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Review

"Winners" and "Losers" of the Bivalve Evolution

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Abstract

Bivalves are nowadays represented by several thousand species of variable sizes and shapes. Additionally, thousands more species occurred during their 500-million-year long evolution. Present on Earth since the Cambrian, the class Bivalvia experienced periods of gradual evolution, interspersed with periods of rapid changes. Some groups of bivalves, namely clams, oysters, scallops, and marine mussels, managed to survive a series of extinctions, and their descendants still thrive in modern oceans and seas. Other groups, such as the rudists, completely disappeared from marine environments, after undergoing successful evolutionary radiation. In this study, we consider the possible reasons for the longevity of some bivalve orders and discuss the possible causes of demise of several once-successful clades. As expected, a small body size, large number of specimens, infaunal mode of life, motility, and long-living planktonic larvae proved to be evolutionary advantages during stress periods. The ability to harbor chemosymbionts could be an additional benefit during biotic crises.

Keywords: Mollusca; Bivalvia; geological history; extinctions; survivors; symbionts

1. Introduction

Thousands of years ago, bivalve shells were used by prehistoric men for trade, jewelry, and art. Scientific studies of the Mollusca have flourished since the 17th century and particularly during the 18th and 19th centuries, when many valuable collections were gathered and described, focusing on bivalve taxonomy and anatomy. Progressively, besides determinations, researchers assessed the new data on bivalve ecology and evolution, e.g., [1–6].

The development of genetics contributed to extensive revisions of the mollusk taxonomy, bringing order to several tens of thousands of species [7–14]. The class is divided into the subclasses Protobranchia (with sister orders Nuculida and Solemyida, based on molecular markers) and Autobranchia (Figure 1), with estimated splitting in the middle, Ordovician. Protobranchs possess well-developed feet and bring food to their mouth via palp proboscides. Their monophyly is not beyond doubt. Autobranchia's (Autolamellibranchiata sensu [15]) common ancestor developed a feeding gill, an innovation considered responsible for the Ordovician bivalve radiation and for the development of the infaunal mode of life [14].

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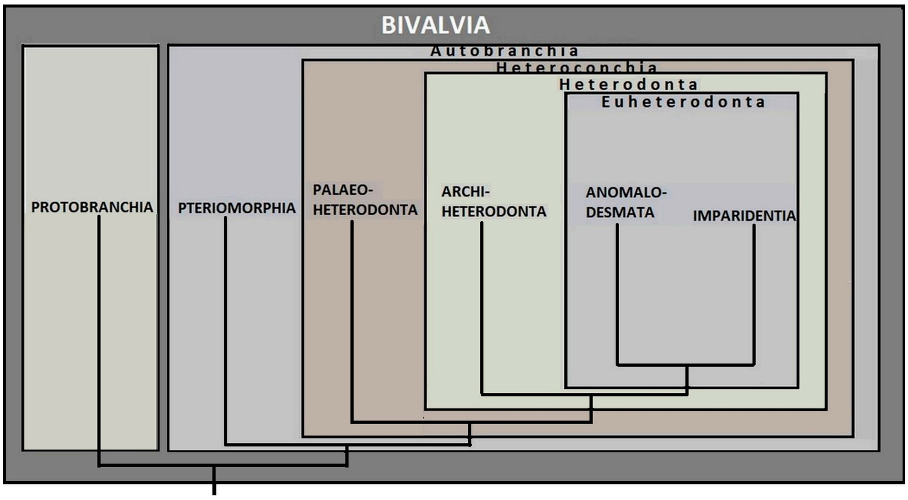

Figure 1. Simplified phylogenetic scheme of the class Bivalvia (after [11]; modified from [16]).

Several studies were recently published considering the bivalve geological history and evolution, e.g., [17–23], revealing the bivalve "slow start", despite the abrupt Cambrian explosion typical for many other clades [24–26]. The Great Ordovician Biodiversification Event (e.g., [27–29]) was more effective in the bivalve evolution, establishing all six major bivalve clades that are still known today. Nevertheless, even during this event, bivalves did not show a burst of functional disparity relative to taxonomic diversity, as stated by [22]. The first bivalves seem to be positioned near the sediment–water interface, being epifaunal, or shallow infaunal, with the gradual development of adaptations, such as byssal anchoring and siphonal communication with water bodies [22].

Additionally, in the past few decades, several studies have been published trying to understand bivalve extinctions and survivals on a wider level, e.g., [30–34]. After mass extinctions, cosmopolitan bivalve genera, similar to many other groups, tend to increase, while endemic genera decrease or become extinct [35].

Approximately in the same period, studies occurred considering symbiosis with microorganisms in bivalves and its importance in adaptation to various environments [9,31–34,36–44].

When studying the causes of extinction of any fossil taxon, we need to consider both biological traits and environmental stress caused by local or global geological events. When studying bivalve taxa with living descendants (including our evolutionary "winners"), such data are available. The problem occurs when we try to figure out what happened to the genera/families with no living relatives. In that case, information is derived from shell morphology, sedimentology and, sometimes, stable isotope research [31,32,36,45–48].

Several factors can impact the abundance of bivalves in the fossil record, similarly to all other fossil groups. Among them, fossil size, skeleton mineralogy, geographic distribution, and uneven sampling can affect the composition of fossil collections [21,31,49]. Many authors studied the impact of mineralogy and life position on bivalves' ecologic diversity and their response to stress events, particularly mass extinctions [21,23,32]. Most of them presumed that mineralogy did not play a crucial role in bivalve survival during stress periods, while the infaunal or epifaunal mode of life affects species diversity (e.g., [50]). The feeding mode can also have an effect on survival during biotic crises. When studying the Triassic bivalve extinction, Ref. [21] noticed that detritivorous bivalves were less affected than shallowly buried filter feeders, particularly the fast motile taxa. Deep infaunal taxa and "swimming" bivalves seemed to be the least affected by the crisis. Sedentary, unattached suspensivorous taxa, no matter whether epifaunal or semi-infaunal, were even more affected than the cemented bivalves [21].

