., Vachard, D., 1979. Sur l'âge givétien de la formation de Chalonnes (Bassin d'Ancenis, sud-est du Massif armoricain) et ses conséquences. Comptes Rendus de l'Académie des Sciences de Paris D 289, 241-244.

Ducassou, C., Strullu-Derrien, C., Ballèvre, M., Dabard, M.-P., Gerrienne, P., Lardeux, H., Robin, C., 2009. Age and depositional environment of the Saint-Anne Formation (Armorican Massif, France): the oldest (Emsian) evidence for mountain erosion in the Variscan belt. Bulletin de la Société Géologique de France 180, 529-544.

Ducassou, C., Ballèvre, M., Lardeux, H., Robin, C., 2011. Evidence for pre-orogenic, Early Devonian extension in the Variscan belt: stratigraphy and structure of the Palaeozoic cover of the Mauges (Armorican massif, France). International Journal of Earth Sciences 100, 1451-1475.

Ducassou, C., Poujol, M., Ruffet, G., Bruguier, O., Ballèvre, M., 2014. Relief variation and erosion of the Variscan belt : detrital geochronology of the Palaeozoic sediments from the Mauges Unit (Armorican Massif, France). In: Schulmann, K., Martínez Catalán, J.R., Lardeaux, J.-M., Janoušek, V. Oggiano G. (Eds), The Variscan orogeny: extent, timescale and the formation of the European crust, Geological Society of London Special Publication 405, pp. 137-167.

Feist, R., 1977. Le Siluro-Dévonien du sud-Est de la Montagne Noire (Hérault, France) et ses faunes de trilobites. Thèse Doctorat Etat, Université des Sciences et Techniques du Languedoc, 251 p.

Feist, R., 1985. Devonian stratigraphy of the southeastern Montagne Noire (France). Courrier Forschungs-Institut Senckenberg 75, 331-352.

Feist, R., Groos-Uffenorde, H., 1979. Die "Calcaire à polypiers siliceux » und ihre Ostracoden-Faunen (Oberes Unter-Devon ; Montagne Noire, S-Frankreich). Senckenbergiana Lethaea 60, 85-187.

Feist, R., Schönlaub, H.-P., Bultynck, P., 1985. Faciès et biostratigraphie (conodontes) du passage Dévonien inférieur-moyen dans la Montagne Noire (France). Hercynica 1, 81-97.

Feist, R., Ivanov, K.S., Sapelnikov, V.P., Ancigin N.Y.Y., Ivanov, S.N., Mizens, L.I., Bikbayev, A.Z., Lubov, L.V., 1997. Correlations between the evolution of benthic faunal communities and convergent movements of lithospheric blocks from the Silurian to the Late Devonian in the mid-Palaeozoic Uralian basin. Tectonophysics 276, 301-311.

Flügel, H.W., 1975. Die Geologie des Grazer Berglandes. Mitteilungen der Abteilung für Geologie, Paläontologie und Bergbau am Landesmuseum Joanneum SH1, 6-288.

Frank, W., 1898. Beiträge zur Geologie des südöstlichen Taunus, insbesondere der Porphyroide dieses Gebiete. Bericht der Oberhessischen Gesellschaft für Natur- und Heilkunde zu Giessen 32, 42-77.

Franke, W., 2000. The mid-European segment of the Variscides : tectonostratigraphic units, terrane boundaries and plate tectonic evolution. In: Franke, W., Haak, V., Oncken, O., Tanner, D. (Eds), Orogenic processes: quantification and modelling in the Variscan belt, Geological Society of London Special Publication 179, pp. 35-61.

Franke, W., Oncken, O., 1995. Zur prädevonischen Geschichte des Rhenohercynischen Beckens. Nova Acta Leopoldina Neue Folge 71, 53-72.

Ganichaud, R., 1927. Note préliminaire sur la structure du massif corallien de Châteaupanne (Synclinal d'Ancenis). Bulletin de la Société Géologique et Minéralogique de Bretagne 8, 4-6.

García-Alcalde, J.L., Truyols-Massoni, M., Pardo-Alonso, M., Bultynck, P., Carls, P., 2000. Devonian chronostratigraphy of Spain. Courrier Forschungs-Institut Senckenberg 225, 131-144.

García-Alcalde, J.L., 2015. La sucesión del Emsiense más alto-eifeliense basal (Devónico) en el Dominio Astur-Leonés de la zona Cantábrica (N de España) y su faune de braquiópodos. Trabajos de Geología 35, 41-98.

Garcia-Lopez S., Sanz-Lopez J., 2002. Devonian to lower Carboniferous conodont biostratigraphy of the Bernesga valley section (Cantabrian Zone, NW Spain). Cuadernos del Museo Geominero 1, 163-205.

Gerrienne, P., Gensel, P.G., Strullu-Derrien, C., Lardeux, H., Steemans, P., Prestianni, P., 2011. A simple type of wood in two early Devonian plants. Science 333, 837.

Gerrienne, P., Gensel, P.G., 2016. New data about anatomy, branching, and inferred growth patterns in the Early Devonian plant *Armoricaphyton chateaupannense*, Montjean-sur-Loire, France. Review of Palaeobotany and Palynology, 224, 38-53.

Godefroid, J., 1968. Contribution à l'étude du Couvinien entre Wellin et Jemelle (bord sud du bassin de Dinant). Académie Royale de Belgique, Classe des Sciences, Mémoires 2ème série 17, 1-87.

Godefroid, J., 1971. Morphologie interne de Gypidulinae couviniens. Annales de la Société Géologique de Belgique 94, 45-72.

Godefroid, J., Blieck, A., Bultynck, P., Dejonghe, L., Gerrienne, P., Hance, L., Meilliez, F., Stainier, P., Steemans, P., 1994. Les formations du Dévonien inférieur de la Vesdre, de la Fenêtre de Theux et du Synclinorium de Dinant (Belgique, France). Mémoires pour Servir à l'Explication des Cartes Géologiques et Minières de la Belgique 38, 1-44.

Halfar, A., 1879. Über eine neue Pentamerus-Art aus dem typischen Devon des Oberharzes. Zeitschrift der Deutschen Geologischen Gesellschaft 31, 705-715

Hall, J., 1893. Palaeontology of New York. An introduction to the study of the genera of the Palaeozoic brachiopoda, 8(2), pp. 177-317.

