

THE WAXWEILER PROJECT, EODEVONIAN HETEROSTRACAN PTERASPIDOMORPHS AND MYTHOLOGY OF THE BIG FIVE

Le projet Waxweiler, les Ptéraspidomorphes hétérostracés éodévonien et le mythe des 'Big Five'

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All audience abstract. – Waxweiler is a small city in Eifel, West Germany. Several quarries for extracting black shale are open there. They regularly yield a fossil assemblage of Early Devonian age. This includes, in particular, a new small pteraspide heterostracan, i.e., a 'primitive' jawless, armoured fish without paired fins, known as the 'Waxweiler-Form'. It is represented by many complete or near-complete individuals which are used for re-interpreting a series of palaeontology topics. The latter include morphology and anatomy, systematics (taxonomy, phylogeny, nomenclature, classification), evolutionary biology (evolutionary trends, ecology, ethology), palaeoenvironments and especially those of the Old Red Sandstone that is a post- and late-Caledonian or Ellesmerian as well as pre-Variscan molassic megafacies. Other elements of the assemblage are other fishes, molluscs, ostracodes, eurypterids, lingulids, plants, trace fossils. Another important locality is Odenspiel in Bergisches Land. It delivers another new pteraspide which is most probably of the same clade as the 'Waxweiler-Form'. It does show convergence with the psammosteid Drepanaspis which is usually another component of Early Devonian fossil assemblages of the Ardennes-Rhenish Slate Massif. Both discoveries will lead to new geobiological interpretations of the end-Proterozoic (Ediacaran) to Mid-Palaeozoic Biodiversification events, including crises and radiations.

Résumé tout public. – Waxweiler est une petite commune rurale de l'Eifel de l'ouest de l'Allemagne. Plusieurs grandes carrières pour l'extraction de schistes noirs y sont ouvertes. Ils fournissent régulièrement un assemblage fossile du Dévonien inférieur. Celui-ci comprend : un nouveau petit hétérostracé ptéraspide, c'est-à-dire un poisson cuirassé 'primitif' sans mâchoires et sans nageoires paires, connu sous le nom de 'Waxweiler-Form'. Cette espèce est représentée par de nombreux individus complets ou presque complets, qui sont utilisés pour réinterpréter une série de sujets de paléontologie actuelle. Ceux-ci comprennent les thèmes suivants : morphologie & anatomie, systématique (taxonomie, phylogénie, nomenclature, classification), biologie évolutive (tendances évolutives, écologie, éthologie), paléo-environnements et tout particulièrement les Vieux Grès Rouges qui sont des litho-faciès post- à tardi-calédoniens et pré-hercyniens. Les autres éléments de l'assemblage fossile sont d'autres poissons, des mollusques, des ostracodes, des plantes, des traces fossiles. Une autre localité importante est celle d'Odenspiel en Bergisches Land. Elle a fourni un autre ptéraspide nouveau qui est probablement du même clade (= ensemble d'organismes) monophylétique que la 'Waxweiler Form'. Ce second ptéraspide offre une convergence probablement écophénotypique avec le psammostéide Drepanaspis qui est un autre élément des assemblages fossiles de type Waxweiler. Ces deux découvertes conduiront à de nouvelles interprétations géobiologiques des événements de biodiversification de la fin du Protérozoïque (Édiacarien) au Paléozoïque moyen, en particulier les crises et les radiations.

Key words. – Ediacaran, Cambrian, Ordovician, Silurian, Devonian, geobiology, evolution, adaptation, convergence, fossils, databases, analogic and numerical modelling.

Mots clés. – Édiacarien, Cambrien, Ordovicien, Silurien, Dévonien, géobiologie, évolution, adaptation, convergence, fossiles, banques de données, modélisations analogiques et numériques.