2. Materials and Methods

During this study, we considered the bivalve orders still present on Earth after at least 360 Ma of evolution as "winners" (since the Ordovician, Silurian, or Devonian) and studied their ecological parameters to see what made them so successful (Table 1). It was more complicated to decide which groups to consider "losers". We could not avoid peculiarly shaped rudists, although they thrived in oceans for more than 70 Ma, but they are the representatives of a body plan that has no modern counterparts. Also, within otherwise successful bivalve orders, some subgroups evolved, flourished, and vanished in geologically rather short time periods (less than 50 million years). Such groups, e.g., large alatoconchids, rock-building lithiotids, or chondrodonts (Table 2), were our choice to understand what made them more prone to extinction compared to their relatives. We decided to take into consideration the fossil categories at least on the family level.

The data for this study were acquired from a variety of paleontological and biological published papers (cited in the text and quoted in the References), corroborating verified bases: WoRMS (taxonomy), Paleobiology Database (shell composition, life mode, locomotion, feeding mode, geographic distribution, and age range), and International Commission on Stratigraphy (stratigraphic age).

This study comprises the basic data on the once-widespread bivalve taxa, which was significantly attributed to the diversity of biota and environments and provided the bioclastic material for the thick sequences of carbonate rocks. The locally distributed clades (in most cases, freshwater), and those first occurring after the Devonian Period, were not taken into consideration. We studied the ecological characteristics of such successful clades, in order to see how some of them managed to survive throughout harsh crises, while the others rather abruptly vanished from the fossil record.

Table 1. Comparison of life habits, shell composition, distribution, and age range of bivalve orders present on Earth for more than 360 million years [32,38,40,43,51,52]. Uncertian or unknown microsymbionts are marked by a question mark.

Order	Shell Mineralogy	Life Mode	Locomotion	Feeding	Microsymbionts
Nuculida	Aragonite	Infaunal	Slow	Detritivore	Chemosynthetic ?
Solemyida	Aragonite	Infaunal	Facultatively	Suspension-feeder	Chemosynthetic
Nuculanida	Aragonite	Infaunal	Facultatively	Combined	Chemosynthetic
Arcida	Aragonite	Epifaunal Infaunal	Facultatively	Suspension-feeder	Chemosynthetic
Mytilida	Aragonite Mg-calcite	Epifaunal Infaunal	Stationary	Suspension-feeder	Chemosynthetic, Photosynthetic ?
Ostreida	Mg-calcite	Epifaunal	Stationary	Suspension-feeder	Variable
Pectinida	Mg-calcite Aragonite	Epifaunal	Facultatively	Suspension-feeder	Chemosynthetic, Photosynthetic
Limida	Aragonite Mg-calcite	Epifaunal	Facultatively	Suspension-feeder	Not known
Carditida	Aragonite	Infaunal	Facultatively	Suspension-feeder	Chemosynthetic, Photosynthetic
Lucinida	Aragonite	Infaunal	Facultatively	Suspension-feeder	Chemosynthetic

Table 2. List of bivalve taxa that became extinct during geological history at the family and/or order level, with their life habits and shell composition. Extinct orders/families are marked by a dagger symbol (†). Uncertian or unknown microsymbionts are marked by a question mark.

Order Family	Shell Mineralogy	Life Mode	Locomotion	Feeding	Microsymbionts
Fordillida † Both families	Aragonite	Epifaunal	Stationary	Suspension-feeder	Chemosynthetic ?
Megalodontida † All families	Aragonite	Infaunal	Facultatively mobile	Suspension-feeder	Photosynthetic ? Chemosynthetic ?
Myalinida † Alatoconchidae †	Aragonite Low Mg-calcite	Semi-infaunal	Stationary	Suspension-feeder	Photosynthetic ? Chemosynthetic ?
Myalinida † Inoceramidae †	Low Mg-calcite	Epifaunal	Facultatively mobile	Suspension-feeder	Chemosynthetic
Hippuritida † all families	Low Mg-calcite Aragonite	Intermediate-level epifaunal, Gregarious	Stationary	Suspension-feeder	Chemosynthetic
Trigoniida Megatrigoniidae †	Aragonite	Infaunal	Facultatively mobile	Suspension-feeder	Not known
Ostreida Bakevelliidae †	Aragonite Low Mg-calcite	Epifaunal	Stationary	Suspension-feeder	Chemosynthetic, Photosynthetic
Ostreida Halobiidae †	Aragonite Low Mg-calcite	Epifaunal	Stationary	Suspension-feeder	Chemosynthetic
Ostreida Plicatostylidae †	Low Mg-calcite	Epifaunal	Stationary	Suspension-feeder, Photosymbiotic	Chemosynthetic, Photosynthetic
Ostreida Chondrodontidae †	Low Mg-calcite Aragonite	Epifaunal	Stationary	Suspension-feeder	Not known

3. Bivalve Survivors

Bivalves common in modern seas and oceans have their roots in an early bivalve evolution, some of them being present on Earth for more than 480 million years (Table 1, Figure 2).

Long-existing orders Nuculida Dall, 1889 and Solemyida Dall, 1889 belong to the subclass Protobranchia Pelseneer, 1889 (Figure 1). Order Nuculanida J. G. Carter, D. C. Campbell & M. R. Campbell, 2000 is traditionally placed within the protobranchs, although, based on molecular markers, they should be placed within the subclass Autobranchia [14]. Orders Arcida Stoliczka, 1871, Mytilida A. Férussac, 1822, Ostreida A. Férussac, 1822, Pectinida Gray, 1824 and Limida Moore, 1952 from the infraclass Pteriomorphia Beurlen, 1944 (Figure 1) are also represented in rocks older than the Carboniferous period (358.86 Ma).

