

# Ecology of Devonian ostracods: application to the Frasnian/Famennian boundary bioevent in the type region (Dinant Synclinorium, Belgium)

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**Abstract** Three mega-assemblages and six assemblages of ostracods numbered 0 to V are recognised in the Devonian. They are indicative of lagoonal environments, semi-restricted environments and marine environments above and below fair-weather wave-base or storm wave-base. The water energy, the oxygenation and the temperature of marine waters seem to be the most important factors controlling the distribution of ostracods in the Devonian. These ostracod assemblages and mega-assemblages are also recognised in the Silurian and the Carboniferous. The ecological study of ostracods in the southern border of the Dinant Synclinorium, the type region for the definition of the Frasnian and Famennian stages, proves that the Late Devonian mass extinction is related to a period of hypoxia of marine waters followed and probably linked to a regression close to their boundary. The hypoxia is marked by the occurrence of the Myodocopid Mega-Assemblage, and its acme corresponds to the *splendens* Zone/*sigmoidale* Zone boundary of the parachronology based on Entomozoid ostracods. The sea-level fall is attested by the occurrence of ostracods indicative of semi-restricted water conditions in several sections, and particularly at Sinsin where stacked valves due to very small waves related to the lap are observed. Thus, the study of ostracods shows that intrinsic factors linked to the global tectonic regime are the most important factors explaining the Late Devonian mass extinction. The Frasnian/Famennian historic boundary of Gosselet

(*Annales de la Société géologique du Nord*, 4, 303–320, 1877) corresponding to the recovery of the mega-fauna after the acme of this mass extinction marks in reality the return to true marine water conditions after the semi-restricted marine episode. The Matagne Fm, the Senzeille Fm and the position of the F/F boundary in the Synclinorium of Dinant are discussed.

**Keywords** Ostracods · Palaeoecology · Palaeoclimatology · Stratigraphy · Devonian · Mass extinction

## Introduction

The small bivalve crustacean ostracods are certainly the best fossil group useful to reconstruct Palaeozoic environments. Their great abundance, diversity and presence in all kind of niches in aqueous environments, from fresh to hypersaline waters, from low to high latitudes and from high altitudes on continents to deep settings in oceans at the very least present day, are the principal reasons. Ostracods lived in the upper part of soft sediments, on the bottom and on plants, and some species are nekto-benthic or nekto-planktonic. The principal environmental factors influencing their distribution are the salinity, temperature, nature of substrate, oxygen content, food supply and water motion. Their mode of preservation (carapaces or dissociated valves of adults and instars, sorted valves and carapaces, stacked valves, etc.) provided valuable information on palaeoenvironments. Numerous papers, books and reports of meetings treat with the palaeoecology of ostracods (e.g. Puri 1966; Oertli 1971; Whatley and Maybury 1990; Groos-Uffner et al. 2000, etc.).

With the exception of the entomozoid ostracods characterised by their fingerprint ornamentation, the biostratigraphic value of ostracods during the Palaeozoic is weak comparatively to the

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biostratigraphic value of conodonts chosen by the International Commission on Stratigraphy (ICS) to fix stages boundaries during the Devonian (Casier 2008, 2013). The parochronology based on entomozoid ostracods was established by Rabien (1954) and has been little modified since then (See Groos-Uffenorde et al. 2000). But the role of ostracods in biostratigraphy is important because their palaeoecological study permits appreciation of the value of stratigraphical decisions based on conodonts. The study of the Devonian/Carboniferous (=D/C) Global Section and Point (=GSSP) at La Serre in the French Montagne Noire (Klapper et al. 1993) is a good example. The study of ostracods in the D/C GSSP demonstrates that a great part of the fauna in this section is reworked (numerous ostracods present in microbreccia and oolites!), and also the presence of a tectonic discontinuity close to the boundary linked to the presence of two beds not in accordance with the general evolution of facies observed in the section (Casier et al. 2002; Casier and Pr eat 2009). Recently, Kaiser et al. (2007) have recorded *Siphonodella sulcata* (Huddle, 1934), defining the base of the Carboniferous, below the fixed D/C boundary and the entry of this conodont species during the above-mentioned gap may be suspected. Researches are currently in hand to propose a new definition of this boundary and to propose a new GSSP (see Corradini et al. 2016). Recently (SDS Newsletter, n o 29, 2014, p. 50), I have drawn the attention of the Subcommittee of Devonian Stratigraphy members to the Puech de la Suque section studied by Feist (1990, 1995) (see also Girard 1996 and Casier et al. 2001) also in the Montagne Noire. This section is easily accessible and continuous, rich in fossils and conodonts, and exposes the Hangenberg Event.

Studies of Palaeozoic and particularly of Devonian ostracods have been undertaken since the 1970s by the author. The Devonian is an important period for Earth history because at that time, continents were colonised by plants and vertebrates and also because the Late Devonian is marked by one of the most important mass extinctions (one of the Big Five!) recognised since the base of the Phanerozoic (See the synthesis of McGhee 1996; Racki 2005; Bond and Wignall 2008). The Frasnian/Famennian (=F/F) boundary bioevent corresponds to the acme of the Late Devonian mass extinction.

The Belgian localities cited in the text are shown on Fig. 1. All the specimens figured in Figs. 3, 4, 5, and 6 are stored in the collection of the OD Earth and Life History of the Royal Belgian Royal Institute of natural Sciences.