I. - INTRODUCTION

Waxweiler is a small locality in the west of Germany, situated in the Eifel region within the Hautes Fagnes – Eifel Natur Park (http://www.botranger.be/index.php?id_surf=&surf_lang=de). A series of huge quarries devoted to black shale extraction, yielded a wealth of splendidly preserved fossils of Early Devonian age, i.e., ca. 413 million years Before Present (413 My BP, viz., before year 1950 which was established as a standard year with nearly 0 radio-isotope in atmosphere, before the series of numerous anthropic experiments had went on from 1945 to 1996: https://fr.wikipedia.org/wiki/Liste_d%27essais_nucl%C3%A9aires). The locality gives its name to the project under focus here. We will see how much important are Waxweiler and other equivalent localities around, as concerned with a series of basic questions in palaeontology: fish evolution, systematics (phylogenetics, taxonomy, nomenclature, classification), palaeobiology (growth, development, ecology, ethology),

biostratigraphy, palaeoecology, historical palaeobiogeography, palaeoenvironments, palaeohistology, biogeochemistry, retro-tectonic and/or retro-diagenetic deformations, assemblages, semantics, philosophy and history of palaeontology, geobiology. Waxweiler is indeed an actual Konservat-Fossil-Lagerstätte and perhaps also a Konservat-Fossil-Lagerstätte. It is one of the most diversified localities with a high disparity and quite abundance of various fossils such as fish (jawless heterostracans, jawed placoderms), ostracods, bivalves, lingulids, plants, trace fossils. Eurypterid remains have not been discovered yet. This locality does correspond to a geobiological event that pertains to the end of the very first peak of palaeobiodiversity of the Palaeozoic. The latter occurred in the Lower Devonian, either Lochkovian or Pragian and was named The Great Eodevonian Biodiversification Event (GEBE, Blieck, 2015). Later, this appeared to be the acme of the Early-Middle Palaeozoic Biodiversification, that is, the main phase of a continuous, latest Proterozoic to early Palaeozoic biodiversity rise of life on Earth

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(Blieck, 2018).

II. - THE WAXWEILER PROJECT

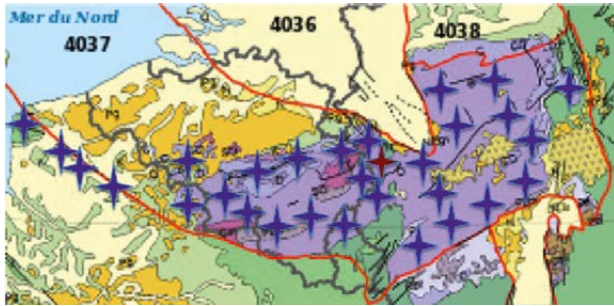


Fig. 1. — Simplified geological map between the Channel and the Rhine River, including the Boulonnais Inlier in the West & the Ardenne-Rhenish Slate Massif (ARSM) in the Centre and East. Blue stars- heterostracan-bearing localities; red star- Waxweiler; purple- Palaeozoic rocks; blue- Jurassic; green- Cretaceous; orange- 'Tertiary'; pale yellow- Quaternary; lighter blue- North Sea; pale brown with small 'v'- volcanic rocks.

Fig. 1. — Carte géologique simplifiée du Pas de Calais au Rhin, comprenant la boutonnière du Boulonnais à l'ouest et l'Ardenne-Massif Schisteux Rhénan à l'est. Etoiles bleues pour les localités à hétérostracés, rouge pour Waxweiler ; violet pour le Paléozoïque, bleu pour le Jurassique, vert pour le Crétacé, orange pour le 'Tertiaire', jaune-pâle pour le Quaternaire, bleu clair pour la Mer du Nord, brun pâle avec de petits 'v' pour les volcanites.

Waxweiler is located in the heart of the Ardenne-Rhenish Slate Massif (ARSM), west of the Rhine Graben, east of the Ardenne Sub-Massif. It shows a Lower Devonian sedimentary series with, *inter alia*, Emsian black shales. The latter are dark grey to black thinly laminated, organic- and metal-rich argillites having been slightly metamorphosed during the late- and post-Caledonian tectonic phase, also known as the early or pre-Hercynian tectonic phase. This phase did occur in the western French Armorican Massif, the French Central Massif, the Vosges Massif continued in the West-German Black Forest Massif, the Harz Mountains and all along the SW-NE trending branch of the Variscan, Mid-European Mountain Belt (see, e.g., Meilliez *et al.*, 1992; Fig. 1-2 here).

