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Cambrian explosion and Ordovician biodiversification or Cambrian biodiversification and Ordovician explosion?

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ABSTRACT

In this study, we examine how metazoan biodiversity has accumulated from the late Precambrian until the Silurian at various scales of taxonomic organization using compilations of the First Appearance Data (FAD) of global marine Metazoa from the datasets available in the Paleobiology Database (PBDB) and primary literature. The results indicate that all animal phyla appear during the late Precambrian and the earlier parts of the Cambrian, which corresponds to the usual concept of the Cambrian Explosion. However, at lower taxonomic ranks, a significant increase of first appearances is observed during the Ordovician, corresponding to an Ordovician Explosion of animal orders, families and genera. The cumulative counts of metazoan FADs at these lower taxonomic ranks reveal a gradual and long-term increase of diversity, reflecting a single large-scale radiation that started in the late Precambrian and lasted at least until the Silurian. This scenario corroborates recent studies that point towards a single long-term radiation during the early Palaeozoic, without clearly distinguishable global diversity explosions during discrete intervals.

1. Introduction

The general public often relates the famous Cambrian *Fossil-Konservat-Lagerstätten* (e.g., Chengjiang Biota, China; Burgess Shale, Canada; Sirius Passett, Greenland; etc.) to the Cambrian Explosion, as portrayed, among others by Stephen Jay Gould (1989). On the other hand, some authors consider the Cambrian Explosion and the Great Ordovician Biodiversification Event as biodiversity peaks in global datasets of taxonomic richness (e.g., Rasmussen et al., 2019; Fan et al., 2020). However, both the Cambrian Explosion (CE) and the Great Ordovician Biodiversification Event (GOBE) should be considered as conceptual terms only (Servais et al., 2023a). The CE refers to the relatively short time interval during the late Precambrian and the early Cambrian when nearly all modern animal phyla and body plans (*Baupläne*) appeared (e.g., Briggs, 2015). Conversely, the GOBE is considered to be the most rapid increase in marine metazoan biodiversity of the entire Phanerozoic that occurred during the Ordovician (Webby, 2004), with diversity increases being mostly visible at lower taxonomic ranks (in particular, families, genera and species). Given that various events seem related to

different evolutionary trends, namely the intrinsic developmental organization leading to diversified body plans and the filling of ecospace (e.g., Bambach et al., 2007), in this paper we study how metazoan biodiversity has accrued at various hierarchical taxonomic levels through time with the aim to better understand large-scale diversity trends in the Palaeozoic natural history of Metazoa. This approach may allow another perspective on the early Palaeozoic radiations focusing on the spatio-temporal interaction of diversification mechanisms to explain patterns.

Based on the data from the Paleobiology Database, we compiled the First Appearance Data (FAD), i.e., the first occurrences of taxa in the fossil record, of all metazoan groups, at the level of different taxonomic ranks: orders, families and genera. For the rank of phyla, we used primary literature to compile the first occurrences. One of the objectives of our study is to document the possible temporal asymmetries in global signals of first appearances. A further aim is to evaluate whether, for some particular intervals, ‘explosions’ of first appearances occurred, and if so, at what taxonomic ranks, which may provide insight into underlying mechanisms driving biodiversity. Within this framework, we then

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evaluate whether the data on first occurrences confirm a Cambrian explosion and an Ordovician event.

2. Methods

In order to observe the first occurrences of all fossils at different taxonomical levels, we use the data available from the Paleobiology Database, PBDB (<https://paleobiodb.org/#/>), that is currently the most complete database available for the ranges of Phanerozoic marine organisms. To investigate the tempo and mode in the origination of marine life during the early Palaeozoic, we ran a comparative analysis of First Appearance Data (FAD) using a multi taxonomic-level approach (i.e., from phyla to genera). We here investigate the levels of phylum, order, family and genus, that are easily accessible. Phyla-level data were compiled from primary literature, whereas order, family and genus-level data were downloaded from the PBDB. Our download was performed on August 30, 2023 using as target a list of 24 phyla (in alphabetical order): Agmata, Annelida, Arthropoda, Brachiopoda, Bryozoa, Chaetognatha, Chordata, Cnidaria, Ctenophora, Echinodermata, Entoprocta, Hemichordata, Hyolitha, Lobopodia, Mollusca, Onychophora, Petalonamae, Phoronida, Platyhelminthes, Porifera, Priapulida, Proarticulata, Protozoa and Vetulicolia (Table 1). We used the tool ‘Diversity over time’ of the database to obtain raw counts of the taxa crossing upper boundaries of geological stages and the taxa confined to a single interval (N_{FI} : number of taxa that cross the top boundary only; N_{FL} : number of taxa confined to an interval; Foote, 2000). The FAD analysis was performed at the stage-level ranging from the Ediacaran (part) to the Silurian. All types of preservation were considered, resulting in 195,782 occurrences, but we excluded records for which the stratigraphic position, or taxonomic status is uncertain, retaining 149,149 records.