### Ecology of Palaeozoic ostracods: main steps

Based mainly on studies of Rabien (1954, 1956), Zagora (1968), Polenova (1971), Becker (1971, 2000), Blumenstengel (1973) and on numerous personal studies, Becker (in Bandel



**Fig. 1** Localisation map of Senzeille, Sinsin, Hony, Lambermont and other Belgian localities cited in the text

and Becker 1975) distinguished three ostracod ecotypes in the Devonian established on the carapace morphology (ornamentation, thickness of shells, shape and size) and related to energy levels:

1. The Eifelian ecotype corresponding to the “sandig-kalkige Fazies Typ” of Blumenstengel (1973) is composed mainly of benthonic palaeocopid, platycopid and metacopid ostracods. The Beyrichiid type of Polenova (1971) belongs to the Eifelian ecotype.
2. The Thuringian ecotype corresponding to the “Th uringischer Typus” of Zagora (1968) and to the “kalkig-tonige Fazies Typ” of Blumenstengel (1973) is characterised by a sparse ostracod fauna predominated by spiny benthic podocopids.
3. The Entomozoacean ecotype corresponding to the “tonige, hemipelagische Fazies Typ” of Blumenstengel (1973) is characterised by pseudoplanktonic entomozoid ostracods.

For Becker (in Bandel and Becker 1975), these ecotypes are frequently mixed, and particularly the Thuringian ecotype with the Eifelian or the Entomozoacean ecotypes.

But, the usage of the term “ecotype” was the subject of several misinterpretations criticised by Becker (2001a, b). The ostracods representative of Becker’s ecotypes were frequently assimilated to represent ecozones, and consequently not in accordance with the intentions of the author. These misinterpretations are in part due also to the inappropriate use of the word ecotype by Becker (Casier 2004). By definition, an “ecotype” describes a group of plants or animals belonging to one single species, genetically adapted to a particular habitat but able to cross freely with other ecotypes of the same species (Abercrombie et al. 1980).

In 1987, Casier (1987a) recognised five ecozones numbered I to V in the Frasnian of Belgium. These ecozones characterised restricted carbonaceous environments (=ecozone I), shallow marine carbonaceous environments (=ecozone II), marginal basin environments generally argillaceous (=ecozone III), deeper basin environments (=ecozone IV), and basin environments poor in dissolved oxygen (=ecozone V). The ecozones IV and V are referred to the Thuringian and Entomozoacean ecotypes of Becker (in Bandel and Becker 1975). Later, Casier (in Casier and Pr at 1991) recognised also a brackish lagoonal environment characterised by leperditicopid ostracods (=ecozone 0 though the “0” does not exist in the Latin numeration), and Casier et al. (1995) reported ecozones 0 to III to the Eifelian ecotype of Becker (in Bandel and Becker 1975).

Later, Casier and Lethiers (1998a) emended the Eifelian ecotype of Becker (in Bandel and Becker 1975) in order to take into account the great importance of podocopids in that ecotype.

In 2003, Casier replaced the Entomozoacean ecotype by a Myodocopid ecotype because cypridinoid ostracods are frequently associated with entomozoid ostracods in poorly oxygenated environments (Casier 1988a) and because these two super-families belong to the Order Myodocopida.

From 1995 (Casier et al. 1995) onwards, the “ecozones” have been progressively replaced by “assemblages” and the genetically connoted ecotype replaced by the more neutral term “mega-assemblage” (Casier 2004).

### Ecology of Palaeozoic ostracods: present state of expertise

Three mega-assemblages are presently recognised in the Devonian: the Eifelian, the Thuringian and the Myodocopid Mega-Assemblages (Fig. 2).

#### The Eifelian Mega-Assemblage

The Eifelian Mega-Assemblage on continental shelves is composed of four assemblages numbered 0 to III (Fig. 2).

**The assemblage 0:** characterised exclusively by large leperditicopid ostracods, is indicative of lagoonal environments. These ostracods are occasionally associated with Characea (Malec et al. 1987) and this association may indicate brackish waters (Casier and Pr at 1991; Casier et al. 2015).

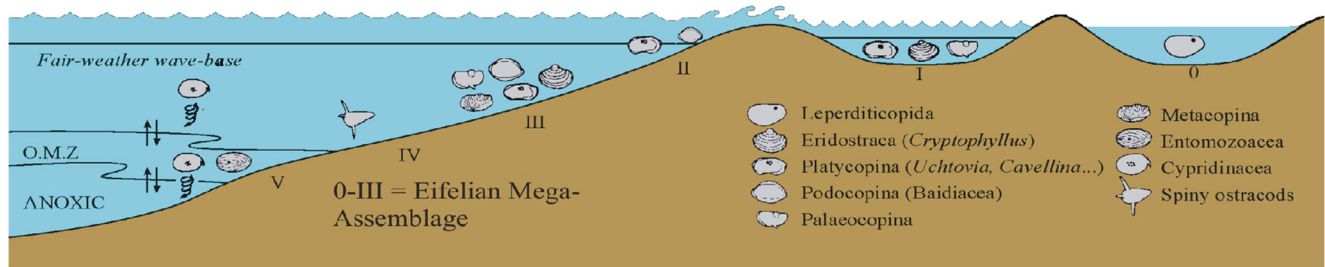
Assemblage 0 is e.g. well represented in the Trois-Fontaines Formation (=Fm) in Belgium and France, and is probably indicative of a wet and warm climate during the early Givetian (Casier et al. 2015). This assemblage is also recognised among others in Germany (Kegel 1933), Poland (Malec et al. 1987) and South China (Wang 1988).