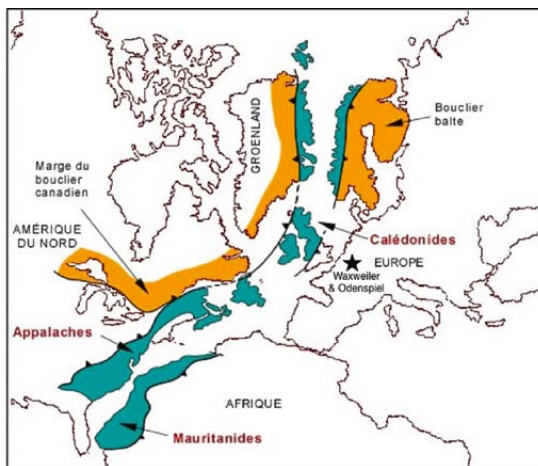


Fig. 2. — Reconstruction of the North-Atlantic, Early-Middle Palaeozoic mountain belts after <http://www2.ggl.ulaval.ca/personnel/bourque/s1/derive.html>. Blue is for the Appalachian-Caledonian mountain belts, orange for the basement shields.

Fig. 2 — Reconstitution des chaînes de montagnes du Paléozoïque inférieur et moyen de l'Atlantique Nord d'après <http://www2.ggl.ulaval.ca/personnel/bourque/s1/derive.html>. Chaînes de montagnes appalachiennes-calédoniennes en bleu, boucliers en orange.

Original collections were made by German amateur palaeontologists such as Peter Bardenheuer (Düren, Germany) who proposed the material of the 'Waxweiler-Form' (*sensu* Friman, 1986 a-b; fig. 3-4 here), for study to the present author. I proposed it to a then young student in Berlin, Markus Otto who, in turn, did not fulfill the project. Thus, the material was sent back to me.



Fig. 3. — The 'Waxweiler-Form' of P. Bardenheuer. Full length of animal is ca. 4 cm. The crescent-shaped pineal plate is clearly visible in the mid-line at ca. 1/4 of the head length from its tip to the posterior end of the dorsal shield. Armoured head on top. Near complete trunk and caudal paddle bottom left. © P. Bardenheuer's image.

Fig. 3. — La 'Waxweiler-Form' de P. Bardenheuer. Longueur totale de l'animal env. 4 cm. La plaque pinéale en forme de croissant est nettement visible au milieu à env. 1/4 de la longueur entre le bord antérieur de la tête et le bord postérieur du bouclier dorsal. Carapace céphalique en haut. Carapace presque complète du tronc avec sa palette natatoire caudale en bas à gauche. © Cliché P. Bardenheuer.

The main aim of the Waxweiler Project is to:

- study the fish (vertebrate) fauna of Waxweiler and Odenpiel and their surrounding localities in the ARSM,
- study all elements of its accompanying assemblage with 'invertebrates', plants, traces and eventually microfossils,
- synthesize these results in all possible fields of Palaeozoic geobiology by using all possible hard or computer, technical tools, i.e., hammers, field lenses, acid and mechanical preparations, CT-Scan, SEM, HD optical microscopy, morphometry, 3D reconstruction and eventually holographic techniques.

This will not be made in a single year. It was initiated as a third-year Bachelor's Degree practical learning (Hautier, 2018) and will be hopefully continued later. Collaboration is planned with both the colleagues of (i) the Senckenberg Institute and Museum of Natural History in Frankfurt.a/Main (Senckenberg Institut u. Natur-Historisches Museum, <http://www.senckenberg.de>; Drs E. Schindler, P. Königshof, R. Brocke *et al.*), and (ii) the Bavarian Land Collection of Palaeontology & Geology in München (Bayerische Staatssammlung für Paläontologie und Geologie und GeoBio-Center LMU, München, <http://www.geo.uni-muenchen.de/depearthenv/sektionen/paleo/index.html>; Dr A. Lopez-Arbarello).