Havlicek, V., 1955. The brachiopoda of the Branik and Hlubocepy limestones in the immediate vicinity of Prague. Sbornik Ustredniho Ustavu Geologického (oddil Paleontologicky) 22, 535-665 (in Czech with Russian and English summaries).

Heritsch, F., 1915. Beiträge zur geologischen Kenntnis der Steiermark. VII - Die Stellung der Pentamerus-Kalke der Umgebung von Graz. Mitteilungen Naturwisschaftlicher Verein für Steiermark 51, 92-106.

Heritsch, F. 1918. Beiträge zur geologischen Kenntnis der Steiermark. IX. Die Fauna des unterdevonischen Korallenkalkes der Mittel-Steiermark nebst Bemerkungen über das Devon der Ostalpen. Mitteilungen Naturwisschaftlicher Verein für Steiermark 54, 7-52.

Heritsch, F., 1935. Oberstes Unterdevon und unteres Mittedevon bei Graz. Sitzungsberichte der Akademie der Wissenschaften, Mathematisch Naturwissenschaftliche Klasse (I), 144, 187-197.

Hinze, C., 1971, mit Beiträge von Duphorn K., Hannak, W., Heinemann, B., Hermann, A. & Hermann, F. Blatt Clausthal-Zellerfeld, Geologische Karte niedersachsen 1/25000, Erl. Blatt Nr 4128, Niedersächsiche Landes-Amtes für Bodenforschung, Hannover, 166 p.

Hubmann, B., 1993. Ablagerungsraum, Mikrofazies und Paläoökologie der Barrandeikalk – Formation (Eifelium) des Grazer Paläozoikums. Jahrbuch der Geologischen Bundesanstalt 136, 393-461.

Hubmann, B., 2003. Plabutsch-Formation: nomen novum pro Barrandeikalk (Mitteldevon, Grazer Paläozoikum). Stratigraphia Austriaca (Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschftlichen Kommissionen) 16, 269-292.

Hubmann, B., Suttner, T., 2007. Siluro-Devonian Alpine reefs and pavements. Geological Society of London Special Publication 275, 95-107.

Huckriede, H., Wemmer K., Ahrendt H., 2004. Palaeogeography and tectonic structure of allochthonous units in the German part of the Rheno-Hercynian belt (Central European Variscides). International Journal of Earth Sciences 93, 414-431.

Kegel, W., 1953. Das Paläozoikum der Linderner Mark bie Giessen. Abhandlungen des Hessischen Landesamtes für Bodenforschung 7, 1-55.

Kegel, W., 1976. Erläuterungen zur Geologischen Karte von Hessen 1/25000, Blatt Nr 5417 Wetzlar 2, ergänzte Auflage). Hessisches Landesamt für Bodenforschung, Wiesbaden, 137 p.

Kim, I.-S., 1997. Trilobiten aus dem Greifensteiner Kalk (Grenzbereich Unter-Mittel Devon). Palaeontographica A245, 157-205.

Khodalevich, A. N., 1939. Upper Silurian brachiopods of eastern slope of the Urals. Trudy Ural'skogo Geologicheskogo Upravleniia. Izdanie Uralgeoupravleniia, Sverdlovsk 135 p. (in Russian).

Krömmelbein, K., Hotz, H.-E., Kräusel, W., Struve, W., 1955. Zur Geologie der Eifelkalkmulden. Beihefte zum Geologischen Jahrbuch 17, 1-204.

Langenstrassen, F., 1972. Fazies und Stratigraphie der Eifel-Stufe im östlichen Sauerland. Göttinger Arbeiten zur Geologie und Paläontologie 12, 1-106.

Langenstrassen, F., Müller, H., 1982. The lower/middle Devonian boundary in the Sauerland (Latrop anticline and Wittgenstein syncline, eastern Rheinische Schiefergebirge). Courrier Forschungsinstitut Senckenberg 55, 337-344.

Lardeux, H., Cavet, P., 1994. Paleozoic of the Ligerian Domain. In: Keppie, J.D. (Ed.), Pre-Mesozoic geology in France and related areas, Springer Verlag, Berlin, pp. 152-156.

Lardeux, H., Weyant, M., 1993. Conodontes et Tentaculites (Dacryoconarides) du calcaire de Valet en Chaudefonds (Dévonien inférieur, Massif armorician, Anjou). Revue de Micropaléontologie 36, 19-28.

Lecompte, M., 1962. Faciès et stratigraphie dans le Dévonien inférieur et moyen de la Belgique. In: Erben, H.K. (Ed.), Symposium Silur-Devon Grenze, Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 143-150.

Lecompte, M., 1967. Le Dévonien de la Belgique et le Nord de la France. In: Oswald, D. H. (Ed.), International Symposium on the Devonian System, Calgary, 1967. Alberta Society of Petroleum Geologists, Calgary, 1, 15-52.

Lecompte, M., 1970. Die Riffe im Devon der Ardennen und ihre Bildungsbedingungen. Geologica et Palaeontologica 4, 25-71.

Le Maître, D., 1929. La faune des couches à Sp. cultrijugatus de Fourmies. Annales de la Société Géologique du Nord 54, 27-74.

Le Maître, D., 1932. Amphigenia Bureaui Oehlert et ses gisements dans les calcaires dévoniens du bassin d'Ancenis. Annales de la Société Géologique du Nord 56, 263-273.

Le Maître, D., 1934. Etude sur la faune des calcaires dévoniens du bassin d'Ancenis. Calcaire de Chaudefonds et calcaire de Chalonnes (Maine-et-Loire). Mémoires de la Société Géologique du Nord 12, 1-267.

Le Maître, D., 1935. A propos d'un travail de M. Heritsch sur le Dévonien de Graz. Annales de la Société Géologique du Nord 59, 107-109.

Le Maître, D., 1960. Les faciès hercyniens de la bordure sud-orientale du Massif armoricain. Bulletin de la Société d'Etudes scientifiques d'Angers nouvelle série 2, 89-94.

Lessuise, A., Streel, M., Vanguestaine, M., 1979. Observations palynologiques dans le Couvinien (Emsien terminal et Eifélien) du bord oriental du synclinorium de Dinant, Belgique. Annales de la Société Géologique de Belgique 102, 325-355.

Lotz, H., 1900. Die Fauna des Massenkalks der Lindener Mark bei Giessen. Schriften der Gesellschaft zur Beförderung der gesammten Naturwissenschaften zu Marburg 13, 197-236.