**The assemblage I:** characterised by a very poor diversity, and sometimes by a very great number of specimens. This assemblage is indicative of semi-restricted water environments and the species belong principally to the euryhaline platycopids but also to the metacopids, palaeocopids and Eridostracina. If the salinity is very close to the normal marine level, some podocopids may be present. Today, the Mediterranean Sea, the Marmara Sea and the Black Sea are different examples of semi-restricted environments.

In the Givetian of Belgium and France, the Assemblage I is characterised by one or several species belonging principally to the platycopine genera *Cavellina*, *Coeloenellina* and to the Eridostracina genus *Cryptophyllus* in the Fromelennes Fm (Milhau 1983, Maillet et al. 2013a). This occurrence is indicative of an important change of climatic conditions from wet and warm during the early Givetian (Assemblage 0, see above) to very arid in the late Givetian (Assemblage I) probably related to the Taghanic Event defined by House (1985) (Casier et al. 2015). This biocrisis is marked by the important faunal renewal of ostracods close the middle/late Givetian boundary recognised by Maillet et al. (2013b, 2016) in the Givet type region, in the Ardenne and also in Spain.

The Assemblage I is present in the base of the Famennian of several Belgian sections (Senzeille, Sinsin, Hony, Lambermont). At Sinsin, ostracods are abnormally abundant. In some very rich samples, 98% of the ostracod fauna is composed of only five species, and in one sample, 95% of these ostracods belong to *Ovatoquassilites avesnellensis* (Lethiers, 1973) (Casier and Devleeschouwer 1995). At Senzeille, Assemblage I is present in the base of the lower member of the Senzeille Fm (see Fig. 6e).

Stacked valves of ostracods are sometimes observed in environments characterised by ostracods belonging to the Assemblage I. This arrangement is favoured by the assemblage monospecificity and by the abundance of dissociated valves. Ostracods grow by ten or so moltings and dissociated valves of last moults of the same species mixed during a long period, fitted in (Fig. 3). Such stacked valves are observed in very shallow slightly but continuously agitated waters, by very small waves due to the lapping, on shore of lake or lagoon (Guernet and Lethiers 1989). I have observed such arrangement of valves on the shore of a contemporary sebkha in the Gourara (Algerian Sahara), and also in samples collected in the Shungura Fm (Quaternary) of the Omo Valley in Ethiopia (see Casier and Pr at 1991, pl. 3, Figs. 9 and 10). In the Devonian, stacked valves are abundant e.g. in the very base of the Famennian at Sinsin (Casier and Devleeschouwer 1995). Stacked valves are sometimes present in the Givetian, e.g. in the Terre d’Hauris Fm in Belgium and France (Casier and Pr at 1991). Kesling and Soronen (1957) reported some stacked valves in a Givetian lagoonal environment in the Michigan (USA). But, stacked valves due to small waves related to the lap have been sometimes erroneously



**Fig. 2** Ostracod assemblages and mega-assemblages recognised in the Devonian. The Eifelian Mega-Assemblage is composed of four assemblages numbered 0 to III indicative of lagoonal (Ass. 0), semi-restricted (Ass. I), marine above (Ass. II) or below (Ass. III) fair-weather wave-base or storm wave-base environments. The Thuringian Mega-Assemblage

(IV) is indicative of a deeper calm and maybe colder marine environment, and the Mydocopida Mega-Assemblage (V) is indicative of poorly oxygenated waters (after Casier (1987a), (2008), Casier et al. (1995), Bultynck et al. (2001), etc.)

attributed to the retention of moults (see Fig. 135, p. Q193 in Treatise on Invertebrate Palaeontology (Moore (Ed.) 1961).

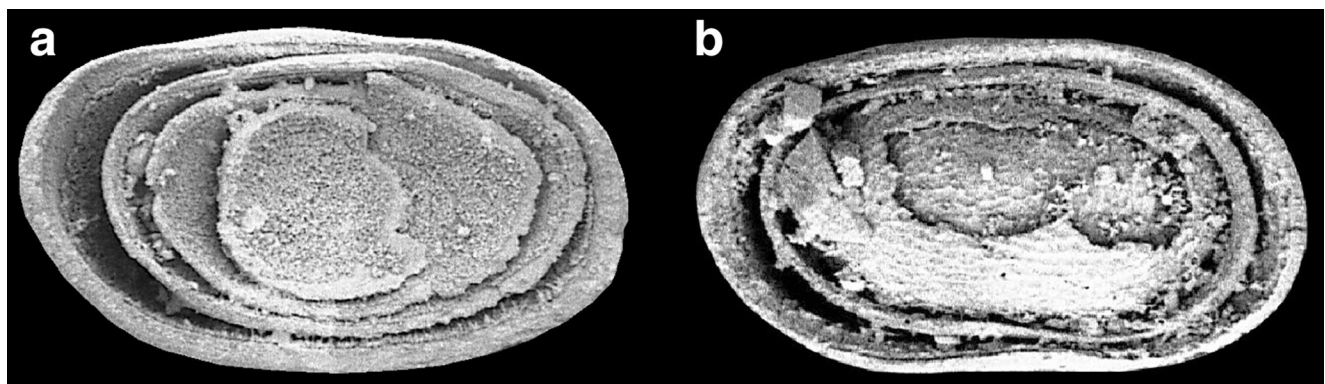
**The assemblage II:** characterised by a moderately diversified ostracod fauna belonging principally to large and thick shelled podocopids and platycopids. Juvenile forms are generally absent and carapaces are frequently broken in this assemblage. The Assemblage II is indicative of very shallow open-marine agitated environments above fair-weather wave base.