I was invited by Prof. Dr. Adriana Lopez-Arbarello to study, in the München collection, a series of very well 3D-preserved, new psammosteid-like specimens that are named here 'Drepanaspis of Odenpiel' (Lopez-Arbarello & Blieck, 2010; Fig. 5 here). This was collected in Odenpiel, a locality of Bergisches Land, Germany. It turns out to probably be of the same clade as the 'Waxweiler-Form' and a few other 'bizarre' pteraspids with apparently homologous features to the 'Waxweiler Form' and the 'Drepanaspis of Odenpiel'. These 'bizarre' forms were collected in Spitsbergen («some aberrant form of Pteraspidomorphi, related to real Pterasp-

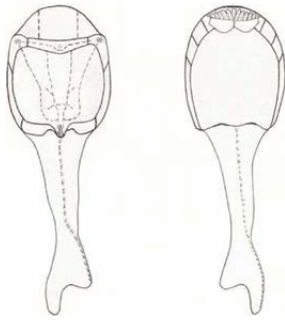


Fig. 4. — Provisional reconstruction of the 'Waxweiler-Form' by P. Bardenheuer (see also Friman 1986a, fig. 5: 9). Dorsal (left) and ventral (right) views of both head carapaces and trunk and tail scale cover. The caudal paddle is slightly distorted for convenient view. This provisional reconstruction is to be tested. The adult animal was 2 to 6 cm long.
Fig. 4. — Essai de reconstitution de la 'Waxweiler-Form' par P. Bardenheuer (voir aussi Friman 1986a, fig. 5 : 9). Vues dorsale (gauche) et ventrale (droite) des carapaces de la tête et du tronc avec la couverture d'écaïles de la queue. La palette natatoire caudale est légèrement tordue pour des raisons de représentation. Cette reconstitution provisoire demande à être vérifiée. L'animal adulte faisait 2 à 6 cm de longueur.

pids» Føyn & Heintz, 1943, fig. 14 and p. 34; from the Late Devonian Wijde Bay Formation), and Lithuania (*Skalviaspis narbutasi* Karatajūtė-Talimaa, 1989, from the East Baltic Lower Devonian). What is 'bizarre' is that all latter taxa seem not to have an external dentine layer of the bone of their dermal carapace. They seem phylogenetically related to the Central-West US taxon *Protaspidae* or *Protaspidae* (*sensu* Blicek, 1984; Pernègre & Elliott, 2008; "Protaspis"-Gruppe of Friman, 1986b, p. 99). If confirmed, this hypothesis leads to establish a monophyletic group (clade) for all these taxa.



Fig. 5. — Dorsal view of a near-complete specimen of the 'Drepanaspis of Odenspiel' ('Drepanaspis-artiger Fisch' sensu Lopez-Arbarello & Blicek, 2010, fig. 2: specimen BSPG 2009 I 22). Head armour on top left, trunk and caudal fin armour at right. The head carapace bony plates and the thick bony trunk scales are slightly displaced for diagenetic or tectonic reasons. The black and white label gives the metric scale in cm.
Fig. 5. — Vue dorsale d'un individu presque complet du 'Drepanaspis d'Odenspiel' ('Drepanaspis-artiger Fisch' sensu Lopez-Arbarello & Blicek, 2010, fig. 2: spécimen BSPG 2009 I 22). Carapace céphalique en haut à gauche, carapace du tronc et de la nageoire caudale à droite. Les plaques osseuses de la tête et les grosses écaïles du tronc sont légèrement déplacées les unes par rapport aux autres pour des raisons diagénétiques ou tectoniques. L'étiquette noir et blanc donne l'échelle en cm.

