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Evolutionary biology

Cambrian origin but no early burst in functional disparity for Class Bivalvia

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Both the Cambrian explosion, more than half a billion years ago, and its Ordovician aftermath some 35 Myr later, are often framed as episodes of widespread ecological opportunity, but not all clades originating during this interval showed prolific rises in morphological or functional disparity. In a direct analysis of functional disparity, instead of the more commonly used proxy of morphological disparity, we find that ecological functions of Class Bivalvia arose concordantly with and even lagged behind taxonomic diversification, rather than the early-burst pattern expected for clades originating in supposedly open ecological landscapes. Unlike several other clades originating in the Cambrian explosion, the bivalves' belated acquisition of key anatomical novelties imposed a macroevolutionary lag, and even when those novelties evolved in the Early Ordovician, functional disparity never surpassed taxonomic diversity. Beyond this early period of animal evolution, the founding and subsequent diversification of new major clades and their functions might be expected to follow the pattern of the early bivalves—one where interactions between highly dynamic environmental and biotic landscapes and evolutionary contingencies need not promote prolific functional innovation.

1. Introduction

Biological diversification has many modes, ranging from early bursts to slow accumulations [1–3]. Much work identifying these evolutionary modes uses temporal or phylogenetic patterns in a single macroevolutionary currency, such as taxonomic diversity, ecological functions or morphological disparity, but a richer understanding derives from multi-dimensional analyses [4,5]. For example, 'non-adaptive radiations' [6] produce many taxa with relatively little ecological and morphological differentiation (e.g. woodland salamanders), whereas the Cambrian explosion of metazoan life famously produced an early burst of morphological disparity and ecological function with relatively low taxonomic diversity [7]. Major taxonomic classes or orders established during the Cambrian might also be expected to exhibit rapid ecological expansion; however, most studies of these clades have quantified morphology as a proxy for ecological functional groups [2,3,8,9], potentially confounding these two biodiversity dimensions [10]. In fact, echinoderms showed an early burst in morphology but not in function [11]. Further, early bursts in form or function are generally gauged by timing, without directly testing whether the rise in functional diversity, or disparity, exceeds the null expectation given the pace of taxonomic diversification [1,3]. Whether functional disparity preceded, was
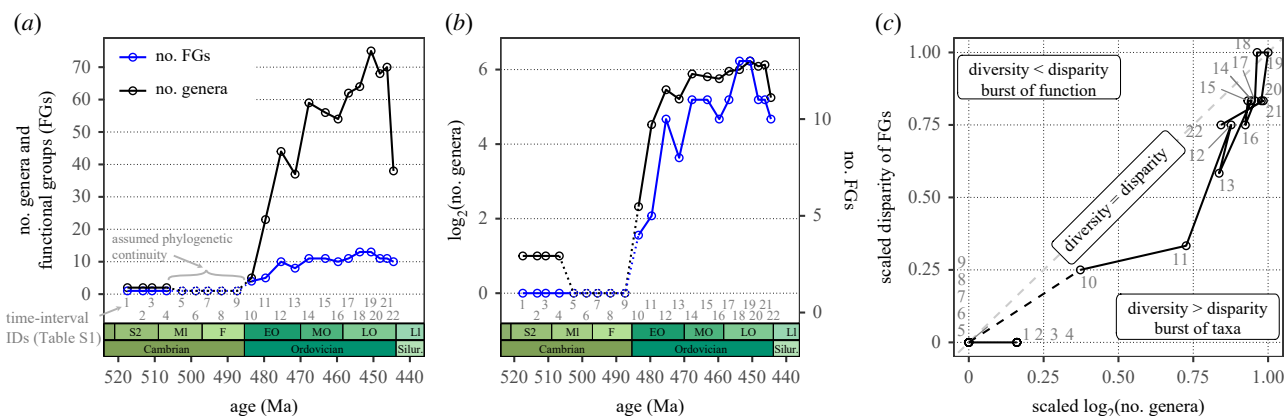
Figure 1. Taxonomic diversification outpaces functional disparification of Bivalvia from its origin in the mid-Cambrian to the end of the Ordovician. (a) Arithmetically, genus diversity accumulates to a greater degree than functional disparity starting in the Early Ordovician. (b) The same as (a) but with functional disparity scaled to the range of logged genus richness. (c) Diversity-disparity analysis of genus richness (logged) and functional disparity.

concordant with, or lagged behind the Ordovician rise in taxonomic diversity, can be tested directly in Class Bivalvia primarily using specific shell traits in their phylogenetic context to infer function.