Lotz, H., 1901. Pentamerus-« Quartzit » und Greifensteiner Kalk. Jahrbuch der Königlich-Preussische Geologische Landesanstalt und Bergakademie zu Berlin 21, 64-80.

Lu, J., Valenzuela-Ríos, J.I., Chen, X., Liao J.-C., 2017. Conodont biostratigraphy of the Nalai section (Guangxi) and new data on the age of the *Zdimir* beds in South China. Bulletin of Geosciences 92, 525-544.

Maillieux, E., 1938. Le Couvinien de l'Ardenne et ses faunes. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 83, 1-57.

Maillieux, E., 1941. Les brachiopodes de l'Emsien de l'Ardenne. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 96, 1-74.

Mohr, K., 1993. Geologie und Minerallagerstätten des Harzes. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, 496 p.

Morzadec, P., 1983. Le Dévonien (Emsien-Famennien) de la rade de Brest (Massif armoricain). Lithologie, cartographie, stratigraphie, paléogéographie. Géologie de la France 4, 269-310.

Morzadec, P., Paris, F., Plusquellec, Y., Racheboeuf, P., Weyant, M., 1988. Devonian stratigraphy and paleogeography of the Armorican Massif (Western France). In: McMillan, N.J., Embr, A.F., Glass, D.J. (Eds), Devonian of the world, Canadian Society of Petroleum Geologists 1, pp. 401-420.

Novak, O., 1888. Bemerkungen über *Pentamerus* (*Zdimir*) *solus* Barrande aus Etage G-g^3 von Hlubočep bei Prag. Zeitschrift der Deutschen Geologischen Gesellschaft 40, 588-590.

Oczlon, M.S., 1994. North Gondwana origin for exotic Variscan rocks in the Rhenohercynian zone of Germany. Geologische Rundschau 83, 20-31.

Oehlert, D., 1881. Note sur le calcaire de Montjean et de Chalonnes. Annales des Sciences Géologiques 12, 1-12.

Oehlert, D., 1887. Brachiopodes. In: Fischer, P.H., Manuel de conchyologie et de paléontologie conchyologique, ou Histoire naturelle des mollusques vivants et fossiles, part II, F. Savy, Paris, pp. 1189-1324,

Pedder, A.E.H., Feist, R., 1998. Lower Devonian (Emsian) Rugosa of the Izarne Formation, Montagne Noire, France. Journal of Paleontology 72, 967-991.

Péneau, J., 1934. Compte-rendu de la réunion extraordinaire de la Société Géologique et Minéralogique de Bretagne à Angers – Châteaubriant – Ancenis (22-26 avril 1930).. Bulletin de la Société Géologique et Minéralogique de Bretagne, nouvelle série 1, 57-132.

Plusquellec, Y., Jahnke, H., 1999. Les tabulés de l'Erbslochgrauwacke (Emsien inférieur du Kellerwald) et le problème des affinités paléogéographiques de l'allochtone « Giessen-Harz ». Abhandlungen der Geologischen Bundesanstalt 54, 435-451.

Renaud, A., 1942. Le Dévonien du synclinorium médian Brest-Laval. Mémoires de la Société Géologique et Minéralogique de Bretagne 7(1), 1-184 ; 7(2), 1-385.

Renaud, A., 1953. Les collections paléontologiques du Musée du Vieux Château de Laval. Imprimerie Goupil, Laval, 39 p.

Renaud, A., 1955. Etude de quelques affleurements emsiens au Nord d'Argentré (Mayenne). Bulletin de la Société Géologique et Minéralogique de Bretagne, nouvelle série 1, 20-35.

Robardet, M., Bonjour, J.-L., Paris F., Morzadec, P., Racheboeuf, P., 1994. Ordovician, Silurian, and Devonian of the Medio-North-Armorican Domain. In: Keppie, J.D. (Ed.), Pre-Mesozoic geology in France and related areas, Springer Verlag, Berlin, pp. 142-151.

Roemer, F.A., 1874. Ueber die ältesten versteinerungsführenden Schichten in dem rheinisch-westfälischen Schiefergebirge. Zeitschrift der Deutschen Geologischen Gesellschaft 26, 752-760.

Rzhonsnitskaia, M.A., 1961. K sistematike I filogenii Pentameracea [On the systematics and phylogeny of the Pentameracea]. Paleontologicheskii Zhurnal 1, 38-49.

Sapelnikov, V.P., Snigireva, M.P., Bikbayev, A.Z., Mizens, L.I., 1995. Zonal subdivisions of Early-Middle Devonian reef deposits of the Urals based on conodonts and brachiopods. Courrier Forschungsinstitut Senckenberg 182, 399-420.

Simon, W., Dahmer, G., 1954. *Zygobolba corbis* (Ostrac.), Leitmarke für den Begin des Mittel-Devons in Oberharz. Senckenbergiana Lethaea 34, 235-245.

Solle, G., 1934. *Conchidium hercynicum* Halfar und die Stellung der Pentamerenkalke im Grazer Devon. Senckenbergiana Lethaea 16, 110- 126.

Strullu-Derrien, C., Ducassou, C., Ballèvre, M., Dabard, M.-P., Gerrienne, P., Lardeux, H., Le Hérissé, A., Robin, C., Steemans, P., Strullu, D.-G. 2010. The early land plants from the Armorican Massif : sedimentological and palynological considerations on age and environment. Geological Magazine 147, 830-843.

Strullu-Derrien, C., Kenrick, P., Tafforeau P., Cochard, H., Bonnemain, J.-L., Le Hérissé, A., Lardeux, H., Badel, E., 2014. The earliest wood and its hydraulic properties documented in c. 407-million-year-old fossils using synchrotron microtomography. Botanical Journal of the Linnean Society 175, 423-437.

Struve, W., 1982. Beiträge zur Kenntnis devonischer Brachiopoden, 23 – Schaltier-Faunen aus dem Devon des Schwarzbach-Tales bei Ratingen, Rheinland. Senckenbergiana Lethaea 63, 183-283.

Struve, W., 1989. Zur Lebensweise von Schaltieren auf mittel-devonischen Karbonat-Plattformen. Natur und Museum 119, 128-139.

Suttner, T.J., Berkyovà, S., 2009. Devonian conodonts of the Plabutsch Formation (Graz Palaeozoic). Regional Devonian Workshop, Prague and Graz, 25-27th May 2009, pp. 42-43.

Suttner, T.J., Chen, X.-Q., 2009. *Zdimir* and related faunas near the Emsian/Eifelian boundary in Austria and China. In: Regional Devonian Workshop, Prague and Graz, 25-27th May 2009, pp. 44-45.