III. - EODEVONIAN HETEROSTRACAN PTERASPIDOMORPHS

The Pteraspidomorphi is a group of jawless vertebrates that lived from the Early Ordovician to the Late Devonian (ca. 470 to 372 My BP = ca. 100 My long). The head is generally covered by a bony dermal armour organized into large dorsal and ventral plates, and the trunk and tail by scales (Fig. 3-5). They had no paired lateral or unpaired midline fins other than the caudal fin. They are united by the presence of acellular bone (aspidin) in the armour. Four clades are included in the Pteraspidomorphi: the Arandaspidia, Astraspida, Eriptychiida and Heterostraci (*sensu* Janvier, 1996). Heterostraci are concerned here. They are known from the Lower Silurian to the Frasnian (Upper Devonian), that is, from 430 to 374 My BP, a geologically-long time slice of 56 million years. This very long time may be compared to the one that has been needed since after the end-Cretaceous and 'disappearance' of dinosaurs for Earth climate to rise up to its present state of global-warming (<https://www.youtube.com/watch?v=81Zb0pJa3Hg>). Heterostracans were collected mainly in sedimentary series originated from Laurentia, Avalonia and Baltica palaeocontinents in the Silurian, and the Old Red Sandstone Continent and Siberia in the Devonian.

Heterostracans have a single paired external branchial opening, and a cancellous (honeycomb-stitch-like) dermal bone. They were diverse, with more than 300 species described to date, but, their diversity or specific richness is under evaluation. The best known heterostracans are the Cythaspidiformes (including amphiaspids) and the Pteraspidiformes (including psammosteids). Both latter taxa are concerned with in Waxweiler and Odenspiel. In addition to these two major, cythaspid and pteraspid, clades there are a number of minor groups whose affinities are uncertain, viz., traquiraspids, cardipeltids, corvaspids, ctenaspids, *Nahanniaspis*, and various tessellated taxa (*Tesseraspis*, *Lepidaspis*, *Aporemaspis*, *Strosipherus-Oniscolepis*...; Blicek & Elliott, 2017; Blicek *et al.*, 2018a).

Geodistribution of heterostracans

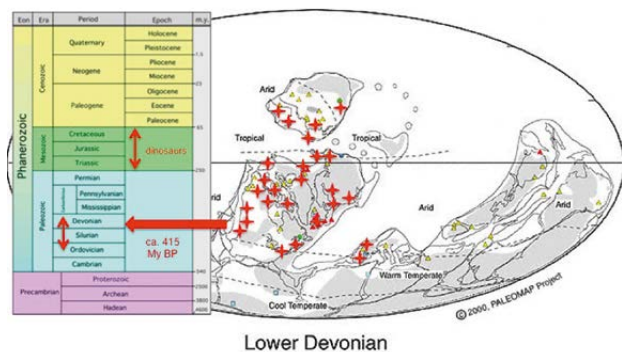


Fig. 6. — Stratigraphic (time) and geographic (space) distribution of Early Devonian heterostracans. This distribution is compared to the dinosaur's one. Palaeocontinents after Chris Scotese's Paleomaps Project (see <http://www.scotese.com/newpage3.htm>).

Fig. 6. — Répartition stratigraphique (temps) & géographique (espace) des Hétérostracés éodévonien. Cette répartition est comparée à celle des dinosaures. Reconstitution paléocontinentale d'après le Paleomaps Project de Chris Scotese (voir <http://www.scotese.com/newpage3.htm>).

From analysis of published palaeobiodiversity curves, heterostracans recently appeared to be one of the major elements of the Great Eodevonian Biodiversification Event or GEBE, *sensu* Bleick (2011). Their major peak is Lochkovian or Pragian in age, that is, early-mid Early Devonian. Whole ostracoderm diversity declines and reaches zero by the Frasnian/Famennian boundary time in the Upper Devonian. It is replaced by a placoderm diversity peak of Mid-Late Devonian age (Fig. 6-7). This must be situated in the trophic relationship frame within the Devonian seas, when ostracoderms were preyed by jawed fishes (gnathostomes), eurypterid arthropods, or other predators such as ammonoid cephalopods (Bleick, 2011). It does correspond to the very first mega-turnover of vertebrate assemblages on Earth through the Phanerozoic. GEBE appears to be the end and acme of the Great Ediacaran to Mid-Palaeozoic Biodiversification on Earth (GEMPB, Bleick, 2018). This topic is aimed at being developed in the forthcoming years.