Unlike trilobites [12] and several echinoderm classes [13], bivalve taxonomic diversity apparently remained low through the Cambrian, producing at most four genera across the first 36 Myr of the Class's evolutionary history [14,15] (electronic supplementary material, figure S1). Bivalves did participate in the ensuing Great Ordovician Biodiversification Event, establishing all six of their major clades [16,17] and generating 176 genera among 50 families (electronic supplementary material, figure S1), before suffering significant losses in the end-Ordovician mass extinction that we treat here as the end of this initial phase of the group's evolution. Bivalve functional disparity also appears to have remained low throughout the Cambrian and rose significantly by the end of the Ordovician [14,18–20]. Here we test whether Bivalvia, which originated during the Cambrian explosion to become one of the most biodiverse animal groups through the Phanerozoic, exhibited an early burst of ecological function over the first 80 Myr of their evolutionary history.

2. Material and methods

Genus-level stratigraphic ranges were used to quantify taxonomic diversity across 22 operational time bins generally corresponding to stratigraphic stages, from the mid-Cambrian to the end of the Ordovician (primarily compiled from [16] and an extensive update to [21]; details in the electronic supplementary material, text S1.1, dataset S1). To quantify functional disparity, we assigned each bivalve genus to a functional group defined on four attributes: feeding, position in the substratum, attachment and mobility (Table S2, as in [22]; electronic supplementary material, dataset S1). This framework captures approximate ecological equivalencies among distantly related taxa and can thus detect stability, shifts and expansions in ecological attributes at macroevolutionary scales [22].

We test an early burst in ecological function against other evolutionary patterns using a diversity-disparity analysis [23], where the accumulation of functional disparity (number of functional groups) is compared to log-transformed diversity (number of genera); genus richness is log-transformed because unimpeded taxonomic diversification is most often an exponential process, whereas a stochastic increase in disparity tends to be linear [23,24]. Both diversity and disparity are range-standardized,

respectively, so that each point in time is scaled to the minimum and maximum number of functional groups or genera attained during the study interval. An early-burst dynamic would involve a greater accumulation of functional groups relative to genus richness. Although the origin of each functional group must be tied to a genus, the trajectory of bivalve diversification could, theoretically, enter the upper left region of the diversity-disparity space during the initial phase of diversification, i.e. exhibit an early burst, if functional groups appear in rapid succession through the first part of the group's history ('burst of function' field in figure 1c). Further, the uneven distribution of bivalve genera among functional groups both today and in the geological past [22,25] and the uneven scatter of bivalve functional groups in morphospace [26] means that functional richness cannot proxy for morphological disparity, or vice versa. Thus, this diversity-disparity analysis is not a mere rescaling of the more common morphology-taxonomy comparisons but instead provides a new, complementary perspective. Uncertainty in diversity-disparity analyses, and thus in the inferred evolutionary dynamic, was assessed through sensitivity analyses assuming different sampling and diversification trends during the study interval (electronic supplementary material, text S2; described in context with the results below).

3. Results

(a) No early burst

Early bivalve evolution did not exhibit an early burst of ecological function relative to taxonomic diversification (figure 1), instead showing little taxonomic diversification and functional disparification through their first approximately 36 Myr. Both genus richness and functional disparity increased at the highest proportional rates through the Early Ordovician (time intervals 10–12 versus 13–20 in figure 1b), but even here, more genera accumulated relative to functional groups (figure 1c). This lag in functional disparity also holds when starting the analysis in the earliest Ordovician (electronic supplementary material, figure S4), which would assume a fundamental change in evolutionary dynamic at that time, possibly associated with the acquisition of a gill adapted for suspension-feeding as well as respiration [14]. From the latest Early Ordovician (interval 13) onwards, new genera accumulated almost exclusively within already established functional groups (points lying below the diagonal line in figure 1c).