Tazawa, J., 1988. *Zdimir* (Devonian Brachiopoda) from the Kitakami Mountains, northeast Japan and its palaeobiogeographical significance. Journal of the Geological Society of Japan 94, 1013-1016 (in Japanese).

Vandenven, C., 1975. Coupe géologique du nouveau tracé de la nationale 4 au sud de Marche (Communes de Waha et de Harsin). Service Géologique de Belgique Professional Paper 2, 1-18.

Zapalski, M.K., Hubert, B.L.M., Nicollin, J.-P., Mistiaen, B., Brice, D., 2007. The palaeobiodiversity of stromatoporoids, tabulates and brachiopods in the Devonian of the Ardennes – Changes through time. Bulletin de la Société Géologique de France 178, 383-390.

Figure captions.

Fig. 1. Location of the studied area.
Localisation de la région étudiée.

Fig. 2. Stratigraphy of the Châteaupanne Unit (modified from Ducassou et al., 2011).
Stratigraphie de l'unité de Châteaupanne (modifié d'après Ducassou et al., 2011).

Fig. 3. Original figurations of: (a) ?*Porambonites robustus* (Barrande, 1879, pl. 80, fig. II), C. *Zdimir solus* (Barrande, 1881, pl. 292, figs. 17-20) and C. *Pentamerus davyi* (Oehlert, 1881) (L = 27 mm, w = 25 mm, t = 16 mm). Following the revision made by Boucot and Siehl (1962), the first two are considered as a brachial and peduncular valve, respectively, of the same species, *Zdimir robustus*. Note the exceptional preservation of the sample drawn by Oehlert as compared to those from Bohemia.
*Figurations originales de : A. ?*Porambonites robustus *(Barrande, 1879, pl. 80, fig. II), B.* Zdimir solus *(Barrande, 1881, pl. 292, figs. 17-20) et C.* Pentamerus davyi *(Oehlert, 1881) (L = 27 mm, w = 25 mm, t = 16 mm). Selon la révision effectuée par Boucot et Siehl (1962), les deux premiers taxons sont considérés comme étant la valve brachiale et pédonculaire, respectivement, de la même espèce,* Zdimir robustus. *On notera la préservation exceptionnelle de l'échantillon dessiné par Oehlert, par comparaison avec ceux de Bohême.*

Fig. 4. Photographs of *Zdimir robustus* from the Chalonnes Formation, Châteaupanne quarry. Sample 75269-1 (L = 37 mm, w = 33 mm, t = 24 mm): A. Pedicle valve; B. brachial valve ; C. frontal view; D. profile view. Sample 75269-2 (L = 30 mm, w = 28 mm, t = 19 mm): E. internal mold in profile; F. brachial view. Both samples are housed in the collections from the Université Catholique d'Angers.
Photographies de Zdimir robustus *de la Formation de Chalonnes, carrière de Châteaupanne. Spécimen 75269-1 : A. valve pédonculaire ; B. valve brachiale ; C. vue frontale ; D. vue de profil. Spécimen 75269-2 : E. vue de profil ; F. vue brachiale d'un moule interne. Ces deux échantillons sont conservés dans les collections de l'Université Catholique d'Angers.*

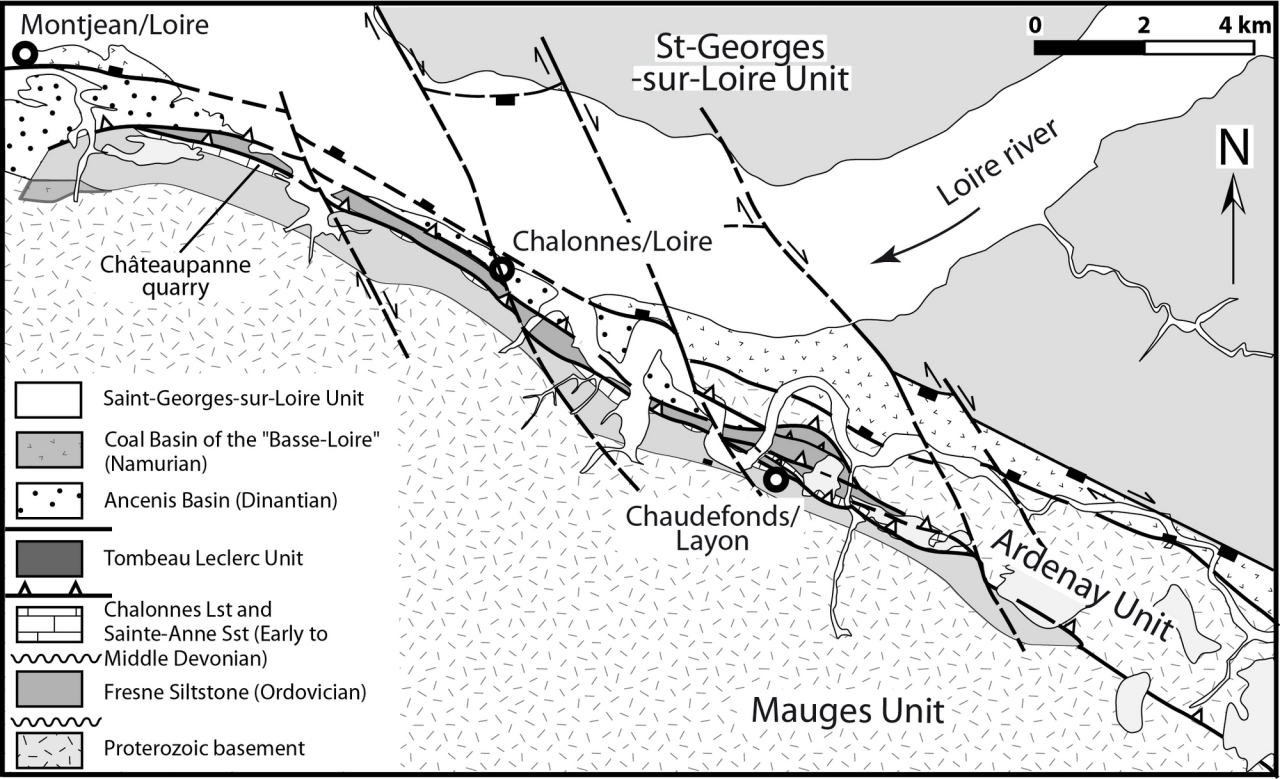
Fig. 5. Serial transverse sections of *Zdimir robustus* (specimen from the collection of the Museum des Sciences Naturelles d'Angers MHNAn.2014.0.100 (L = 27,6 mm, w = 26,5 mm, t = 20,5 mm). Distances are in mm from the top of the ventral umbo. The shell is cut across by a few calcite veins (white). The dashed line emphasizes the boundary between the external lamellar and internal prismatic layers.
Sections transversales sériées de Zdimir robustus *d'après un spécimen du Musée des Sciences Naturelles d'Angers MHNAn.2014.0.100 (L = 27,6 mm, w = 26,5 mm, t = 20,5 mm). Les distances sont mesurées en mm depuis le sommet du crochet ventral. La coquille est reecoupée par quelques veines de calcite (blanc). La ligne tiretée indique la position de la limite entre les couches externes lamellaires et interne prismatique de la coquille.*