3.1. Order Nuculida Dall, 1889

Nuculids are small clams, today mostly present in subtropical to temperate shallow and deep-sea environments (most commonly between 125 and 200 m) [53]. As deposit-feeders, they constantly move in search of food, shallowly burrowing the muddy sands substrate. Present since the Early Ordovician (between 485 and 479 Ma), they are known as a conservative group, showing little diversity variation. Three genera managed to survive the end-Permian extinction, moderately diversifying during the Middle and particularly Late Triassic. They also managed to survive the end-Triassic extinction and fully recovered by the end of the Hettangian [32]. Today they are represented by one family, Nuculidae

J.E. Gray, 1824, with several genera, among which the genus *Nucula* is abundant, widely distributed, and highly diverse [51].

Nuculids can harbor various symbiotic microorganisms, particularly bacteria. It is also presumed that they have chemosymbiotic relationships with sulfur-oxidizing bacteria [41].

3.2. Order Solemyida Dall, 1889

Solemyida are an ancient order of facultatively mobile, infaunal suspension feeders, producing aragonite shells. Solemyids' taxonomy is problematic, and today they are represented by one family, Solemyidae J.E. Gray, 1840, living in marine environments worldwide at depths ranging from 0 to 6000 m, e.g., [54]. Their maximum range, based on fossils, is from the base of the Tremadocian until today (486.85 ± 1.5 Ma-rec) [19,52,55,56].

Solemyidae are also known for their obligate chemosymbiosis with chemoautotrophic and gill-hosted bacteria, which enables them to thrive in oxygen-depleted environments [37,40,41,57–59]. Solemyids in most cases supplement symbiosis with heterotrophic filter feeding [44].

3.3. Order Nuculanida J. G. Carter, D. C. Campbell & M. R. Campbell, 2000

Nuculanida are generally facultatively mobile infaunal deposit feeders producing small aragonite shells. Some nuculanids may partly supplement their diet with suspension feeding. Their maximum range based on fossils is from early Ordovician (486.85 ± 1.5 Ma) until today. The family Nuculanidae lives in marine habitats worldwide and is most common in deep-sea environments. They are infaunal deposit feeders, and supplementary limited suspension feeders, e.g., [60,61]. The family Bathyspinulidae is known for harboring symbiotic sulfide-oxidizing bacteria, which enables them to live in extreme habitats, such as deep-sea hydrothermal vents. Bacteria can be positioned in the gills, or in an internal sac (trophosome) [10]. Such symbiosis has enabled nuculanids to thrive in food and oxygen-depleted environments since the early days of bivalve evolution.

3.4. Order Arcida Stoliczka, 1871

Ark clams are another conservative group, achieving their recognizable adaptations to rather unfriendly environments early on. During their evolution, since the early Ordovician (~450 Ma) [62], they frequently changed their life habits from burrowing to byssate and vice versa [17,32]. The late Paleozoic family Paralellodontidae had long-ranging genera with a wide geographic distribution and high diversity, surviving the end-Permian and Triassic/Jurassic mass extinctions. The order has one living family, which appeared at the beginning of the Jurassic. Modern arcids mostly originate from Jurassic and Cretaceous ancestors, who developed the burrowing life habit and ability to produce a new byssus and live gregariously [32,63,64].

3.5. Order Mytilida A. Férussac, 1822

Members of the order Mytilida, although present on Earth since the early Ordovician (486.85 ± 1.5 Ma) [52], can hardly be considered conservative, developing epi- and endobyssate modes of life. The development of a single posterior inhalant current can be considered an important novelty, enabling the shaping of the characteristic mytilid valve and adaptation of unequal muscles [32,65]. Gregarious behavior, so typical for mytilids, along with the persistent periostracum, represents a successful adaptation to predator attacks [32,66,67]. Additional important abilities were crucial in mytilid evolution, such as their ability to live in the intertidal zone (stressful even in "stable" geological periods), short life cycles, and fast-growing rates [30,32,68,69].

The subfamily Bathymodiolinae harbors chemosymbionts in their gills, which enables them to colonize hostile environments, such as cold seeps and hydrothermal vents [39].

3.6. Order Ostreida A. Férussac, 1822

Ostreida are thick-shelled sessile gregarious bivalves that live cemented to the surface. As they grow, they join forming bioconstructions and oyster reefs, diversifying marine habitats, e.g., [70,71]. They live worldwide in warm and moderately warm seas with average salinity, but freshwater inlets also suit them, and they inhabit brackish waters too (Table 1). The majority of representatives of this order occur in the intertidal and very shallow subtidal environments. However, representatives of the family Gryphaeidae inhabit water depths below 25 m, e.g., [71,72]. As ostreids show variable morphology in the fossil record, and today as well, their taxonomy is sometimes unclear.

Due to their massive calcitic shells, Ostreida have been common fossils in the fossil record (Table 1) since the Late Ordovician (477.1 Ma) [52]. True oysters originated in the Triassic [32]. Certain groups disappeared by the end of the Cretaceous, but they recovered in the Cenozoic era, with a recorded "bloom" in the Neogene.

3.7. Order Pectinida Gray, 1854

Pectinids are a large and diverse group living mostly as vagile epifauna in marine environments. However, some species are byssally attached or cemented to the surface, e.g., (N348, [73]). This order is recorded worldwide, from the intertidal zone to deep-sea environments, e.g., [60]. They are also common in the fossil record due to the high preservation potential of their shell (Table 1), with the oldest known fossils from early Silurian rocks (438.6 Ma) [52].

Pectinida are successful bivalves that have survived all mass extinctions so far. One of the reasons for their success and diversity is their mode of life and morphological innovations developed during their evolution, which enable them to swim by clapping their valves together [32].

3.8. Order Limida Moore, 1952

Limida or "flame scallops" live in a variety of marine habitats. They produce symmetrical valves of various sizes. They can be either attached by byssus or live freely on the seafloor (on the surface or shallowly buried). When disturbed, many of them can swim away by flapping their valves together [74]. The oldest limid fossils were found in the Upper Devonian rocks (365 Ma).

3.9. Order Carditida Dall, 1889

Unofficially called false cockles, there are some doubts on carditid's taxonomical position, some of them being included in the order Venerida. The order has a long fossil record, since the Early Devonian (419.62 Ma), but the classification needs further improvements, e.g., [75]. Members of the order were severely affected by the end-Permian extinction, becoming diverse during the Late Triassic and again highly affected by the end-Triassic extinction. After the end-Cretaceous event they became diverse and rather common [32].