3. Results

The number of FADs per time unit for the different taxonomical levels is shown in Fig. 1. Fig. 1A illustrates the evolution of the first appearance of all animal phyla (complete list presented in Table 1). The

Table 1

List of marine phyla (by alphabetical order) considered here showing their first appearance data (FAD) at the stage-level. References are justificative of temporal data only.

Phyla	FAD (Epoch/Age)	References
Agmata	Terreneuvian/Age 2	Yochelson and Kisselev (2003); Kouchinsky et al. (2012)
Annelida	Terreneuvian/ Fortunian	Landing et al. (2010)
Arthropoda	Series 2/Age 3	Edgecombe and Legg (2013)
Brachiopoda	Terreneuvian/Age 2	Landing et al. (2010)
Bryozoa	Series 2/Age 3	Zhang et al. (2021)
Chaetognatha	Series 2/Age 3	Shu et al. (2017)
Chordata	Series 2/Age 3	Chen et al. (1995); Shu et al. (2010)
Cnidaria	Ediacaran	Van Iten et al. (2014)
Ctenophora	Series 2/Age 3	Zhao et al. (2019)
Echinodermata	Series 2/Age 3	Smith et al. (2013)
Entoprocta	Series 2/Age 3	Zhang et al. (2013)
Hemichordata	Series 2/Age 3	Hou et al. (2011)
Hyolitha	Terreneuvian/ Fortunian	Kouchinsky et al. (2017)
Lobopodia	Series 2/Age 3	Liu et al. (2008)
Mollusca	Terreneuvian/ Fortunian	Kouchinsky et al. (2017)
Onychophora	Series 2/Age 3	Bergström and Hou (2001)
Petalonamae	Ediacaran	Sharp et al. (2017)
Phoronida	Series 2/Age 3	Hou et al. (2017)
Platyhelminthes	Ediacaran	Fedonkin (1985)
Porifera	Ediacaran	Yin et al. (2015)
Priapulida	Terreneuvian/Age 2	Smith et al. (2015)
Proarticulata	Ediacaran	Fedonkin (1985)
Protozoa	Ediacaran	Antcliffe et al. (2011); Xiao et al. (2014)
Vetulicolia	Series 2/Age 3	Gee (2001); Shu (2005)

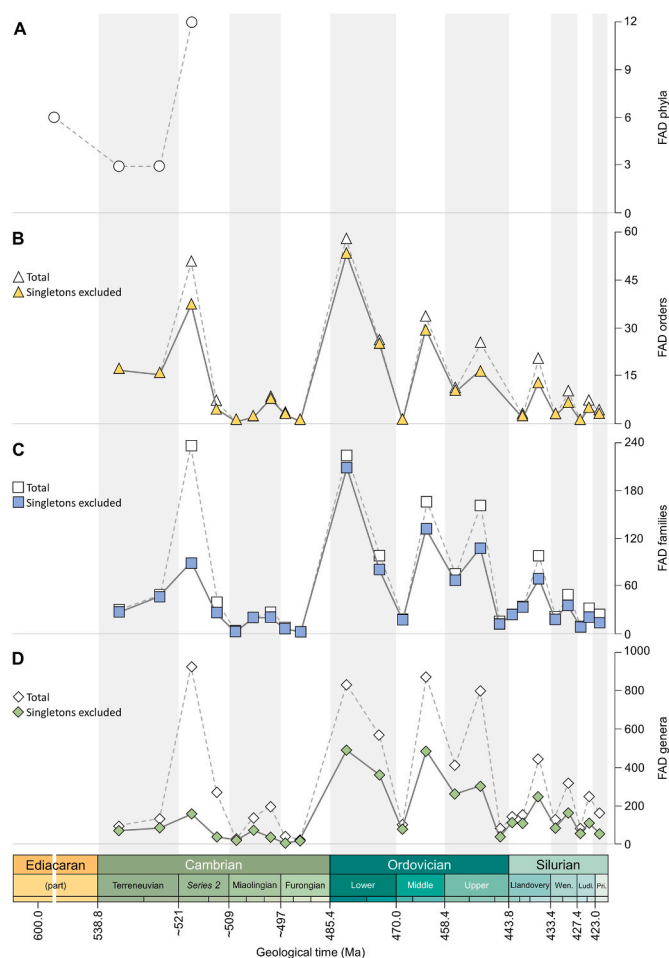


Fig. 1. Dynamics of the number of first appearance data (FAD) of marine metazoans per time unit (data available in Table 1). Comparative analyses performed following a multi-taxonomic level approach involving phyla (A), orders (B), families (C) and genera (D) of marine faunas. Data analysis carried out on total data and without single-interval taxa from Ediacaran (part) to the Silurian.