Although the earliest bivalve functional group never diversified, those originating at the start of the Ordovician
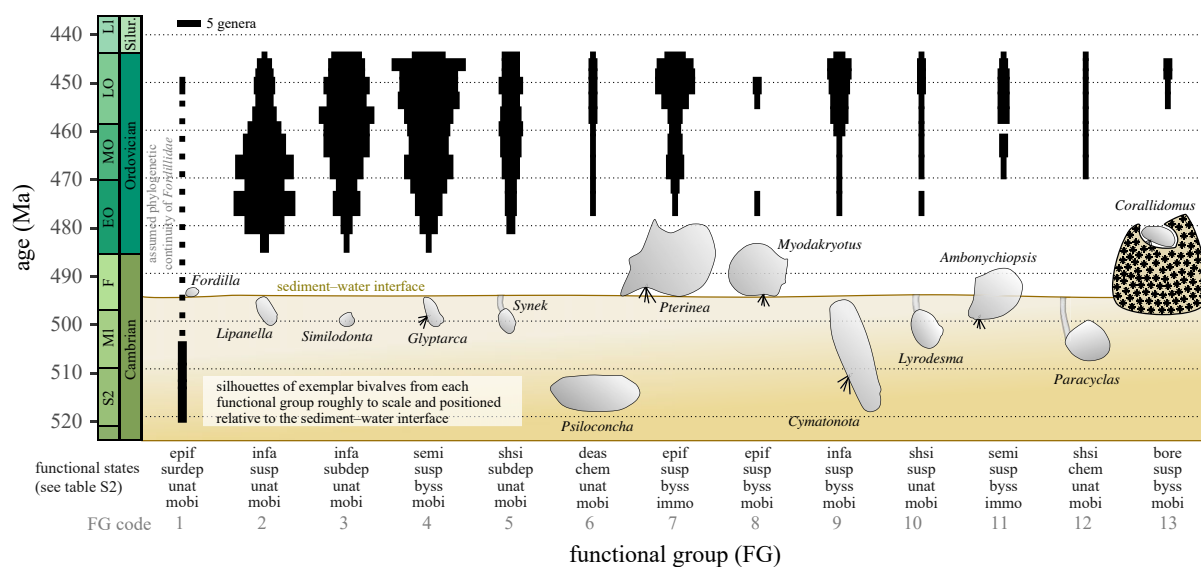
Figure 2. Origination and genus richness of bivalve functional groups through the early Palaeozoic.

accumulated the highest number of genera through the study interval (figure 2; electronic supplementary material, figure S3). One of the earliest groups rapidly attained high richness but declined by the end of the study interval (figure 2, FG-2), while the other two more gradually accumulated genera to remain major constituents of the global biota (figure 2, FG-3–4). Ultimately, 76% of genus richness concentrated in only 31% of functional disparity (136 genera among the four richest functional groups, electronic supplementary material, figure S2), similar to the uneven distributions seen in the Late Permian, Late Cretaceous, and today [22,25].

(b) Sensitivity tests

The Late Cambrian interval of low bivalve diversity might reflect either a genuine extinction event or poor sampling and preservation (time intervals 5–9); both scenarios have been suggested for Late Cambrian echinoderms [27]. However, simulating range extensions of the first and last appearances of genera that occur in time intervals on either side of that low-diversity Cambrian interval results in an even greater accumulation of genera relative to functional groups (i.e. farther below the diagonal 1 : 1 line, electronic supplementary material, text §S2.3 and figure S5).

