

# The mode of life of Devonian entomozoacean ostracods and the Myodocopid Mega-Assemblage proxy for hypoxic events

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## Abstract

The mode of life of entomozoacean ostracods, which belong to the Myodocopida, is controversial. It is generally assumed that they are pelagic, more precisely planktonic or nekto-planktonic, and that their presence is indicative of deep environments. However, a purely morphological study is not sufficient to determine their mode of life. Their relationship with the substrata and other animals, and their response to major environmental changes must be taken into account. These data confirm a swimming mode of life for all the entomozoaceans, and suggest that a nekto-benthic lifestyle, in poorly oxygenated, but not necessarily deep, environments is more probable than a planktonic mode of life. The presence of a Myodocopid Mega-Assemblage proxy for hypoxic events, seems more useful than the differentiation of an "Entomozoid ecotype".

**Key-words:** Ostracods - Entomozoacea - Devonian - Mode of life - Palaeoecology.

## Résumé

Les Entomozoacea constituent une super-famille d'ostracodes appartenant à l'ordre des Myodocopida. Ils ont en commun une taille relativement grande, des valves égales peu calcifiées, et une ornementation souvent comparée à des empreintes digitales. Elle leur confère une grande valeur biostratigraphique. La plupart des ostracodologues estiment qu'ils étaient pélagiques et plus précisément planctoniques ou necto-planctoniques, et que leur abondance dans les sédiments témoigne par conséquent d'une grande profondeur de dépôt. Mais l'étude morphologique seule ne suffit pas pour déterminer leur mode de vie. Leur relation avec le substrat et avec les autres organismes, ainsi que leur comportement lors des changements environnementaux majeurs doivent aussi être pris en considération. Ils montrent que les Entomozoacea étaient plutôt necto-benthiques et opportunistes dans des milieux pauvres en oxygène dissous, mais pas nécessairement profonds. Un Mega-Assemblage à Myodocopida caractérisé par la présence d'Entomozoacea et (ou) de Cypridinacea (= Assemblage V de CASIER *et al.*, 1985; CASIER, 2003) peut servir d'indicateur pour les événements hypoxiques dans le Dévonien.

**Mots-clés:** Ostracodes - Entomozoacea - Dévonien - Mode de vie - Paléocologie.

## Introduction

Ostracods are ecologically sensitive crustaceans, and their study provides valuable information about environmental changes, particularly in the Palaeozoic. For example, studies of more than 40,000 ostracods across the Frasnian - Famennian (F/F) boundary from several sections worldwide confirms that the upper Devonian event was one of the largest Phanerozoic extinctions for ostracods. Approximately 75 percent of all marine ostracod species went extinct close to the F/F boundary (LETHIERS & CASIER, 1999a; CASIER & LETHIERS, 2001), as a result of sea-level changes (CASIER & DEVLEESCHOUWER, 1995) and a hypoxic event (CASIER, 1987a). The survival of several species demonstrates that very shallow marine environments and surface waters were not affected during the extinction (CASIER, 2003).

Entomozoacean ostracods played an important role during the Late Devonian mass extinction. However, their mode of life is controversial. Entomozoaceans are usually regarded as pelagic, more precisely planktonic or nekto-planktonic. The goal of our paper is to demonstrate that a nekto-benthic mode of life in poorly oxygenated environments is more probable for this group of ostracods.

The Super-family Entomozoacea PRIBYL, 1951 belongs to the Order Myodocopida SARS, 1866. Entomozoaceans are characterized by relatively large carapaces with weakly calcified sub-equal valves (Fig. 1 and Pl. 1, Figs 9, 10, 12-15 show some species of entomozoaceans), the presence in some species of an adductor sulcus (= nuchal furrow), and a ribbed ornamentation frequently compared to fingerprints (see OLEMPSKA, 1992, for a detailed study of their shell structure). Entomozoaceans were abundant from the Silurian to the Upper Carboniferous.