data available from literature confirm that all phyla appeared during the late Precambrian, the early Cambrian Terreneuvian Series and the Cambrian Series 2. The most significant numbers of FADs are recorded for the last interval. These first occurrences of phyla correspond to the usual concept of the Cambrian Explosion: there is an ‘explosive’ appearance of all animal phyla during a time interval of about 50 million years. This interval has often been interpreted as relatively short, when considering geological time, but was evidently not instant, especially given that FADs per definition underestimate the actual time of origin.

There is a striking difference in the FADs per time unit of the lower taxonomical levels obtained from the data in the PBDB. For the orders, families and genera, the highest numbers of FADs all occur in the Early Ordovician (Fig. 1B, C, D). Only when singletons (taxa that are only present in a single stratigraphical interval) are included, very high numbers of FADs are also recorded in the Cambrian Series 2, possibly reflecting high levels of endemics or short temporal ranges. The numbers of FADs of orders, families and genera during the Middle and Late Ordovician and during the Silurian remain high, but continuously decrease after the Early Ordovician.

Fig. 2 illustrates the cumulative analyses of FADs per time unit for the different taxonomical levels. There is a clear increase in the number of animal phyla between the Ediacaran and Cambrian Series 2, where all phyla have been recorded. The Cambrian Explosion, i.e., the appearance of all phyla, ended thus during Cambrian Series 2 (Fig. 2A).

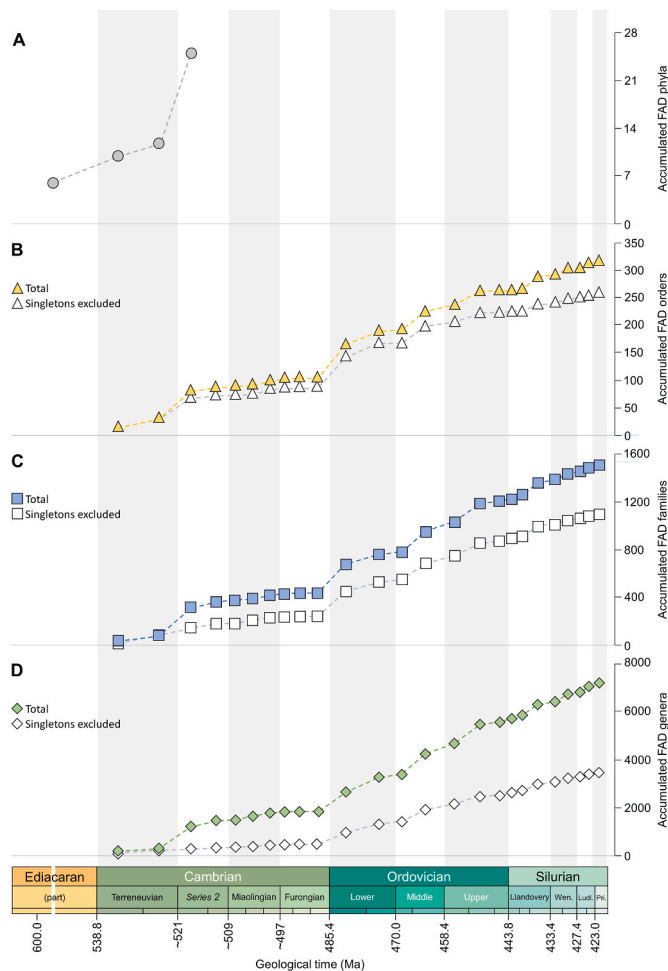


Fig. 2. Cumulative analysis of first appearance data (FAD) of marine metazoans per time unit. Legend as Fig. 1.

The accumulation of the FADs of orders, families and genera (Fig. 2B–D) shows a continuous increase between the Ediacaran and the end of the Silurian. This accumulation appears linear, however, and a possibly cascading increase in diversity can be observed at the base of the Ordovician, when numerous new orders, families and genera have been described and recorded in the PBDB. In addition, the slope of increases for families and genera is different between the Cambrian and the Ordovician–Silurian, with steeper cumulative curves after the Cambrian–Ordovician boundary (Davies’ test for non-constant regression slope: $p < 0.001$), even when accounting for differences in the number of occurrences per stage.