Fig. 6. Geographical distribution of *Zdimir* occurrences in western and central Europe (see text for references).

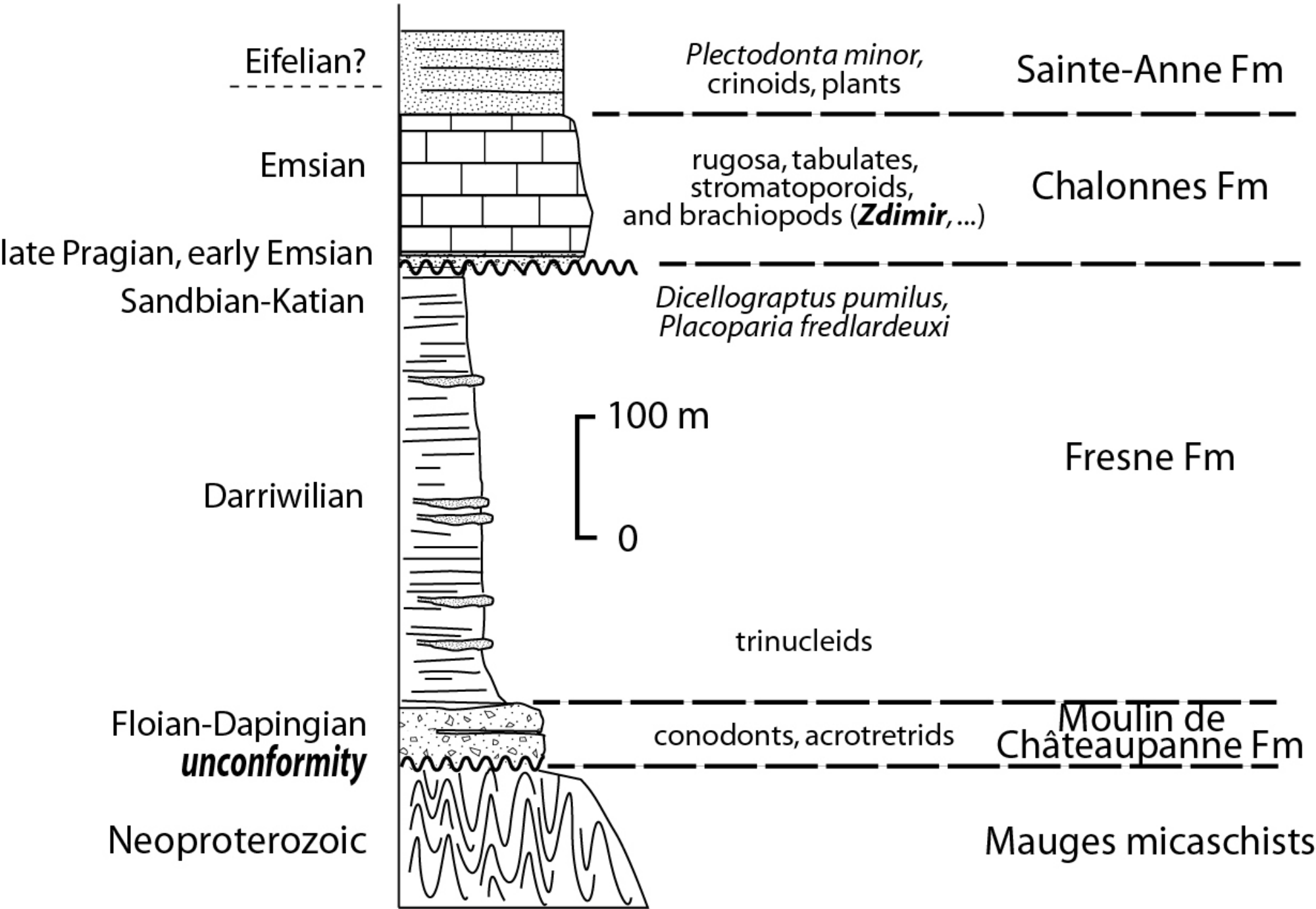
Distribution géographique du genre Zdimir *en Europe occidentale et centrale (les sources sont données dans le texte pour chaque localité).*

Fig. 7. Stratigraphical distribution of *Zdimir* occurences in western and central Europe. The diverse columns are referred to numbers that are reported on figure 6. *Zdimir* occurrences in sections that have been dated using conodonts and/or tentaculitids are shown in black, otherwise they are displayed in grey (e.g. Chalonnes and Plabutsch formations). The vertical extent of *Zdimir* in a specific column (i.e. the height of the black segment) is either restricted to its known range in a specific formation (e.g. the Moniello Formation according to Arbizu et al., 1979), or taken (conservatively) as the whole formation when its vertical distribution within this formation is not known (e.g. the Trebotov Limestone). This maximizes the uncertainties associated with the vertical distribution of *Zdimir*. For sake of reference, key conodont- biozones are displayed on the rigth of the figure.