3.10. Lucinida Gray, 1854

Lucinida are one of the most diverse chemosymbiotic bivalves, widely distributed in various marine habitats, from the intertidal zone to more than a 2500 m depth [40,76]. According to [76], symbiosis seems obligatory in this order. Chemosymbiosis has been recorded in the families Lucinidae and Thyasiridae [59,76–78], with symbiontic bacteria located in their gills. The order Lucinida appeared during the Paleozoic, with the earliest probable representatives recorded in the Middle Ordovician [79] and more common findings in the Late Silurian [80], from [76].

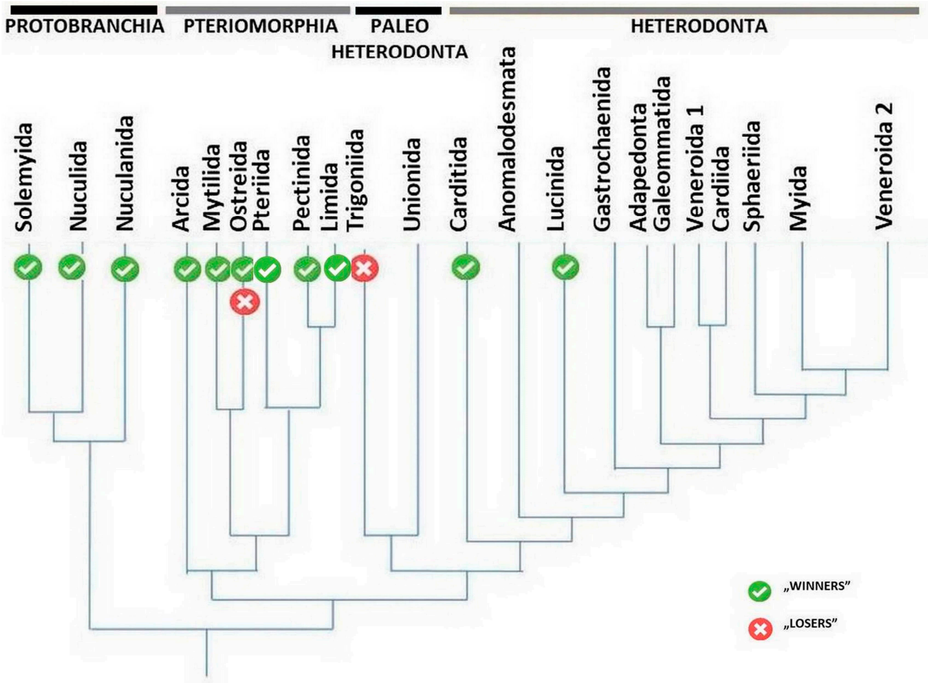

Figure 2. Phylogenetic tree representing the main bivalve orders (based on [12,13,81], modified from [82]), with marked evolutionary "winners" and some of the "losers" from this study.

4. Extinct Bivalve Orders

While studying the bivalve evolution, not many taxa can be considered "evolutionary losers". A few bivalve orders completely vanished from ancient seas (Table 2), in most cases after a long period of time. Nevertheless, several fossil groups deserve to be particularly highlighted as short-lived stars, either at the order or at the family level.

4.1. Order Fordillida Pojeta, 1975

The extinct order Fordillida (Table 2) is represented by one superfamily, Fordilloidea Pojeta, 1975, comprising two extant families, Camyidae and Fordillidae [8,83]. These small, oldest-known bivalves thrived in the early to middle Cambrian seas between 525.5 and 504.5 Ma [52].

The small shells do not exceed 25 mm in height; they had a single hinge tooth in each valve and their anterior adductor muscle was larger than the posterior. Fossils were found in North America, Greenland, Europe, the Middle East, Asia, and Australia. Their life habit is supposed to be "epibenthic gliding–creeping on microbial mats". They probably had a pedal-palp feeding mode, with a ventrally emergent foot [20]. Some scientists believe that these early clams may have harbored bacterial symbionts to colonize anaerobic environments [55].

4.2. Order Megalodontida Starobogatov, 1992

The extinct order Megalodontida (Table 2) comprises large, facultatively mobile infaunal suspension feeders that inhabited shallow tropical seas from 452.8 to 66 Ma, from the base of the Katian to the top of the Maastrichtian [52]. They are characterized by massive hinge teeth and umbonal thickening.

Within the order, the most common family Megalodontidae had a narrower age range, from the Devonian to the Jurassic period (438.6 to 145.06 Ma) [52], being particularly abundant in the Triassic Dachstein Limestone of the Northern Alps. Sometimes, they are known as "cow's-foot clams". It is presumed that they had photosymbionts placed on the mantle margin of gaping valves [42,45,84].

4.3. Order Myalinida Paul, 1939

The extinct bivalve order Myalinida is a part of the subclass Pteriomorphia, together with the extant orders Mytilida, Ostreida, and Pectinida (Figure 1). Myalinid fossils have been found in the rocks of the early Ordovician to the end of the Cretaceous (477.1–66 Ma) [52].

Myalinids produce aragonite shells. They were epifaunal, facultatively mobile suspension feeders [52,85]. Among this order, two families were particularly well known for their size and abundance: Paleozoic Alatoconchidae and Mesozoic Inoceramidae.

4.3.1. Family Alatoconchidae Termier et al., 1973

Large (up to 1 m-long), dorso-ventrally compressed alatoconchids lived in the early to middle Permian (from 283.3 to 259.51 Ma) [52]. The most common genus was *Shikamaia* Ozaki, 1968 (in some papers = *Tanchintongia* Runnegar and Gobbett, 1975) on the carbonate shelves of the shallow tropical seas [48,86–89]. The shells were composed of aragonite or low Mg-calcite. Their life habit is described as semi-infaunal by some authors, while [50] suggests the more probable epifaunal way of life. Alatoconchids were suspension feeders.