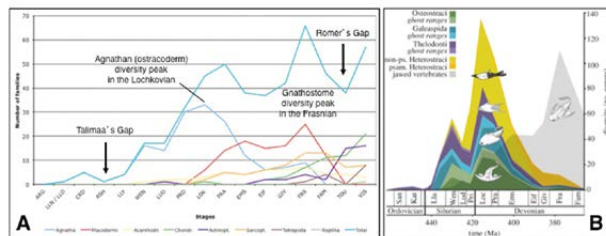


Fig. 7. — Biodiversity curves of (A) Ordovician to Carboniferous Lower Vertebrates, and (B) Ordovician to Devonian ostracoderms (jawless, ossified fishes; left) and placoderms (armoured jawed fishes, in grey; right) after Bleick (2017). © Palaeobiodiversity & Palaeoenvironments, Fischer Verlag.

Fig. 7. — Courbes de biodiversité des Vertébrés inférieurs ordoviciens à carbonifères (A) et des Ostracodermes (poissons ossifiés sans mâchoires) et Placodermes (poissons cuirassés à mâchoires) ordoviciens à dévoniens (B, respectivement à gauche et à droite) d'après Bleick (2017). © Palaeobiodiversity & Palaeoenvironments, Fischer Verlag.

IV. - THE BIG FIVE

« In *Africa*, the big five game animals are the *lion*, *leopard*, *rhinoceros* (both *black* and *white* species), *elephant*, and *Cape buffalo*. The term «big five game» (usually capitalized or quoted as «Big Five») was coined by *big-game hunters* and refers to the five most difficult animals in Africa to hunt on foot [in fact, after hunters themselves, the water buffalo is the most dangerous]. Subsequently the term was adopted by *safari* tour operators for marketing purposes » (https://en.wikipedia.org/wiki/Big_five_game). 'The Big Five' expression was given for the five major biotic crises of Phanerozoic Time on Earth (Fig. 8).

A new interpretation of 'The Big Five' is given on Fig. 8 bottom. It does not show the classical division into an Ediacaran 'origination' (not shown on figure), the 'Cambrian Explosion', the GEBE (Great Ordovician Biodiversification Event), the 'Palaeozoic Plateau' and end-Permian-early Triassic (P/T) biotic crisis, a.k.a., 'The Great Dying' (Wikipedia, 2018), usually interpreted as the major Phanerozoic biotic crisis. Contrarily, we show a simpler model with an Ediacaran to Early-Middle Palaeozoic Biodiversification, GEBE, a Late Palaeozoic 'Plateau', P/T crisis and a Meso-Cenozoic Biodiversification (Fig. 8 bottom). This analogic model will be tested through statistical analyses made in collaboration with various scientists. Even simpler interpretations were published. They are out of the scope of the present short paper, but, will be evaluated as well.