## Previous statements concerning the mode of life of entomozoaceans

MATERN (1929) considered the majority of entomozoaceans to be active swimmers. KUMMEROW (1939) and RABIEN (1954) compared entomozoaceans to modern Halocypridacea and surmised a nektonic or planktonic

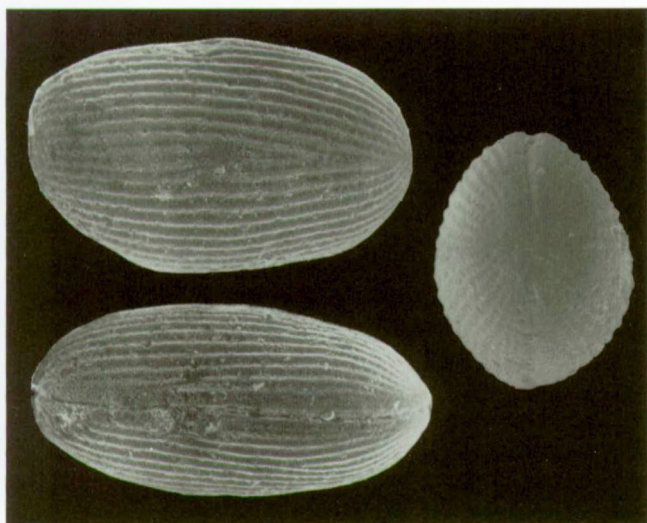


Fig. 1 — *Richterina (Volkina) zimmermanni* (VOLK, 1939). An example of streamlined entomozocean in lateral, dorsal and anterior view. Matagne Formation. Boussu-en-Fagne, Belgium. Collection IRScNB n° a1211. x50.

life habit for this group. On the contrary, the discovery of thick shelled silicified carapaces of entomozoceans led BLUMENSTENGEL (1965, 1973) to suggest that they were heavily calcified and consequently that they were benthic organisms. BECKER (1971) discovered a highly calcified carapace of entomozocean in the Belgian Frasnian, and also concluded that some entomozoceans displayed a benthic mode of life. KOZUR (1972) arrived to the conclusion that they were benthic psychrosphaeric ostracods.

Referring to TRIEBEL (1941), GRÜNDEL, (1962, 1965) and BECKER (1976), GOODAY (1983) summarised the morphological evidence for a planktonic life habit for entomozoceans: 1. the presence of a thin, weakly calcified, often streamlined carapace; 2. a convex ventral margin, and 3. the tendency of the carapace to be rounded with a high surface-volume ratio. In addition, GOODAY (*Ibid.*) suggested that the presence of flange-like ribs of some species may increase the surface area of the shell and retard its sinking velocity, and that their worldwide distribution, together with their abundance in facies which are often virtually devoid of other fossils, are supplementary arguments for a planktonic existence. However, GOODAY (*Ibid.*) noted that the carapace morphology of entomozoceans provides no clear evidence for either a planktonic or benthic existence, and he concluded that both these life habits may have been represented within the group. He compared some species of entomozoceans with modern species belonging to the Thaumatoocyprididae and considered that there is no convincing morphological basis for rejecting the hypothesis that at least some entomozoceans were benthic or nektobenthic.

After the study of entomozoceans present in the Matagne black shale Formation, in Belgium, CASIER

(1987a,b, 1988c) arrived to the conclusion that entomozoceans were probably nektobenthic, and adapted to survive in poorly oxygenated, but not necessary deep, environments. However this statement was not supported by GROOS-UFFENORDE & SCHINDLER (1990), for whom a nektobenthic mode of life for entomozoceans cannot be assumed because they have not been affected during global events, particularly the Upper Kellwasser Event in the Late Devonian. Their abundance in the Upper Kellwasser Horizon, which according to GROOS-UFFENORDE & SCHINDLER (1990) lacks benthos, and their rapid evolution are supplementary arguments against a nektobenthic lifestyle. Conversely, and also in the Proceedings of the Tenth International Symposium on Ostracoda, WILKINSON & RILEY (1990) arrived at the conclusion that entomozoceans present in five marine horizons in the Namurian of Northern England were nektobenthic component of the dysaerobic community. The fauna associated with the Namurian entomozocean in northern England represents low diversity high-abundance assemblages typical of a late Palaeozoic dysaerobic environment, and conclusively WILKINSON & RILEY (*Ibid.*) considered the entomozocean an integral opportunistic vagrant nektobenthic component of the dysaerobic assemblage, colonizing during brief spells when the oxygen level was suitably high.