In the Givetian and Frasnian of Belgium and France, ostracods of the Assemblage II are associated to widespread biostromal or reefal units with stromatoporoids, rugoses and tabulate corals. Ostracods of the Assemblage II are widespread e.g. in the slope deposits of the red marble reef of the Beauchâteau quarry close to Senzeille (Casier 1988b; see also Fig. 6a). This assemblage is also very frequent in samples collected in the Givetian Mont d’Hauris Fm in Belgium and France (Casier et al. 2011).

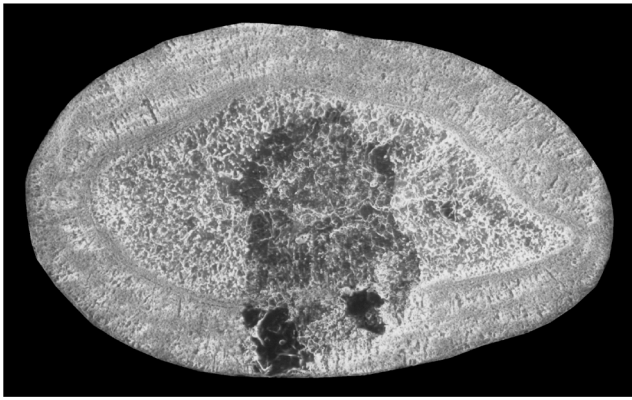
In the Assemblage II, oolites are occasionally present and sometimes they have grown by accretion around an ostracod. I have observed such oolites in the base of the Frasnian in the Tailfer section along the Meuse River in Belgium, and also close to the D/C boundary in the GSSP at La Serre, in the French Montagne Noire (Fig. 4).

**The assemblage III:** most diversified and cosmopolitan ostracod assemblage belonging to the Eifelian Mega-Assemblage. This assemblage contains the majority of ostracod orders (podocopids, metacopids, palaeocopids, platycopids and Eridostracina) and is indicative of environments below fair-weather wave base and sometimes below storm-wave base.

In the Assemblage III, the relative proportion of metacopids and podocopids varies with the deepness water depth: Podocopids conversely to metacopids decrease in number of species and specimens with the deepening and consequently the metacopid/podocopid ratio maybe used as bathymetric indicator (Casier 1987a). This change is probably related to the oxygen content and to the reduction of the agitation of bottom waters (Casier *ibid*), but other factors such as the nature of the substrate, the turbidity, the light penetration, the presence of a flora and the mode of alimentation certainly also play a role. The metacopids are alleged filter-feeders and the podocopids alleged deposit-feeders (Adamczak 1969; Lethiers and Whatley 1994). In the southern border of the Dinant Synclinorium, the Assemblage III is represented e.g. in the Valisettes Fm (Fig. 6b) and in the upper member of the Senzeille Fm (Fig. 6f).



**Fig. 3** Stacked valves of ostracods due to very small waves related to the lap in the base of the Famennian of the Sinsin section (see Casier and Devleeschouwer (1995), for the precise localisation of specimens, the magnifications and the numbers of collection)



**Fig. 4** Oolite having grown by accretion around the ostracod species *Bairdia extenuata* Nazarova, 1951. Upper Famennian, La Serre D/C GSSP (see Casier et al. 2002, for the precise localisation of the specimen, the magnification and the number of collection)

In a deep setting, below storm wave base, only metacopid and palaeocopid ostracods are present, and in this case, the Assemblage III corresponds to the Malvinokaffric ecotype introduced by Lethiers et al. (2001) as demonstrated by the study of ostracods present in the Belen Fm at Pisacavina, in Bolivia (Casier in Racheboeuf et al. 2012). Ostracods described from Bolivia and Argentina (Lethiers et al. 2001; Casier in Racheboeuf et al. 2012; Salas et al. 2013) and from South Africa (Becker et al. 1994) appertain to the Assemblage III of the Eifelian Mega-Assemblage, but are of course characteristic of a Malvinokaffric Realm.

#### The Thuringian Mega-Assemblage

The Thuringian Mega-Assemblage (=Assemblage IV, Fig. 2) is characterised by very thin shelled spiny ostracods belonging principally to the podocopids associated with some metacopids and palaeocopids. They are characteristic of very calm (and probably colder) marine environments below storm-wave base. The characteristic fineness of their carapaces is certainly an adaptation to such environments. They are also cosmopolitan and, compared to the ostracods belonging to other assemblages, they seem to have evolved slowly during the Palaeozoic.

Ostracods belonging to the Thuringian Mega-Assemblage are generally found recrystallised in silica, and after acid processing for the extraction of conodonts. We can surmise that their carapaces are probably destroyed during the processing used generally to extract ostracods, and particularly during the crushing. In limestones, ostracods are frequently extracted by the hot acetolysis method (see Crasquin-Soleau et al. 2005). We can also surmise that their thin shelled carapaces are more frequently destroyed during the diagenesis process. So, I have observed thin shelled ostracods with spiny extensions in thin sections of samples collected at Bou Tchrafine in Morocco, but not in the same samples processed by the acetolysis

method (Casier et al. 2010). I have also found a spiny *Healdia* converted to baryte in a sample collected in the Ermitage Mbr in the Sourd d’Ave section, in Belgium after acid processing for extraction of conodonts (Casier 1987b, Pl. 1, Fig. 9). The thinness of podocopid carapaces in deep water setting explains maybe also the decrease in number of species and specimen of podocopids related to the deepening in the Assemblage III of the Eifelian Mega-Assemblage.