4. Discussion

It is not within the scope of this paper to discuss the macroevolutionary facets of the early Palaeozoic radiations in detail and to fully assess all aspects of the biodiversity dynamics (including alpha, beta and gamma diversities) during this interval. We simply propose another perspective on the biodiversifications of marine metazoans than those recently promoted in the form of global (integrating all available data from all continents) biodiversity (taxonomic richness) curves (e.g., Rasmussen et al., 2019; Fan et al., 2020).

Following Eble (1998), who plotted the first appearances of phyla, classes and orders during the late Precambrian and the Phanerozoic, we have plotted the first appearance of all animal phyla, orders, families and genera, with a focus on the late Precambrian and early Palaeozoic (Cambrian to Silurian). Eble (1998) noted the highest peaks of FADs of

phyla and classes in the early Cambrian, whereas the FADs of orders reached a maximum in the Early Ordovician. Here, we confirm these results, but we provide additional data at the family and genus level.

4.1. Cambrian biodiversification

More or less sophisticated statistical methods and different compilations have provided different biodiversity curves based on more or less complete (or manifestly incomplete) datasets. In the global biodiversity curve based on the Geobiology Database (GBDB), Fan et al. (2020) recognized a strong diversity increase in the Terreneuvian, whereas Rasmussen et al. (2019) see this increase much later, during Cambrian Series 2, based on data of the PBDB. In both studies these diversity increases are interpreted as the Cambrian Explosion.

Our investigation shows that all metazoan phyla appeared during the late Precambrian and the earlier parts of the Cambrian, with a peak of FADs in the Cambrian Series 2, corresponding to the diversity peak of Rasmussen et al. (2019), which is logical, because our data are derived from the same dataset. There are also peaks of FADs in Cambrian Series 2 at the levels of order, family and genus (Fig. 1B–D). However, many of these occurrences are singletons, i.e., they are only recorded at a single interval, possibly reflecting the endemic character of many taxa in the dataset.

The accumulation of the FADs shows a continuous increase of the number of lower taxonomic entities, terminating in some sort of plateau during the late Cambrian. The apparently stable taxonomic richness during the late Cambrian is most probably an artefact, because the PBDB is lacking data for the latest parts of the Cambrian, leading to the Furongian Diversity Gap (Harper et al., 2019). Recent studies have shown that this gap is actually not present in the GBDB (Deng et al., 2023) and that it can be interpreted as a sampling failure in the PBDB (Du et al., 2023).

4.2. Ordovician explosion

There are no new metazoan phyla originating in the fossil record after the earlier part of the Cambrian. However, at lower taxonomic levels, the highest numbers of FADs are all recorded in the Early Ordovician, especially when singletons are excluded. There is indeed a significant increase between the late Cambrian (where the PBDB records a Furongian Biodiversity Gap) and the Early Ordovician. This dramatic first appearance in the fossil record of new orders, families and genera could be termed the Ordovician ‘explosion’ of life. In contrast to the Cambrian Explosion, such a term has never been used before, although the rapid diversification at lower taxonomic levels could also be interpreted as explosive.

The accumulation of FADs (Fig. 2) indicates a continuous, long-term increase of taxonomic diversity at the order, family and genus levels. A particularly strong increase during the Middle Ordovician, where some authors see an ‘event’ (e.g., Stigall et al., 2020), is not visible in our dataset. However, there is a clear step up at the base of the Ordovician, but overall, there is a general continuous increase between the early Cambrian and the late Silurian, although the increase of FADs of orders, families and genera appears more rapid after the Cambrian. The important shift at the Cambrian–Ordovician boundary can thus be interpreted as the onset of the GOBE.

4.3. Cambrian explosion and Ordovician biodiversification or Cambrian biodiversification and Ordovician explosion?

Depending on the use and interpretation of the datasets (species richness curves versus number of FADs) and depending on the taxonomic rank (phyla and classes versus lower taxonomic ranks such as orders, families and genera) different trajectories and peaks in biodiversity are observed in the databases, leading to various terminologies that may attract the public attention to different degrees. Explosion, event and

revolution are terms that have been widely used to describe some aspects of the early Palaeozoic radiations, and that often have curried significant media interest (see Servais et al., 2023a).

The debate about ‘explosions’ and ‘events’ in the early Palaeozoic is actually mostly about terminology. The use of the term Cambrian Explosion started about 20–30 years before that of the GOBE, i.e., both terms were developed by different generations of scientists. Precambrian and Cambrian palaeontologists very often have a biological background and work as palaeobiologists, whereas many Ordovician palaeontologists have traditionally a more geological background. Perhaps as a result, the Cambrian Explosion represents a palaeobiological concept (by biologists), that cannot be linked to a single geological ‘event’ (by geologists). On the other hand, the GOBE has been defined in the 1990s by geologists, within the context of event stratigraphy, which was a popular research field at that time (see discussion in Servais et al., 2021, 2023a).