Furthermore in the Proceedings of the same symposium, BECKER & BLESS (1990) considered CASIER (1987a,b)'s argument that entomozoceans may have a nektobenthic, nearshore lifestyle to be inconclusive. They did not observe mixed Eifelian and entomozocean assemblages, and consider this to be evidence that the entomozoceans did not live in near-shore environments.

Finally, OLEMPKA (1992) suggested that the extremely fragile thin ornamentation over the whole carapace of entomozoceans is apparently inconsistent with a benthic mode of life, and that the extremely high flanges may be an adaptation to a planktonic life habit. However, for several species with rather heavily calcified shells and relatively short flanges, OLEMPKA (1992) suggested that an epiplanktonic as well as a planktobenthic life habit is conceivable. It is herein suggested that the presence of longitudinal canals in the carapace of some entomozoceans may have assisted in the exchange of respiratory gases and such a function could have been important for entomozoceans in stagnant and possibly dysaerobic waters.

#### No argument relevant for a benthic mode of life for the entomozoceans

No particular evidence points conclusively to a genuine benthic mode of life for the entomozoceans. Generally, the principal argument for a benthic life habit is the presence of well calcified and silicified carapaces in some specimens, which has led some authors to suggest that some or all entomozoceans possessed a heavy, thick calcified carapace. The epigenesis in silicon dioxide is

frequent during the fossilisation, and there is no doubt that the heavy calcification of rare carapaces is related to the same phenomenon. The heavy calcified carapace discovered by BECKER (1971) in the access path to the Lion quarry, Belgium, is probably an example of *Entomoprimitia (E.) concentrica* (MATERN, 1929), a very abundant species in the Belgian late Frasnian. Such discoveries prove only that the carapaces of entomozoceans were relatively thick, a feature demonstrated recently by OLEMPKA (1992). This author confirmed LANGER (1973)'s statement that the carapace of entomozoceans consists of a thin outer layer which formed the ornamentation, and a thicker more complicated inner layer. The ornamentation on the upper surface of the inner layer was generally erroneously interpreted to represent the ornamentation on the internal surface of the valve (OLEMPKA, *Ibid.*). In other words, the "internal" moulds of authors showing the ornamentation corresponds really to exfoliate carapaces. It is undoubtable that only the outer layer of the carapaces of entomozoceans were weakly calcified, an adaptation to a swimming life habit. The flange-like ribs strengthening the carapace displayed by some species belonging to the genus *Richterina* confirm this.

One argument for a genuine benthic mode of life for entomozoceans, would be the absence of a rostral incisure through which swimming appendages can protrude (GOODAY, 1983). RABIEN (1954) suggested that the antero-ventral curvature of the carapace observed in some entomozoceans might correspond to such a structure, but GOODAY (1983) demonstrated that the same curvature observed in the recent thamatocypridids bears no obvious relationship to the first and second antennae, the swimming appendages. However, the absence of a rostral incisure is not an argument for a genuine benthic mode of life, because that structure lacks in numerous recent swimming ostracods (GOODAY, *Ibid.*).

#### **No argument relevant for a nekto planktonic mode of life for the entomozoceans**

The weakly calcified, sometimes streamlined carapaces *e.g.*: *Richterina (V.) zimmermanni* (VOLK, 1939) (see Fig. 1), occasionally with postero-dorsal spines (possibly used for the balance of the valves and for the stabilisation of the carapaces *in e.g.* some species of *Entomoprimitia* and *Franklinella*), with flange-like ribs (strengthening the carapace and used probably for aerofoils *in e.g.* *Richterina (R.) goodayi* OLEMPKA, 1992), with longitudinal canals (lightening the carapace; see OLEMPKA, 1992, fig. 8), and with antero-ventral spurs (a structure incompatible with a benthic mode of life in the genus *Franklinella*), indicate a swimming life habit for entomozoceans, but not necessary a nekto planktonic mode of life.

A worldwide distribution of entomozoceans would be an argument for a nekto planktonic mode of life, however this affirmation is overstated: several species are known from Belgium to the Russian Platform, and North Africa but the relationships with Southern France, China and

North America are limited to rare species, even though all these regions were close during the Late Devonian. Several indisputable benthic species belonging *e.g.* to the podocopid ostracods show more widespread geographic distributions compared to that of entomozocean species!