The discrete nature of functional groups and their inherent link to genus origination may lower the probability of recovering an early-burst dynamic in the Cambrian or the Early Ordovician. However, prescribing each of the first 13 genera originating in the study interval to one of the 13 distinct functional groups results, on average, in a greater accumulation of functional disparity relative to taxonomic richness for three Early Ordovician intervals (nos. 11–13, electronic supplementary material, figure S6). Thus, an early burst was theoretically possible given the data structure, but is inconsistent with the observed pattern, even if the Cambrian *Pojetaia* and *Fordilla* occupied different functional groups [28]. Recovering this early-burst dynamic would require at least a doubling of functional disparity above the five functional groups known in the earliest Ordovician—not from unsampled genera, but by re-assigning approximately 22% of the genera in interval 10 to other, distinct functional groups currently unknown from that time

(electronic supplementary material, figure S6). This scenario appears unlikely given the general consensus on the distinctive modes of life indicated by the shell form of Ordovician bivalves [18,29,30]. The more inclusive nature of functional groups should also make them more robust to sampling than genus-level diversity, a bias running counter to the results reported here.

A simulation that comes closer to 'replaying life's tape', allowing genera to originate at any point through the study interval and belong to any functional group, results most often in a slight excess of functional disparity relative to genus diversity (electronic supplementary material, figure S7). Although the initial accumulation of diversity relative to disparity is higher for the observed data, the 95% confidence intervals of the rescaled, simulated series overlap the observed one for all but three time points, most dramatically the earliest Ordovician, where genera accumulated more rapidly than functional disparity (electronic supplementary material, figure S7). Thus, the observed long Cambrian lag appears to be unlikely under random diversification, but the relative rates of accumulation of taxonomic diversity and functional disparity are not inconsistent with such stochastic diversification dynamics—and not an early burst.

4. Discussion

The observed diversity-disparity trajectory and the sensitivity analyses rule out an early burst dynamic for this initial phase of bivalve evolution, owing to the greater production of new genera relative to new functional groups. This result is not a rescaling of the relationship between taxonomy and morphology, as the functions assigned to genera were determined from fossil material using a subset of traits in their phylogenetic context (most after [31]), along with direct evidence of living position (e.g. [18,32]). Thus, functional disparity is not strictly tied to overall morphological disparity, permitting the comparison between diversification patterns as measured in multiple macroevolutionary currencies.

Finer subdivision of ecological functions is unlikely to dramatically alter these findings. The largest body sizes for both infaunal and epifaunal bivalves evolved later in this

study interval [28,33], and extensive tiering within soft and hard substrata developed later in the Phanerozoic, as the Ordovician suspension feeders and deposit feeders lack evidence for long siphons [15,34] and the oldest deep-boring bivalves are mid-Silurian [35]. Only the chemosymbiotic solemyoids lived deep within the sediment (electronic supplementary material, dataset S1). Bivalve functional disparity did not saturate during the Ordovician radiation, increasing with continued taxonomic diversification to 17, 30 and 49 functional groups by the Late Permian, Maastrichtian and Recent ([22,25], electronic supplementary material, figure S8), suggesting that the bivalve body plan remained capable of producing many additional functions through the Phanerozoic [36].

The initial diversification of bivalves appears to be a two-phase process, but these phases do not correspond to those seen in other well-studied Early Palaeozoic groups. Trilobites, blastozoans and crinoids generally show a burst of higher taxa and morphospace occupation (often presumed to reflect functional diversification [8,36,37]). Instead, bivalves exhibited a significant macroevolutionary lag [23,29,38] between their Cambrian origin (approx. 521 Ma) and their taxonomic and functional diversification (starting approximately 485 Ma), perhaps also seen for bryozoans ([39,40] but see [41]). Indeed, the lone Cambrian bivalve functional group was always genus-poor and was lost in the Ordovician, assuming that *Neofordilla* was phylogenetically and ecologically close to the Cambrian forms. Phylogenetically, the failure of Cambrian, stem-group bivalve families to diversify does not fit the general expectation of an expansion-and-decline stem-group dynamic [42]. This lag and the subsequent Ordovician diversification have been attributed to various evolutionary and environmental drivers. An extinction event evidently collapsed the cosmopolitan Cambrian bivalve distribution to siliclastic Gondwanan habitats [43], perhaps delaying the origin of a muscular hydrostatic foot, byssus and/or feeding gill, which opened up a wide range of potential functions [14,30,44]. The onset of their Ordovician diversification coincided with an increase in nutrients and ocean ventilation [45] and the transformation of the seafloor from surfaces stabilized by microbial mats to softer, bioturbated sediments [15,29], with bivalves expanding into both on- and offshore habitats with soft- and hard-ground substrata [43]. Thus, bivalves may be another instance of a clade whose diversification required a chain of derived characters, rather than a single "key innovation" [46,47].