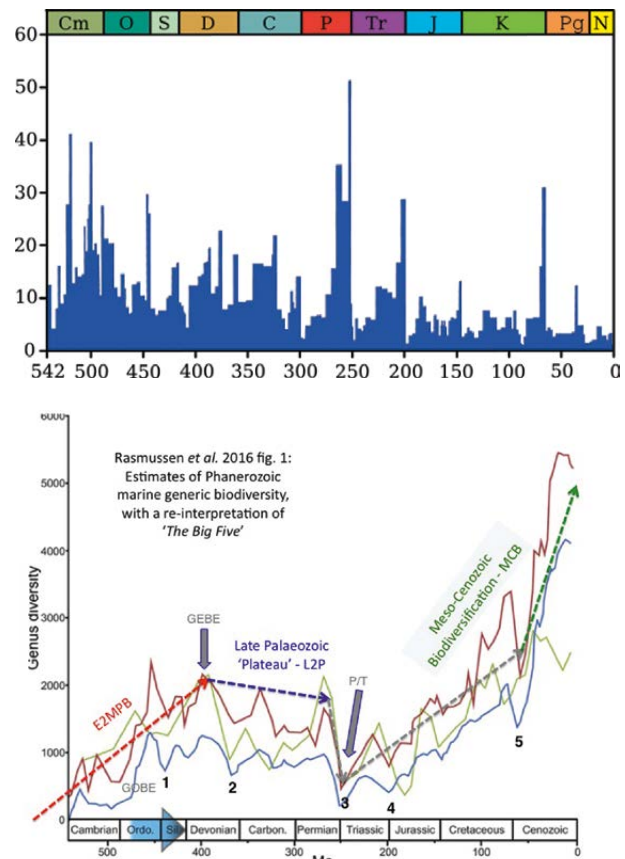


Fig. 8. — Phanerozoic biotic extinctions. Top) Phanerozoic mass extinction intensity after Wikipedia (2018). This graph clearly shows the two-shot end-Permian crisis at the end (right) of the 'P' red box. This biotic event is often considered as the most important Phanerozoic one and is sometimes known as 'The Great Dying'. Bottom) A re-interpretation of 'The Big Five'. Biodiversity curves from Rasmussen *et al.* (2016, fig. 1): red- Sepkoski's curve, blue- Rohde & Muller's curve, green- Alroy *et al.*'s curve. Variations in the palaeobiodiversity of marine organisms (including armoured agnathans and fishes) are re-interpreted as a five-slice analogic model, represented by five differently coloured lines. Other captions: E2MPB- Ediacaran to Early-Middle Palaeozoic Biodiversification whose 'Cambrian Explosion' and 'GOBE' are just shorter-term elements, GEBE- Grande Eodevonian Biodiversification Event, L2P- Late Palaeozoic 'Plateau', P/T- Permian-Triassic Crisis, MCB- Meso-Cenozoic Biodiversification which may in fact correspond to a logarithmic rise, 1-5- «The Big Five» *sensu* Sepkoski (1981) and Sepkoski & Raup (1986).

Fig. 8. — Les extinctions biotiques phanérozoïques. En haut) Intensité des extinctions en masse du Phanérozoïque d'après Wikipédia (2018). Ce graphique montre clairement la crise de la fin du Permien en deux étapes à la fin (à droite) du rectangle rouge 'P'. Cet événement est souvent considéré comme la plus importante des crises biotiques du Phanérozoïque et est parfois dénommé 'La Grande Mort'. En bas) Réinterprétation des 'Big Five'. Courbes de biodiversité in Rasmussen *et al.* (2016, fig. 1): courbes de Sepkoski (rouge), de Rohde & Muller (bleu) et d'Alroy *et al.* (vert). Les variations de la paléobiodiversité marine (incluant celles des agnathes et des poissons) sont réinterprétées sous la forme d'un modèle analogique à cinq phases, représentées par des segments de droites de couleurs différentes. Autres légendes : E2MPB- Biodiversification de l'Édiacarien – Paléozoïque inférieur et moyen dont l'« Explosion cambrienne » et 'GOBE' ne sont que des épisodes à plus court terme ; GEBE- Grande Biodiversification éodévonienne ; L2P- 'Plateau' du Paléozoïque supérieur ; P/T- Crise Permien/Trias ; MCB- Biodiversification méso-cénozoïque ; 1-5- Les «Big Five» *sensu* Sepkoski (1981) et Sepkoski & Raup (1986).