The abundance of entomozoceans in facies which are often virtually devoid of other fossils is another false argument. Entomozoceans are always associated with other ostracods or animals. For example, in the Matagne black shale Formation of Belgium, and in the Cypridien Schiefers of Germany, entomozoceans were always associated with palaeocopid ostracods belonging to the Hollinacea and the Kirkbyacea, and also with bivalves and brachiopods, including lingulids (SARTENAER, 1974; RABIEN, 1954). In the more oxygenated environment of the upper part of the Valisette Formation, formerly exposed in the Senzeille section, Belgium, entomozoceans are associated with diverse fauna including brachiopods, solitary corals, and Eifelian ecotype ostracods, including podocopids, platycopids, metacopids and palaeocopids (CASIER, 1989). Recently we have also demonstrated that entomozoceans are mixed with numerous ostracods of the Eifelian ecotype in the late Frasnian Upper Kellwasser Horizon of the Schmidt quarry parastratotype in the Kellerwald, Germany (CASIER & LETHIERS, 1998), contrary to GROOS-UFFENORDE & SCHINDLER (1990)'s statement.

The third argument for a nekto planktonic mode of life is the rapid evolution of the entomozoceans. Their apparently rapid evolution is in reality linked to their distinctive fine ornamentation. Ostracods are generally of poor biostratigraphic value in the Palaeozoic since criteria of determination are insufficient. They are generally smooth, and due to poor preservation and difficulties of extraction, internal structures of carapaces (hinge, muscle scars...) are only very rarely observable. In addition their morphology is highly controlled by environments and convergent species are frequent. For these reasons numerous species and genera display very long stratigraphic ranges. For example, the podocopid genus *Bairdia* Mc COY, 1844, is recognized from the Ordovician to the Recent! In the Devonian, only the thlipsuraceans, with their strong ornamentation, the spiny ostracods of the Thuringian ecotype of BECKER (*in* BANDEL & BECKER, 1975), and the entomozoceans with their delicate ornamentation comparable to finger prints, have a biostratigraphic value. However, without ornamentation, the number of species distinguishable among the entomozoceans would be considerably reduced, and consequently their apparent rate of evolution would be comparable to the rate of evolution observed for the majority of other ostracods!

#### **A nekto benthic mode of life in dysaerobic environments is the most probable for entomozoceans**

The presence of homoplastic species in the entomozoceans (*e.g.* some *Entomoprimitia* resemble paraparchita-

cean ostracods) is an argument in favour of a relationship with the substrate (CASIER, 1992). OLEMPKA (1992) observed an outermost ridge in some entomozoaceans, another interesting example of convergence. This ridge is comparable to the adventral structure, which continues round the entire valve margin in the palaeocopids, and a nektobenthic life habit is frequently assumed for representatives of this group. GROOS-UFFENORDE (1984) observed that "*Entomoprimitia*" sandbergeri (MATERN, 1929) displays such a structure, and suggested that the species be excluded from the entomozoaceans and moved to the palaeocopids!

As mentioned before, in the Matagne black shale Formation, Belgium, and the Cypridien Schiefers, Germany, entomozoaceans were always associated with palaeocopid ostracods belonging to the Hollinacea and the Kirkbyacea, and also with bivalves (*Buchiola*) and brachiopods (Lingulids, *Chonetes*, *Ripidiorhynchus*, *Ryocarrhynchus* etc...), and it is indisputable that these taxa lived in the same environment. The mode of life of lingulids is well known because they are still alive, and the life habit of chonetaceans is easy to imagine because they displayed spines for the fixation on a muddy substrate. A nektobenthic mode of life is assumed for some palaeocopids (HARTMANN, 1963; BECKER & BLESS, 1990). In fact, all these organisms were adapted to survive in poorly oxygenated environments and this was the case for entomozoaceans. Their weakly calcified carapace might be an adaptation to aid survival in poorly oxygenated, calm waters. OLEMPKA (1992) suggested that the presence of longitudinal canals observed in the carapace of some entomozoaceans may have assisted in exchange of respiratory gases and such a function could have been important for entomozoaceans in dysaerobic waters.