Distribution stratigraphique du genre Zdimir *en Europe occidentale et centrale. Les chiffres en tête des différentes colonnes se rapportent aux localités de la figure 6. Les gisements de* Zdimir *ayant été datés avec des conodontes et/ou des tentaculites sont indiqués en noir ; ceux où un calage biostratigraphique indépendant n'a pu être réalisé sont en gris (par ex. formations de Chalonnes et Plabutsch). L'extension verticale de* Zdimir *dans une colonne donnée (la longueur du segment noir ou gris) représente soit son extension au sein de cette formation quand elle est connue, soit, par défaut, la totalité de la formation dans laquelle* Zdimir *a été observé (par ex. le Calcaire de Trebotov). Cette procédure maximise les incertitudes sur l'extension verticale du genre Zdimir. Les biozones de conodontes sont rappelées, pour mémoire, en marge droite du tableau.*


Montjean/Loire
St-Georges
-sur-Loire Unit
0
2
4 km
N
Loire river
Chalonnes/Loire
Châteaupanne
quarry
Chaudefonds/
Layon
Ardenay Unit
Mauges Unit
Saint-Georges-sur-Loire Unit
Coal Basin of the "Basse-Loire"
(Namurian)
Ancenis Basin (Dinantian)
Tombeau Leclerc Unit
Chalonnes Lst and
Sainte-Anne Sst (Early to
Middle Devonian)
Fresne Siltstone (Ordovician)
Proterozoic basement

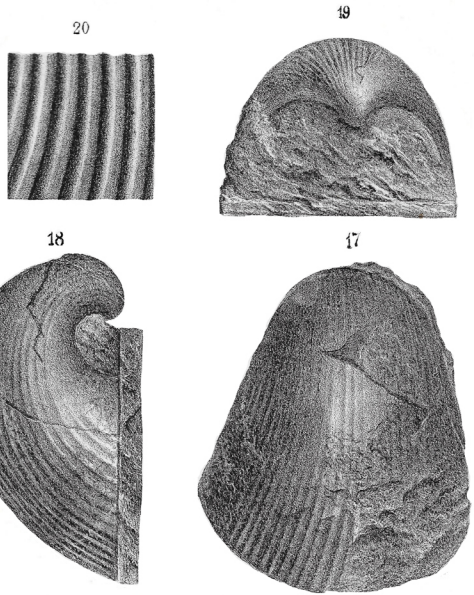
Châteaupanne Unit



?*Porambonites robustus* Barrande 1879

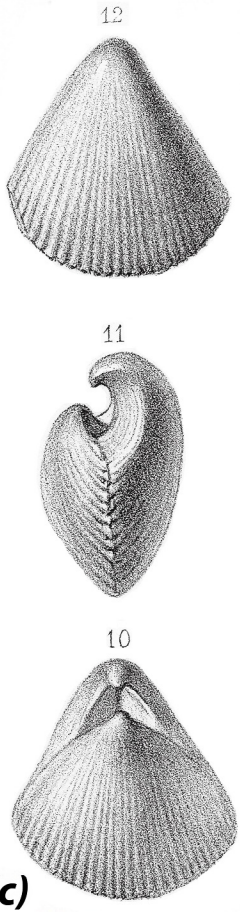
(a)