For clades not participating in the initial Cambrian burst of form and function, shifting environmental conditions, changes to gene-regulatory controls and/or interference from the diversification of other clades with similar functions [7,45,48] may have impeded the proliferation of morphologies or functions in the Ordovician relative to taxonomic diversification. Strophomenid brachiopods showed an Ordovician burst in trait disparity associated with rapid taxonomic diversification [49] and so might resemble the bivalves if evaluated using the approach in figure 1. Rapid morphological evolution in the Cambrian did not always guarantee bursts of functional disparity (e.g. echinoderms [11]). Bivalves may show a related pattern, where most major body plans were established in the Early Ordovician (i.e. the six extant major clades [17]), but those originations did not correspond to relatively high functional disparification.

The origin of each new functional group might promote the rapid accumulation of new genera within it to produce bottom-heavy diversity patterns, reflecting exploitation of vacant ecological space [50,51]. However, only one Ordovician bivalve functional group is bottom-heavy (figure 2, FG-2), while the others slowly accumulate genera or remain genus-poor throughout their Ordovician histories (figure 2), producing a common, skewed distribution of genera among functional groups (electronic supplementary material, figure S2). The first three functional groups to appear in the Ordovician accumulated the greatest number of genera during the study interval (FG-2–4), but richness rankings were unstable both during the Ordovician and beyond. Different functional groups 'dominate' in terms of genus richness by the end-Permian, end-Cretaceous, and today [22,25], suggesting that functional groups wax and wane with the biotic and physical environment, and are not entirely determined by timing or rates of origination. Early evolution of a functional group is thus no guarantee of long-term success—as also seen in the taxonomic and functional declines of the Ediacaran and Cambrian biotas—and early bursts of taxa within functional groups are not required for taxonomic diversification to outpace functional disparification across the entire biota as long as new functional groups enter the system in a more episodic fashion.

5. Conclusion

Diversification is not always concentrated at the inception of a clade or at the founding of a new functional group. Ecological or evolutionary impediments, from pre-empted niche space to developmental limitations, may restrict rapid expansion across biodiversity dimensions. The Early Cambrian was apparently a singular opportunity for new clades to evolve within a relatively empty ecological landscape, perhaps with complex but flexible gene-regulatory controls [7,52]. Although many of the major metazoan body plans and clades were established at this time, bivalves did not undergo an increase in taxonomic, morphologic and functional diversity until the Ordovician, in contrast with several other similarly ranked groups. This macroevolutionary lag may result from a delayed acquisition of key anatomical novelties or a lower degree of morphological modularity than in the more segmented clades that underwent Cambrian radiations [53,54]. Even in their Ordovician diversification, bivalves failed to show a burst of functional disparity relative to taxonomic diversity, although this was not a non-adaptive radiation either. Such concordant patterns may tend to characterize clade radiations occurring outside the Early Cambrian, as seen in the accumulations of biodiversity dimensions in later originating clades, and in recoveries from mass extinctions [55]. The failure of past opportunities to promote rapid and extensive entry into new functions tempers expectations for the macroevolutionary response of global biodiversity to ongoing and impending environmental and climatic crises.

Authors' contributions. S.Z.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft, writing—review and editing; S.M.E.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, visualization,

writing—original draft, writing—review and editing; K.S.C.: conceptualization, data curation, visualization, writing—review and editing; N.M.A.C.: conceptualization, methodology, writing—review and editing; D.J.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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