In short-term, dysoxic conditions, entomozoaceans were poorly diversified. For instance, in the lower Frasnian (*punctata* conodont Zone) observed in the Sourd'Ave section in Belgium, and in the Tempiute Mountain in Nevada, only one species belonging to the genus *Franklinella* has been recorded (CASIER, 1987b; CASIER in SANDBERG *et al.*, 1997). However, when such conditions persisted for a long time, for example in the Belgian Matagne Formation or in the German Cypridien Schiefers, entomozoaceans displayed a gradual diversification, inducing the development of large forms, inconsistent with a nektoplanktonic mode of life.

Our recent study of ostracods present in the late Frasnian of Belgium confirms this life habit (CASIER, 2003). The following assemblages are recognized on the southern flank of the Neuville Massif, within the Dinant Basin (Pl. 1): 1. In the Valisettes Formation enclosing the reef of the Beauchâteau quarry, the ostracod fauna is largely dominated by deposit-feeding thick shelled podocopids indicative of well oxygenated water conditions between fair-weather and storm wave bases; 2. In the upper part of the Valisettes Formation outcropping in the Neuville railway section, ostracods belong to the same assemblage (Assemblage III of CASIER, 1987a; see also CASIER &

PREAT, 2003, fig. 3) which is now dominated by filter-feeding metacopids and palaeocopids. The preponderance of filter-feeding relative to deposit-feeding ostracods is considered to signal the start of an anoxic trend (WHATLEY, 1991; LETHIERS & WHATLEY, 1994), and it is most likely related to the increase in water-depth, which, in turn, would have been responsible for the termination of the reef development as was postulated on basis of detailed sedimentological analysis (BOULVAIN & HERBOSCH, 1996); 3. So extensive was the hypoxia at the Valisettes Formation - Matagne Formation boundary, that ostracods belonging to the benthic Assemblage III disappeared abruptly, and were replaced in the black shales of the overlying Matagne Formation by opportunistic entomozoaceans and by cypridinaceans (Assemblage V of CASIER, 1987a; see also CASIER & PREAT, 2003, fig. 3). These myodocopid ostracods abruptly disappeared 3.5 m below the Frasnian - Famennian boundary in the Neuville railway section, during the peak of anoxia, even though *Palaeophilomedes neuwillensis* CASIER, 1988a, an undisputable nektoplanktonic cypridinacean, survived. The ostracod recovery in the Neuville railway section is marked by the successive entry of *Franklinella sigmoidalis* MULLER-STEFFEN, 1964, and "*Entomoprimitia*" sandbergeri (MATERN, 1929). The most important argument for a nektobenthic mode of life is that the entomozoaceans are affected by extinction events, contrary to the suggestion of GROOS-UFFENORDE & SCHINDLER (1990).

Further evidence is provided by the study of ostracods in the upper Kellwasser Horizon, close to the Frasnian - Famennian boundary, in the Schmidt quarry parastratotype (Kellerwald, Germany). In this horizon, the relative proportions of ostracods belonging to the Eifelian ecotype and to the entomozoaceans reflect variations in the oxygen content of bottom waters, as suggested by variations of the total organic carbon contents (TOC) (CASIER *et al.*, 1999). Entomozoaceans undoubtedly became extinct during the Late Devonian mass extinction in the Schmidt quarry.

Finally, OLEMPKA (2002) also displayed that entomozoaceans became extinct close to the Frasnian - Famennian boundary in the Plucki section in the Holy Cross Mountains, Poland displaying their persistent anoxic deposition in the *linguiformis-triangularis* interval (BOND *et al.*, 2004).

### The Myodocopid Mega-Assemblage

On the basis of the carapace morphology, BECKER (*in* BANDEL & BECKER, 1975) differentiated three ostracod ecotypes (= Ökotypen) for the Devonian, including the "entomozoid ecotype". Since then, cypridinacean ostracods have been discovered in the Frasnian of Germany (BUGGISCH *et al.*, 1983; BECKER & BLESS, 1987), of Belgium (CASIER, 1988a), of France (LETHIERS & CASIER, 1995), and of Poland (OLEMPKA, 2002) (Fig. 2 and Pl. 1, Fig. 11 show a Cypridinacea). Considering that the superfamilies Cypridinacea and Entomozoacea both belong to