Zdimir solus Barrande,1881

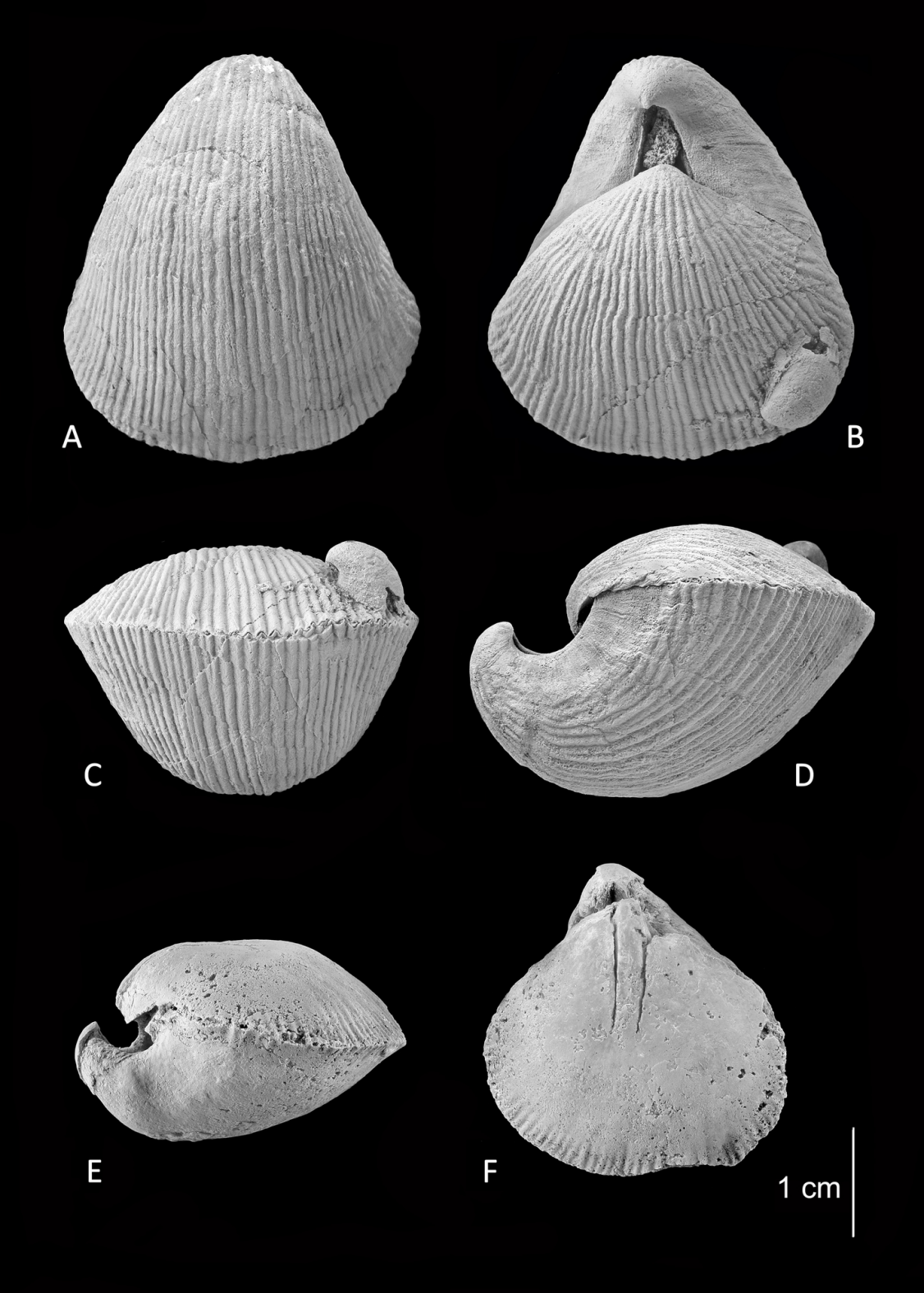


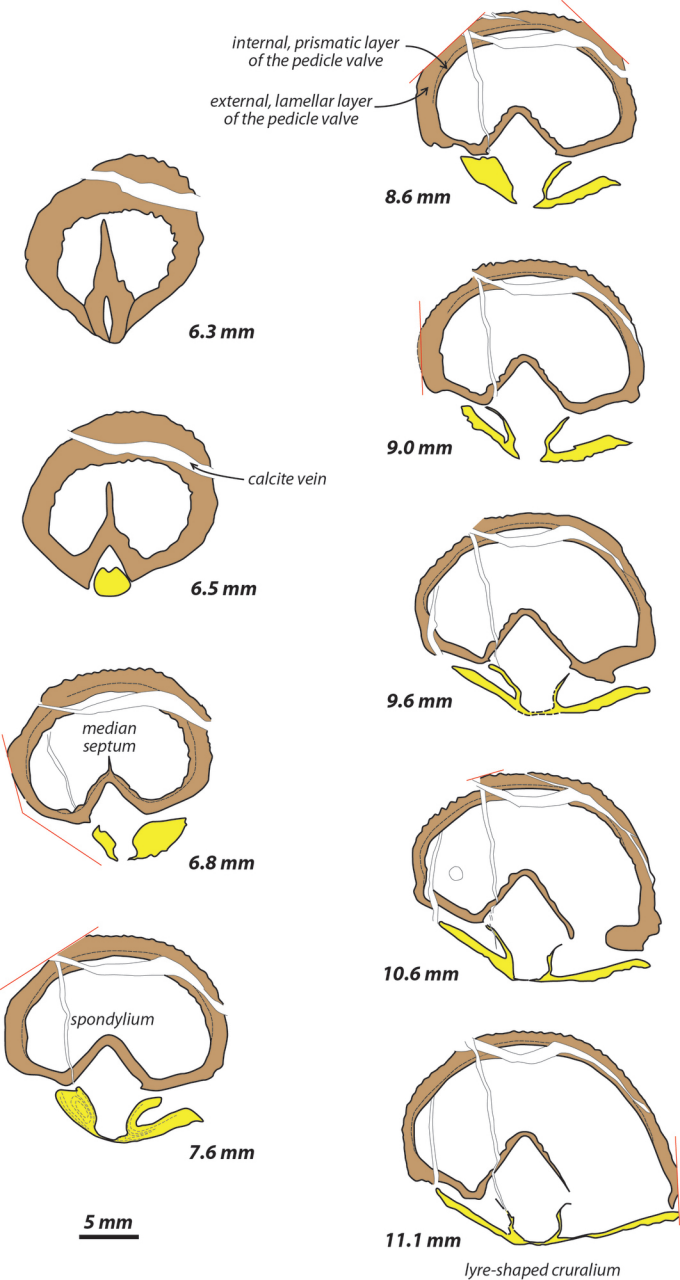
(b)