In deep very calm environments, several species of ostracods belonging to the Metacopina develop spines on their carapaces. *Favulella lecomptei spissa* Zbikowska, 1983, and *Polyzygia neodevonica aragonensis* Gozalo 1994, are two examples of sub-species distinguishable only by the presence of spines (see Gozalo 1994, pl. 14, 15) (Casier et al. 2011). Such subspecies are in reality truthful “ecotypes”!

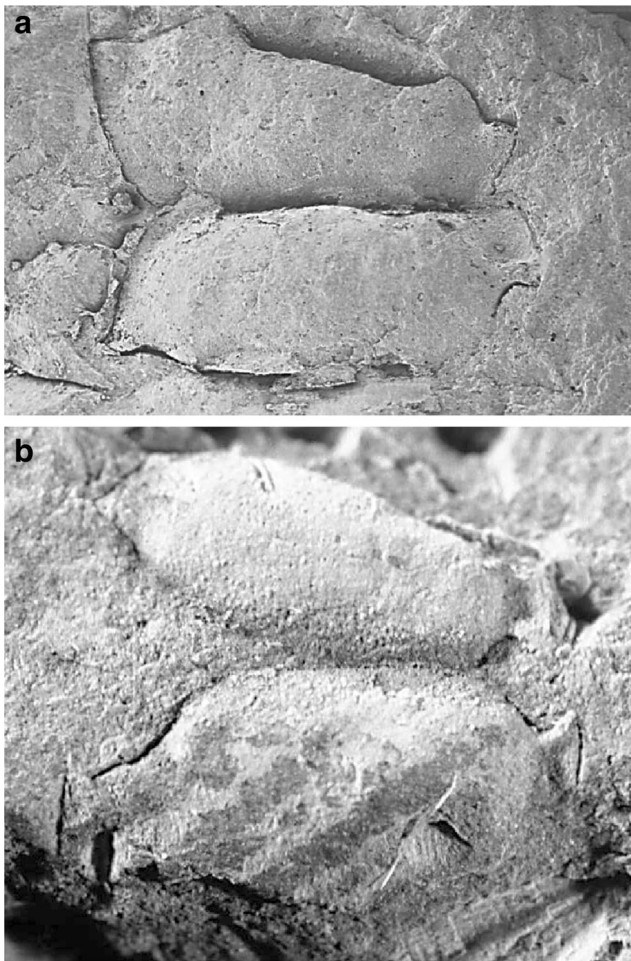
#### The Myodocopid Mega-Assemblage (Fig. 6c, d)

The Myodocopid Mega-Assemblage (=Assemblage V, Fig. 2) is characterised by the presence of Entomozoidea and (or) of Cyprinoidea, and is indicative of poorly oxygenated marine environments.

Cypridinoid ostracods were active swimmers and that is attested by the presence of a large anterior rostrum through which swimming appendages protruded. They are only preserved in poorly oxygenated environments where they are sometimes found in “butterfly position”, valves dissociated but still found together. In this case, they are generally observed with dorsal borders in contact, more rarely with ventral borders (Fig. 5; see also Casier 1988a, Plate 1). A nektoplanktonic mode of life is also attested by their survival during the F/F boundary bioevent in the southern border of the Dinant Synclinorium (see below).

The Entomozoidea are characterised by a finger-print ornamentation conferring to this group their very important biostratigraphic value. But, their mode of life is still in debate. For a majority of ostracodologists, they were also nektoplanktonic but I have developed several arguments in favour of a nektobenthonic mode of life in poorly oxygenated waters (Casier 1988a, 2004). Like Cypridinoid ostracods, they are sometimes found in butterfly position indicative of a very calm environment and of quasi absence of activity on the sea-floor. But, unlike cypridinoid ostracods, entomozoid ostracods are decimated during the F/F boundary bioevent (see below, and Olempska 2002).

The Entomozoidea are cosmopolitan and constitute the most abundant fossil group not only in number of species but also in number of specimens present in the late Frasnian black shale Matagne Fm in Belgium. So, this formation has been formerly called “Assise de la *Buchiola palmata* et de la *Cypridina serrato-striata*” by Mailleux (1912), this last species bringing together a series of entomozoid species. And it is the same case for the German “Cypridinen



**Fig. 5** Cypridinoid (*Palaeophilomedes neuvillensis* Casier, 1988) ostracods in “butterfly” position with the dorsal border in contact (a) and the ventral border in contact (b). They are indicative of the absence of activity on the seafloor (see Casier (1988a), for the precise localisation of the specimens, the magnifications and the numbers of collection)

Schiefers” of Roemer (1851). The so-called Cypridinen group is in reality a series of species belonging to the Entomozoidea.

Figure 6d, e displays ostracods belonging to the Myodocopid Mega-Assemblage in the upper member of the Matagne Fm exposed at Neuville.