Fig. 2 — *Palaeophilomedes neuvillensis* CASIER, 1988. An example of Cypridinacea. Specimen discovered by T. BECKER, in the La Serre coupe C in the Montagne Noire, France. Collection University of Paris 6 n° P6M 1836. x16.5.

the Myodocopida, and, sharing the opinion of BECKER & BLESS (1987) that during the Devonian they lived in the same environments, we suggested it more appropriate to replace the “entomozoid ecotype” by a “myodocopid ecotype” (CASIER, *et al.*, 1985). This was an error of judgment. The recent study of ostracods present in the Neuville railway section (CASIER, 2003) has shown that on the contrary to entomozoaceans, cypridinoid ostracods were not affected during the Late Devonian mass extinction. Moreover, unlike entomozoaceans, cypridinoid ostracods are sometimes found in environments devoid of other ostracods and fossils. Consequently we suggest that not all cypridinaceans and entomozoaceans shared the same life strategy during the Devonian: entomozoaceans were nektobenthic and opportunists in poorly oxygenated environments, whereas all or a part of the cypridinaceans lived in an upper layer of water, maybe close to the surface. Consequently, and by definition, they were not members of the same ecotype, and the “entomozoid ecotype” of BECKER (*in* BANDEL & BECKER, 1975) remains valid but not as emended by the same author in 2001 in order to include the cypridinaceans. In order to distinguish assemblages, a “Myodocopid Mega-Assemblage” characterized by the presence of entomozoaceans and (or) cypridinaceans (= Assemblage V of CASIER *et al.*, 1985; see also fig. 3 *in* CASIER & PRÉAT, 2003) is used in this case, rather than an ecotype, since this removes

ambiguity, especially as the usage of the term ecotype seems to be totally inappropriate in this case. In fact the term ecotype describes a group of plants, more rarely of animals, within a single species, and adapted genetically to a particular habitat but able to cross freely with other ecotypes of the same species (ABERCROMBIE *et al.*, 1980)!

For the same reason, we propose to differentiate an Eifelian Mega-Assemblage constituted of several assemblages (Assemblages 0 to III in CASIER, 1987a; see also CASIER & PRÉAT, 2003, fig. 3) and a Thuringian Mega-Assemblage (= Assemblage V *Ibid.*).

## Conclusions

A purely morphological study is not sufficient to determine the mode of life of entomozocean ostracods. Their relations with the substrate and with other animals, and their response to major environmental changes must be taken into account. These data confirm a swimming life habit for the entomozoaceans, and suggest that a nektobenthic mode of life in poorly oxygenated environments, is more probable than a planktonic or nektoplanktonic mode of life for this group.

The distinction of a “Myodocopid Mega-Assemblage” characterising poorly oxygenated water seems preferable and more useful than the differentiation of an “Entomozoid ecotype” or a “Myodocopid ecotype”, since the term “ecotype” seems inappropriate. Moreover, species belonging to the cypridinaceans and the entomozoaceans did not necessarily share the same environment. This is proved by the fact that cypridinaceans are sometimes found alone (probably during period of intense anoxia) and by the fact that entomozoaceans became extinct during the late Frasnian event whilst cypridinaceans were unaffected by this extinction.

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#### PLATE I

Generalized section of the Frasnian - Famennian boundary beds and their ostracod faunas in the type area (Dinant Basin, Belgium). Most representative ostracod species recovered are shown in successive faunas. The succession of assemblages around the Frasnian - Famennian boundary (= FFB) suggests that the Late Devonian mass extinction was principally linked to a regressive-regressive cycle, and to an anoxic event. The transgression was progressive and culminated below the FFB as suspected by JOHNSON *et al.* (1985); the regression was more rapid and important. O.M.Z. = oxygen minimum zone. See also comments in the text. More details about these ostracod faunas can be found in: CASIER & DEVLEESCHOUWER (1995) for ostracods collected in the Sinsin section (Figs. 1-8); CASIER (2003) for ostracods collected in the Neuville railway section (Figs. 9-22); CASIER (1988b) for ostracods collected in the Beauchâteau quarry (Figs. 23-30). The survival of several species and among them of *Ovatoquassilites avesnellensis* (LETHIERS, 1973) (=Fig. 5) and of the cyprinidacean *Palaeophilomedes neuvillensis* CASIER, 1988 (Fig. 11) shows that very shallow marine environments and surficial waters were not touched during the Late Devonian mass extinction. Ostracods are deposited in the Department of Palaeontology (section Micropalaeontology) of the Royal Belgian Institute of natural Sciences.