Alatoconchid fossils were found in Malaysia, Japan, South China, Iran, Afghanistan, Tunisia, Oman, Croatia, Thailand, Malaysia, the Philippines, and Alaska [52].

Scientists discussed the possibility that alatoconchids might have formed symbiotic relationships with photosynthetic or chemosynthetic microbes, particularly in the genus *Shikamaia*. Initially, they developed a theory on the translucent alatoconch shell layer, enabling them to harbor microalgae. Later, authors studied the oily deposits in which *Shikamaia* was found and disproved this theory [42,48,90].

4.3.2. Family Inoceramidae Giebel, 1852

Inoceramidae is a family of bivalves of various sizes, sometimes reaching more than 1 m in length, e.g., [91]. The largest ever specimen reached 1.87 m [92]. Inoceramide fossils occurred in sediments of the Late Triassic (in some papers even Permian) up to the end of the Cretaceous (227.3–66 Ma) [52], showing considerable variability and rapid evolution [91,93].

They were widely distributed in neritic and bathyal environments all over the world. It is presumed that they had a long-lived planktotrophic larvae. Adults were facultatively mobile, producing low Mg-calcite shells, adapted to filter feeding.

The most probable inoceramid symbionts, particularly for the large Cretaceous taxa, were chemosynthetic bacteria, situated in their gills or other tissues. Such a symbiosis can be inferred from their ecological niches (in oxygen-depleted habitats), from their gill structures, as well as from the stable isotope ratios calculated for the Platyceramus group [36,47].

4.4. Order Hippuritida Newell, 1965

The order Hippuritida represents an extinct order of inequivalve, thick-shelled rudists, with a variety of shell morphologies, sometimes reaching 2 m in height [94]. The order is commonly known under the name rudists. These bivalves lived gregariously as epifauna in the shallow marine environments of the carbonate platforms and shelves during the Late Jurassic and Cretaceous periods, being a part of the pronounced Mesozoic bivalve radiation and forming biostromes and bioherms [94]. Due to their massive shells (Table 2) they are common in the fossil record. The origin of their symbiosis is uncertain. Symbionts were placed in the mantle margins or surface-exposed to light [42].

5. Extinct Bivalve Families from Still-Present Orders

5.1. Order Trigoniida Dall, 1889

Trigoniida are moderately rapid shallow burrowers, characterized by unique shell dentition. The group is better known from the fossil record than from modern environments. Fossils have been found since the early Ordovician (477.1 Ma) until today [52]. Two genera survived the Permian–Triassic Boundary, with the diversity peak during the Carnian and being strongly affected by the end-Triassic mass extinction. They flourished during the Jurassic and the Early Cretaceous, hardly surviving the Cretaceous-Paleogene boundary [32]. Today they are represented by a single genus *Neotrigonia*, which can be considered a living fossil [18,73,95–97].

Semi-infaunal taxa, such as the living genus *Neotrigonia*, have epibiontic algal symbionts, which help the *Neotrigonia* to obtain the best position related to the bottom sediment [98].

Family Megatrigoniidae Van Hoepen, 1929

Megatrigoniidae are extinct saltwater clams, known from the Jurassic and Cretaceous periods, from 170.9 to 66 Ma, according to [52]. They are described as facultatively mobile infaunal suspension feeders, which produced aragonite shells [85] (Table 2). They were particularly common and widespread during the Cretaceous period, leaving fossil evidence on almost all continents.

5.2. Order Ostreida A. Férussac, 1822

Ostreida are generally a very successful order, as previously stated in Section 3 of *Bivalve Survivors*. Still, some of the families had a relatively shorter age range (Table 2).

5.2.1. Family Halobiidae Kittl, 1912

Flat clams of the family Halobiidae were present on Earth from the Middle Devonian to the Middle Jurassic 393.47 to 168.2 Ma, being most common during the Triassic Period. They lived as epifaunal stationary suspension feeders in marine and brackish environments. Their shells were composed of aragonite or low Mg-calcite [52,99–102].

5.2.2. Family Bakevelliidae King, 1850

Bakevelliids, medium-sized inequivalve bivalves, occur in a variety of shell shapes, from elongated and trapezoidal to irregular. They are known as the stationary (endobyssate), epifaunal (semi-infaunal) suspension feeders living in marine and brackish environments almost all over the world. They form aragonite shells with a low amount of magnesium calcite. Their age ranges from the base of the Serpukhovian to the top of the Bartonian (330.3–37.71 Ma) [52]. The direct evidence of symbionts in bakevelliid has not yet been found or studied, but generally, bivalves and other biota living in similar stress environments [103] have dominantly chemosymbiotic relationships.

5.2.3. Family Plicatostylidae Lupher & Packard, 1929 (Cochlearitidae Benini & Loriga, 1977)

This family comprises extinct large (sometimes over 50 cm) stationary suspension feeders, living partly buried in soft sediments of the Early Jurassic carbonate platforms (from 192.9 to 168.2 Ma). Fossils were found in Algeria, Chile, Morocco, and Slovenia [52]. The genus *Cochlearites*, together with gregarious Lithiotis-type bivalves (genus *Lithiotis* and related taxa), formed large bioconstructions (over 60 m in length) along the Tethyan and Panthalassan margins, similar to younger rudists or some modern oysters. Such constructions are sometimes described as “reefs” [46,104–106]. Shells were attached and composed of aragonite or low Mg-calcite [107], rapidly growing and sometimes reaching more than 30 cm.

Apart from being suspension feeders, a photosymbiotic diet is also suggested for the Malleidae family. Vermeij [42] suggests that symbionts might have been placed at the mantle margin around the commisure, and beneath the thin upper valve.

5.2.4. Family Chondrodontidae Freneix, 1960

The family Chondrontidae is represented by the genus *Chondrodonta*, an epifaunal, filter-feeding, oyster-like bivalve, e.g., [108,109]. It lived gregariously and cemented in the shallow-water environments during the Cretaceous period [108]. Due to their calcitic shells, their preservation potential is high (Table 2). Chondrodontids were distributed worldwide in a marine sub-marine environment as biostromes and in association with rudists [109]. Their distribution range is considered from the ? Berriasian to the ? Campanian [109] after Masse et al., 2015 and Freneix & Lefevre, 1967, with a peak during the Lower to Upper Cretaceous period (Aptian and Cenomanian, after [108]).