### The F/F boundary bioevent in the type region for the definition of the Frasnian and Famennian stages

#### Introduction

The Late Devonian mass extinction is responsible for the definitive disappearance of the largest reefal activity known since the beginning of the Phanerozoic, and having its largest extension during the Givetian (Copper 1994). This extinction

is also responsible for the loss of numerous shallow water marine organisms (see the synthesis of McGhee (1996) and Racki (2005)). For ostracods, the study of the F/F GSSP at Coumiac in the French Montagne Noire, and also of the Devils Gate Pass section in Nevada (USA), has demonstrated that the F/F boundary bioevent can be responsible for the disappearance of almost 80% of all species in the marine realm (Casier et al. 1996; Lethiers and Casier 1999; Casier and Lethiers 2001). There is a consensus that the acme of the Late Devonian mass extinction is related to a hypoxic episode responsible notably for the deposition of the Upper Kellwasser Horizon, in Germany. But, the question of whether there is a regression or whether a transgression close to the F/F boundary is still in debate (Bond et al. 2004; Bond and Wignall 2008). A recent study of brachiopods and corals in the Dinant Synclinorium by Mottequin and Poty (2015) has not recognised a sea-level fall close to the F/F boundary.

The study of ostracods in the southern border of the Dinant Basin, Belgium, has demonstrated that these disappearances are linked to a hypoxic episode responsible for the deposition of the black shale Matagne Fm (Casier 1987a), and also to an important regression (Casier and Devleeschouwer 1995). The hypoxic episode is marked by the presence of ostracods belonging to the Myodocopid Mega-Assemblage (Entomozoidea and Cypridinoidea) and is related to the establishment of an Oxygen Minimum Zone (OMZ) such as this one observed and so-called for the first time by Rhoads and Morse (1971) in the Gulf of California (see also Demaison and Moore 1980). The important regression close to the F/F boundary is on the contrary displayed by the occurrence of a poorly diversified but particularly abundant ostracod fauna (Assemblage I) and also of stacked valves due to very small waves related to the lap in the Sinsin section (Casier and Devleeschouwer 1995).

The Frasnian lithostratigraphical scale of Belgium was revised at the end of the last century by the Belgian national Subcommittee of Stratigraphy (Boulvain et al. 1999), and the Devonian lithostratigraphical scale of Belgium has been summarised by Bultynck and Dejonghe (2001). In the type region for the Frasnian and Famennian stages (southern border of the Dinant Synclinorium, Belgium), the Valisettes Fm, the Matagne Fm and the Senzeille Fm, redefined in these works, are the three formations involved in the F/F boundary bioevent. The latest Frasnian red marble reefs belonging to the Petit-Mont Member (=Mbr) disappear in the base of the Valisettes Fm. The Matagne Fm is composed of two beds (or members), but only the second is concerned (see below), and the Senzeille Fm contains two members not formally defined (Bultynck and Martin 1995; see below). Note that Coen-Aubert (2015, 2016) prefers to distinguish three members (Petit-Mont Mbr, Valisettes Mbr, and an underlying member, the Neuville Mbr) grouped in a new formation, the Champ Broquet Fm.

### Stratigraphic remark concerning the F/F boundary

The position of the F/F boundary in the southern border of the Dinant Basin is not clearly fixed for three reasons and two of which are related to the F/F boundary GSSP: (1) The F/F GSSP has been defined at Coumiac (Klapper et al. 1993) in a highly condensed section containing several hard grounds in the upper Frasnian, and the boundary is even fixed precisely above a hardground (Casier and Pr at 2009); (2) The F/F boundary in the GSSP does not correspond to the entry of *Palmatolepis triangularis* Sanneman, 1955, but in reality to the blooming of the conodont *Palmatolepis ultima* Ziegler, 1958 (Klapper 2007); (3) The lithology is not favourable for the extraction of conodonts in the type region and particularly at Senzeille where the historic F/F boundary has been fixed by Gosselet (1877) in shales. This historic boundary corresponds to the renewing of the macrofauna after the F/F bioevent and, as we will see below, to the return to true marine water conditions after a semi-restricted episode. So, at Senzeille, the boundary is certainly below the base of the upper member of the Senzeille Fm where Bultynck found the first *Palmatolepis triangularis* Sannemann, 1955 (Bultynck and Martin 1995). The boundary is probably also below the top of the lower member of the Senzeille Fm where Gosselet fixed the historic F/F boundary after the recovery of the macrofauna. The F/F boundary is maybe fixed at the base of the lower member of the Senzeille Fm, where the recovery of the benthic ostracods belonging to the Eifelian Mega-Assemblage is observed after the hypoxic episode, or at a minimum of 3 m below the base of the Senzeille Fm, where the recovery of the nekto-benthic Entomozoidea belonging to the Myodocopid Mega-Assemblage is recorded in the Matagne Fm. This level corresponds to the boundary between the *splendens* and *sigmoidale* Zones of the zonation based on Entomozoidea. Note that the last *Palmatolepis linguiformis* M uller, 1956, have been found at the top of the Valisettes Fm in the Neuville section (Bultynck et al. 1998).

### Stratigraphic remark concerning the Matagne Fm

Owing to the parachronology established on Entomozoidea by Rabien (1954) and little modified since then (Groos-Uffenorde et al. 2000), we can state that the black shale Matagne Fm is composed of two temporally distinct beds (or members) in the Dinant Synclinorium (Casier 2013). A diachronic relationship is not supported by the zonation established on that group of ostracods. The first bed (or lower member) cropping out in the vicinity of Frasnes, Mariembourg and Boussu-en-Fagne never exceeds the *reichi* Zone of the zonation based on entomozoid ostracods, and the second bed (or upper member) recognised north in the Neuville railway section straddles the boundary between the *splendens* Zone and the *sigmoidale* Zone. These

two members reflect similar environmental conditions as e.g. is the case for the late Frasnian Lower and the Upper Kellwasser Horizons, in the Kellerwald, Germany. I have even envisaged a correlation with these two beds (Casier 1992). The Entomozoidea association found in the base of the upper member of the Matagne Fm at Neuville is comparable to the one observed in the Upper Kellwasser Horizon in the Schmidt quarry, in the Kellerwald (Casier and Lethiers 1998b).