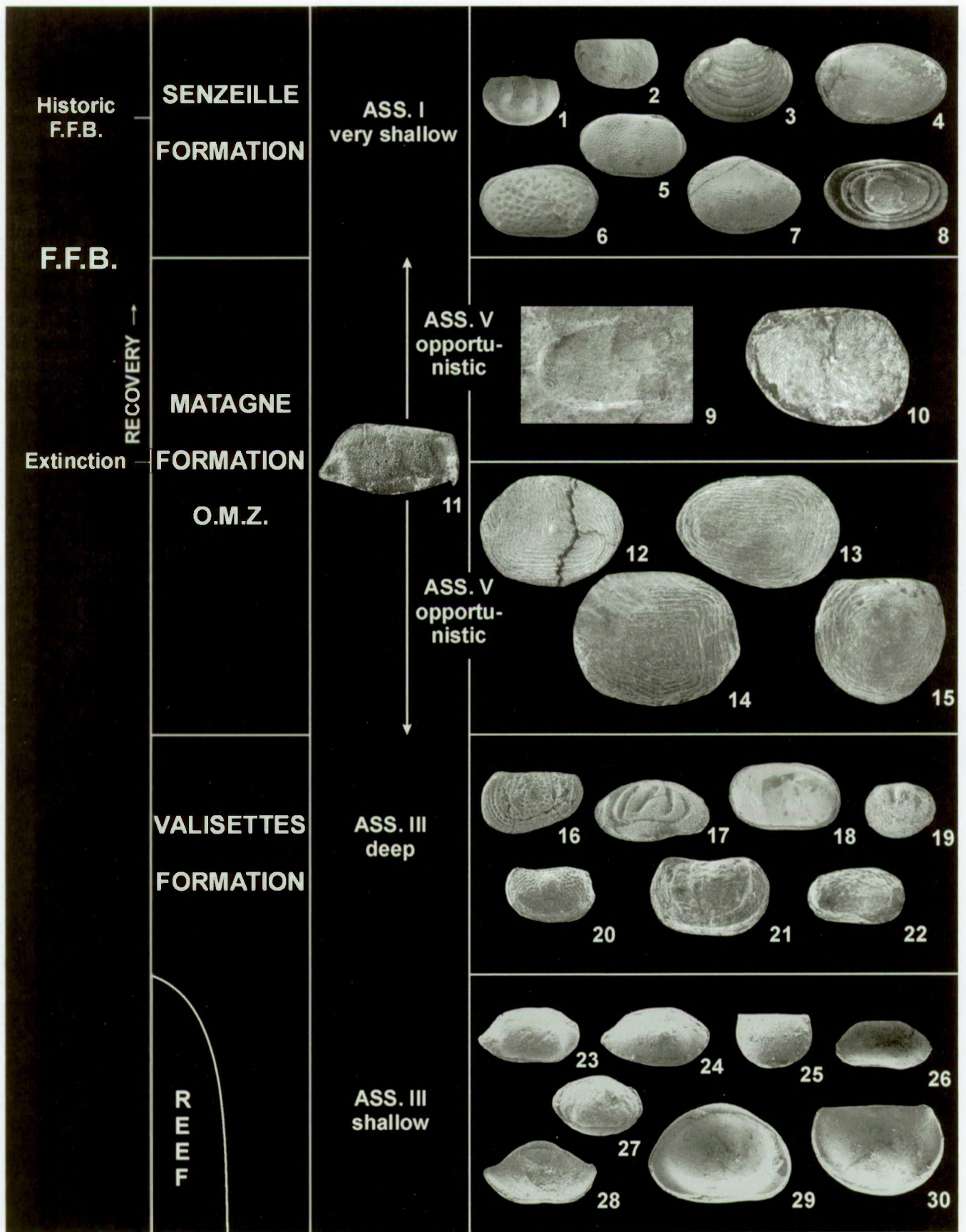


PLATE 1