One of the species, *Chondrodonta joannae*, is used as the late Cenomanian marker in the area of the Upper Cretaceous Adriatic Carbonate Platform, e.g., Polšak, 1967a; Gušić and Jelaska, 1993; and Jurkovšek et al., 1996, after [108].

6. Discussion

When comparing the taxa that survived one or more biotic crises, some of their life habits stand out (Figure 3). On the other hand, we tried to summarize the main extinct taxa and name the biotic crises that led to their extinction (Figure 4).

6.1. Mode of Life of the Successful vs. Extinct Bivalve Taxa

Our list of nine orders surviving on Earth for over 360 Ma comprises the taxa of various sizes, from 2–3 cm (nuculids) to more than 50 cm (some ostreids, lucinids, pectinids, and oysters). Almost all studied groups secrete aragonitic shells or can produce combined (aragonitic/low Mg-calcitic) skeleton. In Table 1 and Figure 3, it can be seen that the infaunal mode of life is more common among the survivors than the epifaunal, although some taxa can take both positions, on or within the sediment, and the two highly successful groups live epifaunally. Almost all studied orders (Solemyida, Nuculanida, Arcida, Pectinida, Carditida, and Lucinida) can be facultatively mobile, or even regularly slowly moving along the sea bottom (Nuculida). The sedentary taxa Mytilida and Ostreida are cemented or byssally attached on the substrate. Suspension-feeders predominate among the survivors, with exception of the orders Nuculida and, partly, Nuculanida, which have retained their peculiar way of detritivory since their early occurrence (Table 1). Considering the solitary or gregarious behavior associated with high abundance (Mytilida, Ostreida), both strategies can be seen among the survivors. We also noticed that the successful taxa obtain additional food supplies from the symbionts, sometimes combining this strategy with heterotrophic filter feeding, as seen in Solemyidae (Table 1, Figure 3). The species *Solemya reidi* even completely lacks the ability to filter feed as an adult, and completely relies on symbionts [37,44,57]. Chemosymbiosis is particularly important for surviving in harsh environments [9,36–44], which obviously increases the surviving rate of some bivalves during biotic crises (Figure 3).

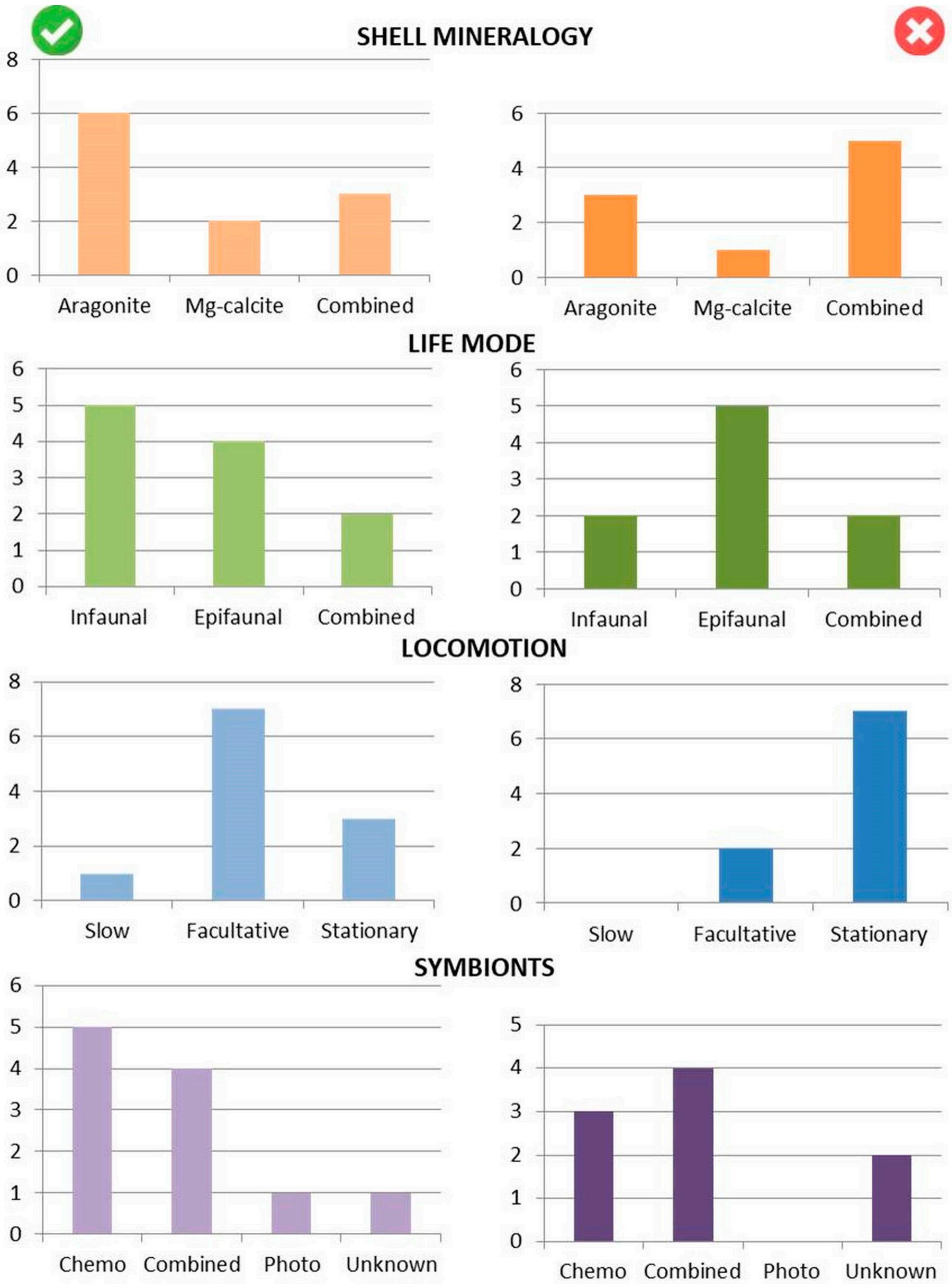

Figure 3. Numerical analysis of bivalve shell mineralogy, life mode, locomotion, and symbiotic relationships with microorganisms of the "winners" (left column) and "losers" (right column) compared in this study. Shell mineralogy does not seem to play an important role in surviving. On the contrary, infaunal mode of life represents an important advantage during biotic crises. Stationary clades are particularly endangered during stress periods, while the symbiosis with chemosynthetic symbionts helps bivalves to survive, not only in harsh environments, but also during extinction periods.