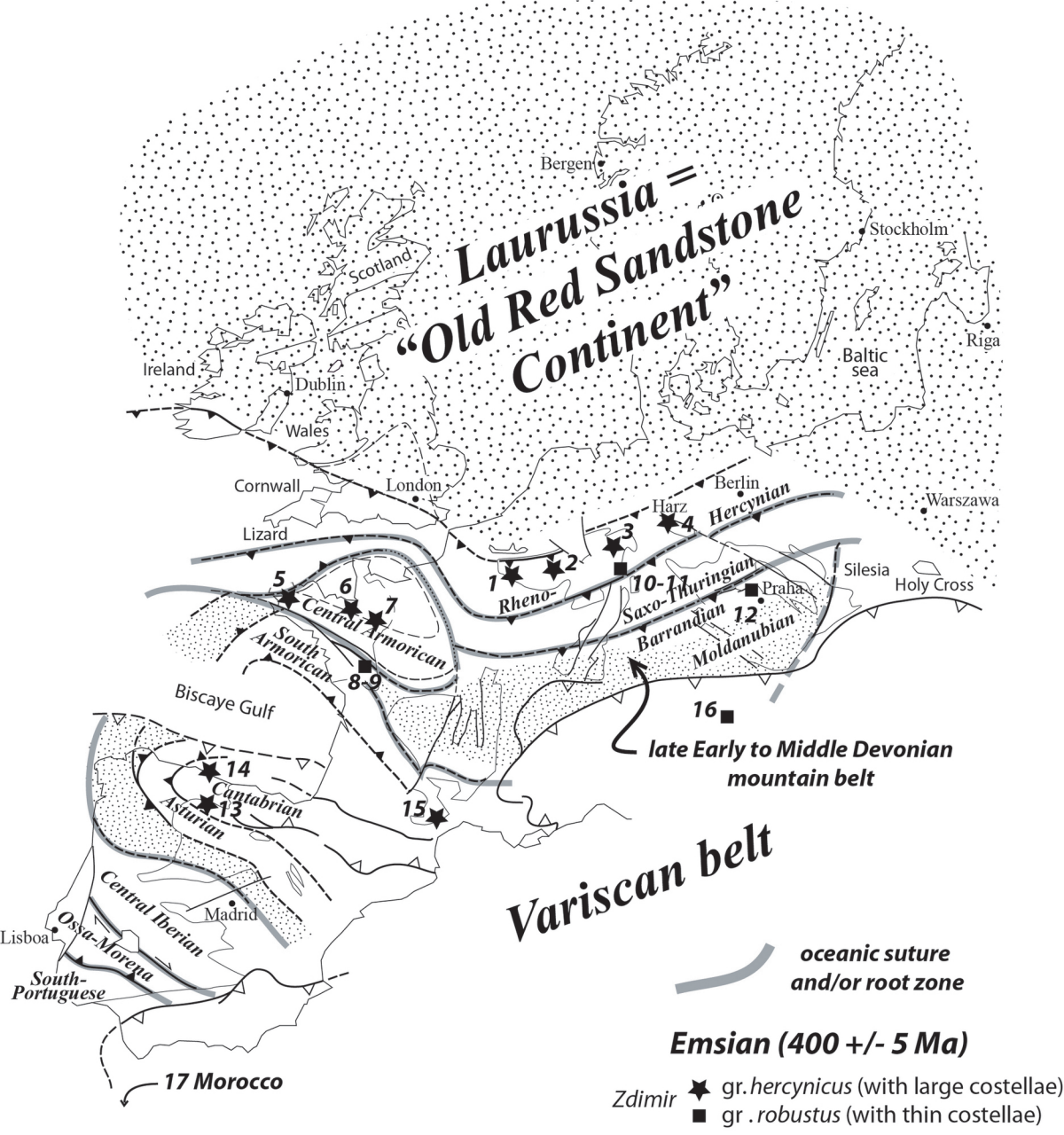
Pentamerus davyi Oehlert 1881

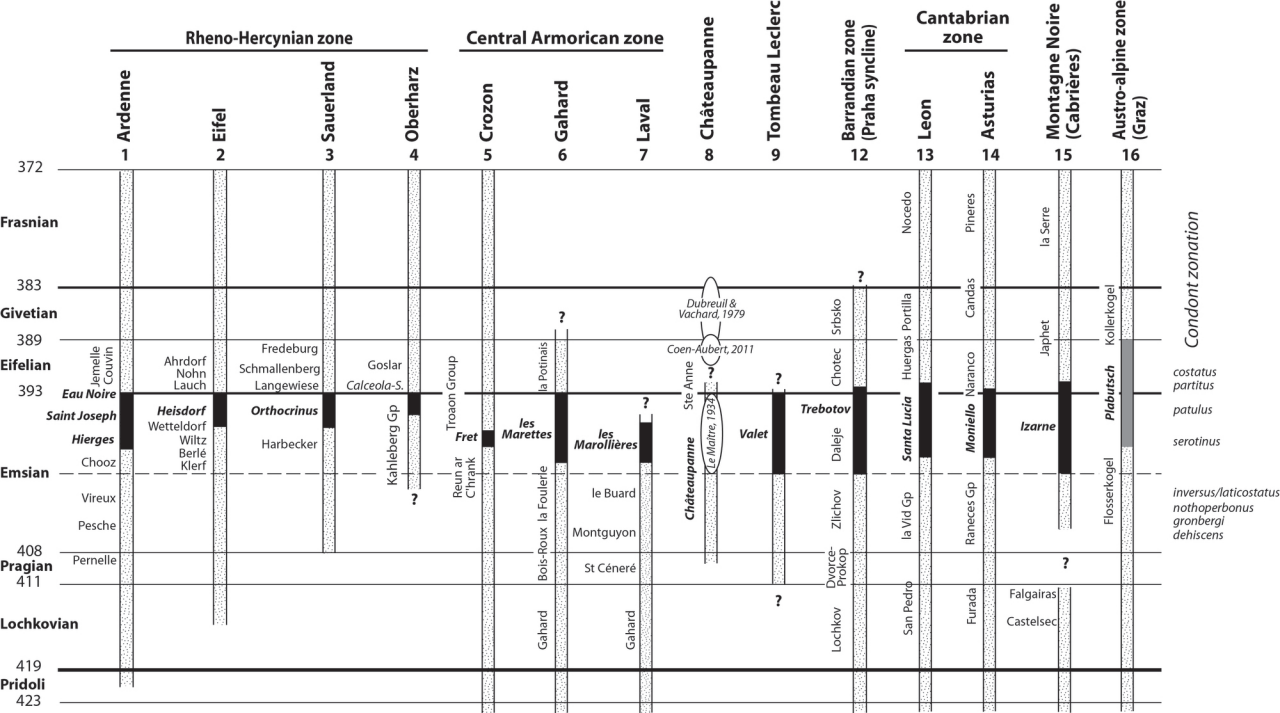


(c)


A
B
C
D
E
F
1 cm


internal, prismatic layer of the pedicle valve
external, lamellar layer of the pedicle valve
8.6 mm
6.3 mm
9.0 mm
calcite vein
6.5 mm
9.6 mm
median septum
6.8 mm
10.6 mm
spondylium
7.6 mm
5 mm
11.1 mm
lyre-shaped cruralium


Laurussia =
"Old Red Sandstone Continent"
Bergen
Stockholm
Riga
Baltic sea
Scotland
Ireland
Dublin
Wales
Cornwall
London
Berlin
Warszawa
Harz
Hercynian
Lizard
Rheno-
Saxo-Thuringian
Praha
Silesia
Holy Cross
Barrandian
Moldanubian
Central Armorican
South Armorican
Biscaye Gulf
late Early to Middle Devonian mountain belt
Variscan belt
Cantabrian
Asturian
Central Iberian
Madrid
Lisboa
Ossa-Morena
South-Portuguese
17 Morocco
oceanic suture and/or root zone
Emsian (400 +/- 5 Ma)
Zdimir
gr. hercynicus (with large costellae)
gr . robustus (with thin costellae)


Rheno-Hercynian zone
Central Armorican zone
Cantabrian zone
Ardenne
Eifel
Sauerland
Oberharz
Crozon
Gahard
Laval
Châteaupanne
Tombeau Leclerc
Barrandian zone (Praha syncline)
Leon
Asturias
Montagne Noire (Cabrières)
Austro-alpine zone (Graz)
1
2
3
4
5
6
7
8
9
12
13
14
15
16
372
Frasnian
383
Givetian
389
Eifelian
393
Emsian
408
Pragian
411
Lochkovian
419
Pridoli
423
Jemelle
Couvin
Eau Noire
Saint Joseph
Hierges
Chooz
Vireux
Pesche
Pernelle
Ahrdorf
Nohn
Lauch
Heisdorf
Wetteldorf
Wiltz
Berlé
Klerf
Fredeburg
Schmallenberg
Langewiese
Orthocrinus
Harbecker
Goslar
Calceola-S.
Kahleberg Gp
Troaon Group
Fret
Reun ar Chrank
la Potinais
les Marettes
Bois-Roux
la Foulerie
Gahard
les Marollières
le Buard
Montguyon
St Céneré
Gahard
Dubreuil & Vachard, 1979
Coen-Aubert, 2011
Ste Anne
Châteaupanne
Le Maître, 1924
Srbsko
Chotec
Trebotov
Valet
Daleje
Zlichov
Dvorce-Prokop
Lochkov
Nocedo
Huergas
Portilla
Santa Lucia
la Vid Gp
San Pedro
Pineres
Candas
Naranco
Moniello
Raneces Gp
Furada
la Serre
Japhet
Izarne
Falgairas
Castelsec
Kollerkogel
Plabutsch
Flosserkogel
Condont zonation
costatus
partitus
patulus
serotinus
inversus/laticostatus
nothoperbonus
gronbergi
dehiscens