Currently, most scientists consider that there was no ‘explosive’ diversification in the Cambrian and that the origination of animal phyla, but also of lower taxonomical ranks did not occur suddenly. Therefore, several authors have avoided the term Cambrian explosion (e.g., Na and Kiessling, 2015), whereas others have declared that the term is inadequate and should be abandoned, because it is misleading (Beasecker et al., 2020).

Similarly, some authors have identified a short-lived ‘event’ in the Middle Ordovician, which is sometimes interpreted as the GOBE by a few authors, in contradiction to its definition by Webby (2004), and following previous studies (see Servais et al., 2023b). Today, it becomes evident that this ‘event’ is mostly based on brachiopod data from a single palaeocontinent (see discussion in Schmitz and Terfelt, 2023). There was clearly no single biodiversity event at a particular interval during the Ordovician that can be observed at a global level (on all palaeocontinents) in all fossil groups. However, a great number of radiations have been observed at different intervals (Servais et al., 2023b).

4.4. The problem with taxonomical levels

As already pointed out in several studies, analyses at different scales provide different results. It is difficult to compare diversity curves based on different datasets, because they commonly use different time bins (temporal scale), but also different taxonomic levels. For example, Alroy et al. (2008) used the generic level for his biodiversity curve with time bins averaging 11 million years, whereas Fan et al. (2020) used the species level at a much higher temporal resolution. The temporal scale can be the origin of biases, with intervals of different duration that cannot be directly compared.

But most importantly, what is a genus and what is a species? What delimits a class, an order, or a family? Are the taxonomical levels used in the databases, for instance in the PBDB, consistent and actually useable?

The definition of all supra-specific levels remains highly arbitrary and varies greatly from one fossil group to another, mainly because different groups of palaeontologists use completely different concepts. Schopf et al. (1975) had already indicated that taxa with higher degrees of morphological complexity display more taxonomic change, suggesting that the number of species, genera and higher taxa recognized within metazoan phyla may directly relate to the number of observable morphological features (as each provides opportunities to differentiate morphospecies). In addition, a palaeontologist working on the Ediacaran, with a limited number of taxa, will logically classify the available biota in another way to a neontologists working on Holocene taxa. In the early Palaeozoic there are a high number of classes and orders that include only an extremely low number of taxa, which would be not conceivable in younger geological periods, where classes and orders include many genera and species. Mesozoic and Cenozoic palaeontologists would probably classify the early Palaeozoic organisms in a completely different way, at different ranks.

In the present study we observe that phyla appear in the Ediacaran-

early Cambrian interval and lower taxonomical ranges appear in greater numbers much later during the Ordovician and Silurian. The question arises if this necessarily reflects an evolutionary pattern. Perhaps not. Perhaps our results mainly reflect a byproduct of the Classification of Life derived from the Linnean system. It is actually not very clear what we count, when we survey the different taxonomical levels. This is not only valid for the present study, but also for most biodiversity studies, where a strong bias is the variable classification by palaeontologists working on different groups at different taxonomical levels. Nevertheless, studies of the palaeontological record, although incomplete and potentially biased, still provide significant patterns to understand diversity processes in deep time. In this context, our analyses performed at various taxonomic levels, despite a number of biases, provide an interesting perspective on metazoan biodiversity during Earth history.

5. Conclusion

1. The analyses of the first appearance data in the fossil record indicates that all animal phyla appeared during the late Precambrian and the earlier parts of the Cambrian, which corresponds to the concept of the Cambrian Explosion.
2. The first appearances in the fossil record of lower taxonomic ranks (orders, families and genera) indicate the highest number of occurrences in the Early Ordovician. This massive occurrence of taxa could thus be interpreted as the GOBE.
3. The cumulative counts of FADs of lower taxonomic ranks indicate a continuous, long-term accumulation of taxonomical diversity during the entire early Palaeozoic, with no significant steps at a particular time period. This corroborates several biodiversity curves that also indicate a single progressive radiation, including the Cambrian explosion and the Ordovician biodiversification.
4. A change in the accumulation of FADs is visible at the base of the Ordovician, after which a more rapid increase of FADs at lower taxonomic ranks persists. This interval could therefore be interpreted as the onset of the GOBE.
5. There is neither a sudden explosion in the Cambrian nor a short-lived global event in the Ordovician.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.eve.2023.100018>.

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