Pushing our reasoning far onward, it shows that the so-called ‘Big Five’ crises in geobiological events and diversifications are a probable pure myth. Some recent and more ancient results show that (1) the Permian-Triassic boundary, considered as ‘the mother’ of ‘The Big Five’, is not that short, abrupt and long as previously thought (Wikipedia, 2018), (2) the post-crisis intervals were not at all devoid of life as exemplified by the earliest, 5 My-long, Triassic case (Hofmann, 2014), and (3) previous modelling arrived to conclude that the development of life on Earth from the Ediacaran to the Present was more probably a ‘Long Quite River’ without strong crises. This was concluded as such by Lane & Benton (2003, fig. 2D): their “*Species curve modeled by extrapolating the differences between the derived parameters of the familial and generic curves*” shows a three-phase development without any strong biotic crisis (Fig. 9). It is comparable to the three-phased numerical model developed by Sclafani & Holland (2013, fig. 9) for local, regional and global species/surface relationships. If correct, this analogy between variously scaled species-time and species-surface diversity curves leads to consider that the Ediacaran-Phanerozoic marine biodiversity does not show any ‘deep trench or graben’ in its development.

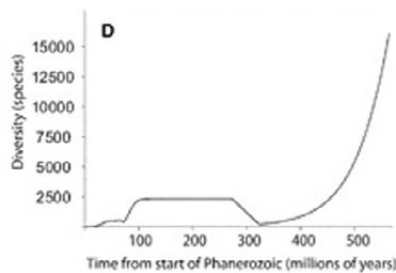


Fig. 9. — Phanerozoic Marine Biodiversity Species Curve modeled by extrapolating the differences between the derived parameters of the familial and generic curves from Lane & Benton (2003, fig. 2D).

Fig. 9. — Courbe de biodiversité spécifique des organismes marins du Phanérozoïque, modélisée par extrapolation des différences entre les paramètres issus des courbes aux rangs familial et générique, d’après Lane & Benton (2003, fig. 2D).

V. - CONCLUSIONS

Waxweiler, Odenspiel and a series of new, unpublished Early Devonian Fossil-Lagerstätten from N France to W Germany through S Belgium and the G. D. of Luxembourg, yield new, often ‘bizarre’ morphologies of lower/early vertebrates. Among the latter, heterostracans are the most significant and useful for local, regional and international, global geobiological problematics. Studies in progress aim at proposing a worldwide, practical and theoretical, analogical and numerical model for palaeontological studies. This programme is part of the *Handbook of Palaeoichthyology* vol. IA, ‘Agnatha’ I (Blieck *et al.*, 2018b). To-day’s palaeontology does again and again show its capability, usefulness and pertinence for human activities, both practically and theoretically. It opens to geoheritage, semantics, history and philosophy of sciences.

Acknowledgments. — We thank all elder and present colleagues, parents and friends who interact(ed) in giving practical and scientific knowledge. Special thanks to Daniel F. Goujet, Philippe Janvier, Hervé Lelièvre, a.k.a., The Three Parisian Musketeers *sensu* Susan Turner (Brisbane, Australia), i.e., all three plus the present author. ‘Sue’, as she is known worldwide, was always inspiringly rich in innovative scientific thoughts. Additionally, she is a talented pastel-painter. This work is dedicated to her as well as to the Three Musketeers team of the East Baltic area, viz., †Elga Mark-Kurik and Tiit Märs (Tallinn, Estonia), †L.A. Lyarskaya (Riga, Latvia), and Valentina N. Karatajūtė-Talimaa (Vilnius, Lithuania). The present author was invited to participate in two field seasons in the W-Rheinisches Schiefergebirge in the region of Koblenz (Alken-an-der-Mosel) and the Eifel in 1999 by the Devonian palaeontologists of the Senckenberg Institut und Museum in Frankfurt-am-Main, E. Schindler, R. Brocke, P. Königshof, U. Jansen, G. Plodowski and V. Wilde as well as their colleagues A. Wehrmann, G. Hertweck & S. Schultka from the Senckenberg in Wilhelmshaven and the Humboldt-Universität zu Berlin respectively. Mr. Peter Bardenheuer (Düren, FRG) is warmly thanked for his field collecting in Waxweiler and the fact that he sent his material for study.

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