By analyzing the life habits of extinct taxa, we also primarily took into consideration the bivalve groups on the order level. Still, among the extant orders Trigoniida and Ostreida, there are some extinct families that were once very successful and widely distributed, such as Megatrigoniidae, Halobiidae, Bakeveliidae, Plicatostylidae, and Chondrodontidae, so we studied their life habits and age ranges as well (Table 2, Figures 3 and 4). Most of the vanished orders or families lived as epifaunal suspension-feeders, with only a few (Inoceramidae and Megatrigoniidae) being facultatively mobile (Table 2, Figure 3). Bivalves with such life habits were the most prone to environmental stress, as previously stated by [21]. While we discuss the extinct taxa here, the data on the possible symbioses are not always confirmed, but they are very useful. Photosynthetic symbiosis was initially presumed for the family Alatoconchidae, but in later studies, chemosymbionts were considered more likely [42]. On the other hand, photosymbiosis, later confirmed via stable isotope analyses [110], helped the rudists (order Hippuritida) to build thick shells and inhabit oligotrophic tropical shallow platform environments all over the world, e.g., [42,111–114]. Although useful under favorable conditions, photosymbionts can be hardly affected during stress episodes (like in modern coral reefs), and contribute to the bivalve extinction.

6.2. Extinctions and Their Victims

The age ranges of the extinct bivalve orders analyzed in this study are highly variable (Figure 4).

The short age range of the Cambrian order Fordillida (525.5–504.5 Ma) was noted by several authors [115]. Intra-Cambrian extinctions are yet to be studied in detail, but these events might be connected with massive eruptions, releasing carbon dioxide and sulfur dioxide into the atmosphere and leading to climate change and ocean acidification and euxinia. Beside the bivalves, these events strongly affected the trilobites, e.g., [116]. Although the representatives of the order Fordillida are extinct, the bivalves that evolved after it are considered its descendants [22].

The order Megalodontida thrived in shallow seas for almost 400 million years (Figure 4), and therefore should probably not be categorized as a “loser”. The reasons for such longevity could be their variable symbionts and semi-infaunal mode of life. Their last occurrence is linked with the end-Cretaceous mass extinction. Megalodontida do not have direct descendants, but they influenced the evolution of lithiotids and rudists [117].

The order Hippuritida was highly important during the Mesozoic Era (Figure 4), representing a typical expression of the Mesozoic Marine Revolution. This important evolutionary episode involved a major restructuring of shallow-marine benthic communities, including bivalves, and gave rise to the Modern Evolutionary Fauna [118]. Rudists developed a variety of morphologies and life modes from their first occurrence in the Oxfordian (Late Jurassic) to their mass extinction at the end of the Cretaceous [119]. In the meantime, environmental changes led to the extinctions of several rudist groups, such as the mid-Aptian temporary demise of caprinoids (global cooling, [120]) and the intra-Cenomanian event, affecting mostly the rudists on Pacific platforms [119]. End-Cenomanian extinction finally hit the caprinids and ichthyosarcolids, while radiolitids thrived along the Tethyan Realm [121]. In the case of rudists, changes in shell mineralogy among the dominant groups even affected the quality of the bottom sediment (composed of crushed bioclasts). Radiolitid and hippuritid calcitic shells produced the deposit susceptible to current reworking [122,123] and seawater chemistry [124] and therefore influenced all benthic life on carbonate platforms. The Late Campanian-Maastrichtian cooling and global regression also affected the evolution and distribution of rudist bioconstructions, but the end-Cretaceous catastrophic events were the last blow to this otherwise successful order. Hippuritida completely vanished and did not evolve into any of the living species [125].