### Stratigraphic remark concerning the lower member of the Senzeille Fm

At Senzeille, 5.5 m of blackish to bluish shales containing some decalcified nodules separate the Matagne Fm and the former “Senzeille Assise”. This bed corresponds to the unit “G” of Gosselet (1877), and to the “transition shales” of Casier (1992), and contains in its upper part the historic F/F boundary of Gosselet (1877). In 1995, Bultynck and Martin proposed to include these “transition” shales in the base of the Senzeille Fm as an informal member 1. Nevertheless, this proposition was not retained by Bultynck and Dejonghe (2001) in their paper on the lithostratigraphic scale of the Devonian of Belgium.

### Succession of ostracod assemblages close the F/F boundary in the southern border of the Dinant synclinorium (Fig. 6)

The succession of ostracod assemblages recognised close to the F/F boundary in the southern border of the Dinant Synclinorium is reported on a synthetic log (Fig. 6) gathering sections located in the vicinity of Senzeille where the historic F/F boundary has been fixed in a railway section by Gosselet (1877). Unit thicknesses are not respected in this synthetic log.

The ostracod fauna present in the Frasnian Valisettes Fm belongs to the Assemblage III of the Eifelian Mega-Assemblage. Figure 6b displays the ostracods extracted from the Neuville railway section (Casier 2003). More precisely, these ostracods have been extracted from samples collected in greenish and purplish shales with rare calcaro-argilaceous nodules capped by a 50 cm thick series of dark nodular limestone beds. The ostracod fauna is rich and diversified in the Valisettes Fm: Metacopid, podocopid and paleocopid ostracods are each represented by five species and the Eridostracina by one species. The environment was marine below fair weather wave base.

The ostracod fauna in the Petit-Mont Mbr straddling the Valisettes Fm and the underlying Neuville Fm belongs to the Assemblage II of the Eifelian Mega-Assemblage. Figure 6a displays the ostracods extracted from samples collected in the slope deposits of the red marble reef of the Beauch ateau quarry (Casier 1988b), and more precisely in the limestone beds extending laterally. The core of the reef is not favourable for the retaining or

for the preservation of ostracods. The ostracod fauna in the Beauchâteau quarry is largely dominated by large and thick shelled podocopids belonging principally to the genera *Bairdia*, *Bairdiocypris* and *Microcheilinella*. See also the red marble reef of the Beauchâteau quarry in Suttner et al. (2016, pp. 88–89).

The ostracod fauna in the upper member of the Matagne Fm belongs exclusively to the Myodocopid Mega-Assemblage. The entomozoid and cypridinoid ostracods on Fig. 6c, d have been also extracted from samples collected in the Neuville railway section (Casier 2003) with the exception of the Cypridinoidea of Fig. 6d collected at Senzeille in a research trench dug close to the former stratotype for the F/F boundary (Casier 1992). The Matagne Fm in the Neuville section is represented by 5.5 m of fine dark-greenish-brown to black shales characterised by the presence of a particular fauna principally composed of *Buchiola* (Pelecypoda), lingulids and chonetids (Brachiopoda), and entomozoids and cypridinoids (Ostracoda). This section is exceptional because the paroxysmal phase of the F/F boundary bioevent may be fixed with precision in a relatively thick and continuous series, between the *splendens* Zone and the *sigmoidale* Zone of the parachronology based on entomozoid ostracods. The boundary between these two zones corresponds probably to the maximum of hypoxia, and only the cypridinoid ostracods living in the upper part of the water-column survived this event in the investigated section. As mentioned above, the association found in the base of the upper member of the Matagne Fm at Neuville is comparable to the fauna found in the Upper Kellwasser Horizon in the Steinbruch Schmidt quarry in the Kellerwald, Germany (Casier and Lethiers 1998b).

In the top of the Matagne Fm at Senzeille, two samples (numbered S86 and S92 in Casier 1992) contain benthic ostracods announcing an improvement of the condition of oxygenation.

The ostracod fauna in the base of lower member of the Senzeille Fm (=unit G of Gosselet 1877; transition shales of Casier 1992; member 1 of Bultynck and Martin 1995) belongs again to the Eifelian Mega-Assemblage. The ostracods on Fig. 6e have been extracted from samples collected in two trenches dug very close to the historic F/F boundary, in reality on the other side of the rails of the former railway. In 1992, I have observed the presence of an abnormally very rich and poorly diversified, but at this time undeterminable, ostracod fauna in the samples collected in the base of this member, and below the F/F historic boundary. Such an association but with very well preserved specimens has been found more recently east, first at Sinsin (Casier and Devleeschouwer 1995, Pl. 1–3), and later in the Hony and Lambermont sections in the vicinity of Liège (unpublished). The ostracods present in the base of the lower member of the Senzeille Fm belong to the Assemblage I of the Eifelian Mega-Assemblage, and they are consequently indicatives of semi-restricted water conditions. Nevertheless, the environment was not so shallow compared

**Fig. 6** Succession of assemblages (a–f) of ostracods close to the F/F boundary in the vicinity of Senzeille railway section where the historic boundary has been fixed by Gosselet (1877). **a** Ostracods from the Petit Mont Mbr in the Beauchâteau quarry (see Casier 1988b, for names, localisations, magnifications and numbers of collection of specimens). **b** Ostracods from the Valisette Fm in the Neuville railway section (see Casier 2003, 2008). **c** Ostracods from the base of the second member of the Matagne Fm in the Neuville railway section (see Casier 2003, 2008). **d** Ostracods from the upper part of the second member of the Matagne Fm at Neuville and Senzeille (see Casier 1989). **e** Ostracods from the base of the lower member of the Senzeille Fm in the west research trench at Senzeille (e1 = *Ovatoquassilites avesnellensis* (Lethiers, 1973). S201. IRScNB n° b6806, ×15; e2 = *Healdianella? tenuistriata* Casier and Devleeschouwer 1995. S201. IRScNB n° a2845, ×25; e3 = *Glezeria minuta* Casier and Devleeschouwer 1995. IRScNB n° b6807, ×33; e4 = *Knoxella fammentiensis* Casier and Devleeschouwer 1995. S205. IRScNB n° b6808, ×55; e5 = *Cryptophyllus sinsinensis* Casier and Devleeschouwer 1995. S98. IRScNB n° a2818, ×15 (see Casier 1992, for the localisation of specimens) **f** Ostracods from the upper part of the lower member and of the base of the upper member of the Senzeille Fm from Senzeille (see Casier 1989)

to Sinsin because in contrast to this section, stacked valves of ostracods are not found at Senzeille.

In the middle and upper part of the lower member and in the upper member (=Senzeille shales *ss* of Casier 1992; member 2 of Bultynck and Martin 1995) of the Senzeille Fm, ostracods become again very diversified (Fig. 6f). They belong to the Assemblage III of the Eifelian Mega-Assemblage and are indicative of the return to true marine conditions below but close to fair-weather wave-base as indicated by the proportion of metacopids and podocopids and the abundance of Paraparchitoidea. The historic F/F boundary of Gosselet (1877) corresponds to the renewal of the macrofauna after the F/F boundary bioevent but above all to the reappearance of true open-marine conditions at Senzeille.

## Conclusions

Three mega-assemblages and six assemblages of ostracods numbered 0 to V are recognised in the Devonian. They are indicative of lagoonal environments, semi-restricted environments and marine environments above and below fair-weather wave-base or storm wave-base. The factors controlling the distribution of ostracods in the Devonian are principally the energy, the salinity, the oxygenation and the temperature of waters. These ostracod assemblages and mega-assemblages are also recognised in the Silurian and the Carboniferous.

The succession of ostracod assemblages close to the F/F boundary in the type region for the definition of these two stages proves indubitably that the Late Devonian mass extinction is related to a period of hypoxia (installation of an oxygen minimum zone) followed by a regression, confirming our earlier statements, with the exception that now, we can surmise that these two events are linked. The hypoxia is marked by the presence of ostracods belonging to the



<p>                   Last <i>P. linguiformis</i>                   Noconodonts             </p>	<p>                 Valisettes Fm             </p>	<p>                 Eifelian Mega-Assemblage Ass III             </p>	<p>                 Eifelian MA Ass II                  Petit Mont Mbr             </p>		<p>                 splendens Z             </p>
<p>                 Noconodonts             </p>	<p>                 Matagne Fm             </p>	<p>                 Upper mbr             </p>	<p>                 Myodocapid Mega-Assemblage             </p>		<p>                 sigmoidale Z             </p>
<p>                 Noconodonts             </p>	<p>                 Senzeille Fm             </p>	<p>                 L mbr      Upper mbr             </p>	<p>                 Eifelian Mega-Assemblage Ass III             </p>		<p>                 nehdensis Zone             </p>

Myodocopid Mega-Assemblage (Entomozoidea and Cyprinoidea) in the upper member of the black shale Matagne Fm, and the sea-level fall is attested by the occurrence of ostracods indicative of semi-restricted water conditions (Assemblage I of the Eifelian Mega-Assemblage) in the base of the lower member of the Senzeille Fm, and below the historic F/F boundary. The acme of the extinction corresponds to the *splendens* Zone/*sigmoidale* Zone boundary of the parachronology based on Entomozoidea. In the southern border of the Dinant synclinorium, the sea-level fall is observed at Senzeille, Hony and Lambermont and particularly at Sinsin where stacked valves due to very small waves related to the lap are observed in thin plates and after the extraction of ostracods by the acetolysis method. The historic boundary corresponding to the recovery of the mega-fauna after the acme of this extinction period marks the return to true marine water conditions after the semi-restricted marine episode. In reality, the palaeoecological study of ostracods displays that intrinsic factors linked to the palaeogeography and consequently to the global tectonic regime are the most important factors responsible for the Late Devonian mass extinction (see also Racki 1998). The gap observed in numerous sections at the F/F boundary level, including the F/F GSSP at Coumiac, results probably from these palaeogeographic modifications. Nevertheless, other factors such as the spread of vascular plants resulting in higher pedogenic weathering rates and increase of the flux of soil-derived nutrients to marine ecosystems (Algeo et al. 1995) or combustion of land vegetation (Kaiho et al. 2013) may have also played a role during the Late Devonian mass extinction.

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#### Compliance with ethical standards

**Conflict of interest** The author declares that he has no conflict of interest.

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