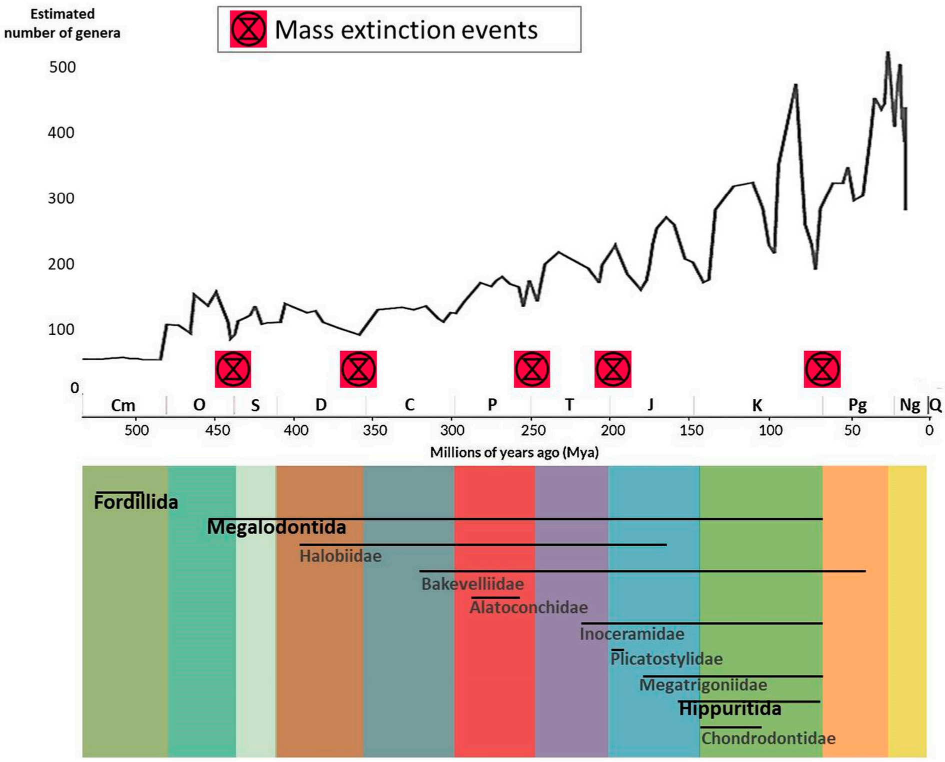

Figure 4. Estimated number of bivalve genera during the Phanerozoic eon, generated using the Paleobiology Database Navigator (modified from [126]), with five most important mass extinction events and age ranges of the described extinct orders (black bolded letters) or families marked (gray letters). End-Cretaceous extinction had a significant impact on the extinction of some previously successful groups. Short age ranges of Alatoconchidae, Plicatostylidae, and Chondrodontidae are particularly interesting. Age ranges are based upon the data from [52].

Many representatives of the intriguing (benthic, planktonic, or pseudoplanktonic) [102] family Halobiidae [127] failed to survive the end-Triassic extinction event, although some of them survived into the Jurassic Period (Figure 4).

The paraphyletic ostreid group Bakeveliidae was successful for almost 300 Ma (Figure 4), but it was strongly affected by the end-Cretaceous extinction event, although they finally vanished at the top of the Bartonian [52,128,129].

Large Permian gregarious Alatoconchidae went extinct at the Guadalupian–Lopingian boundary, the event within the Permian Period, which also affected the large fusulinid foraminifera (Figure 4). Isozaki & Aljinović [89] suggested the abrupt changes in the sea water temperature, ocean acidification, and anoxia, although several authors debuted the causes and scenarios of this (these?) events [130].

The myalinid family Inoceramidae, originating from the Permian Period and surviving for more than 150 Ma, had representatives all around the world, in a variety of marine environments (Figure 4). They had broad adaptive ranges, chemosymbionts, and very likely, long-lived planktotrophic larvae. They evolved rapidly, with an average species range of 0.2–0.5 Ma, declining in the Early Maastrichtian and vanishing around 1.5 Ma prior to the Cretaceous–Paleogene boundary [91,131]. Besides environmental stress, these authors suggest that predation and parasitism also played important roles in their extinction. Myalinida did not directly give rise to any modern bivalve, but some evolutionary links to the recent Mytilida are presumed [81].

Large representatives of the family Plicatostylidae, often called lithiotids, lived gregariously on the Early Jurassic carbonate platforms (Figure 4), producing massive bioconstructions. Lithiotis-type fauna suffered severe losses during the Toarcian Oceanic Anoxic Event, although in some areas, they persisted at least until the Aalenian. The Toarcian event was a part of the biotic crisis at the Pliensbachian–Toarcian boundary, which had the most severe impact on scleractinian corals and was generally selective against sensitive hypercalcifying taxa [132]. Such a selective extinction rate might be connected with their possible symbiosis with microalgae, although [133] put this theory into question.

The extinction of the family Megatrigoniidae (order Trigoniida), active burrowers in near-shore marine habitats [18], coincides with the Cretaceous–Paleogene extinction event (Figure 4). Their modern descendant is considered a living fossil.

The family Chondrodontidae developed a "mud-sticker" strategy of bottom stabilization, often occurring in association with rudist communities, flourishing at their expenses during stress conditions (with high nutrients and fluctuating seawater parameters), preceding the anoxic event [109]. They had discontinuous distribution in the Barremian to the Campanian (?) Tethyan carbonate platforms and finally vanished around 89.8 Ma ago [108], before the Cretaceous–Paleogene boundary (Figure 4).

A complex scenario during end-Cretaceous extinction included the Chixculub impact, wildfires, megatsunamis, nuclear winter, and anoxia; therefore, it is not hard to understand how it affected bivalve communities (see [134,135], and references in these papers). The key factors common to survivors were the ability to feed on carrion or detritus [136], ability to rest, burrowed habitats [137], and the small body size of fauna. Such a pattern was observed among survivors of mass extinctions across nearly all animal lineages [135,138–141].

7. Conclusions

The evolutionary history of bivalves, like in most animal lineages, exhibits both gradual and punctuated patterns.

Mass extinctions had a huge impact on bivalve survival and diversification. Therefore, two categories of bivalves are recognized in this paper: (a) bivalves present on Earth for more than 360 Ma (occurring before the Carboniferous Period), here named "winners"; and (b) bivalves that evolved, flourished, and vanished in geologically short time periods of around 50 Ma, here named "losers".

Among the known Palaeozoic crises, the Middle/Late Permian crisis was fatal for large gregarious alatoconchids ("losers"), but the famous "Great dying" at the Permian–Triassic boundary had less effect on bivalves.

During the Mesozoic Era, bivalve evolution accelerated, on the one hand due to the development of several innovations in the bivalve body plan, and, on the other hand, due to the decline of competing brachiopods. Several Mesozoic biotic crises (particularly end-Triassic, intra-Jurassic, intra-Cretaceous, and end-Cretaceous) affected some highly developed and diverse bivalve groups, causing the extinction of halobiids and lithiotids during the Jurassic Period, chondrodonts during the Cretaceous, and megalodontids, rudists, and most of the trigoniids at the Cretaceous–Paleogene boundary ("losers").

While studying the "winners" and "losers" of the bivalve evolution, we tried to summarize the characteristics common to the surviving taxa. The advantages were a small body size, large number of specimens, wide geographic distribution, infaunal mode of life, ability to move, long-living planktonic larvae and, in some cases, detritivory. Gregarious behavior might generally be advantageous, but in the case of sudden catastrophes or diseases/infestations, may turn into a problem.

Harboring chemosymbionts helps bivalves, not only to thrive in hostile environments, but also to survive the phases of environmental stress and mass extinctions. Therefore, their study deserves more attention in the future.

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