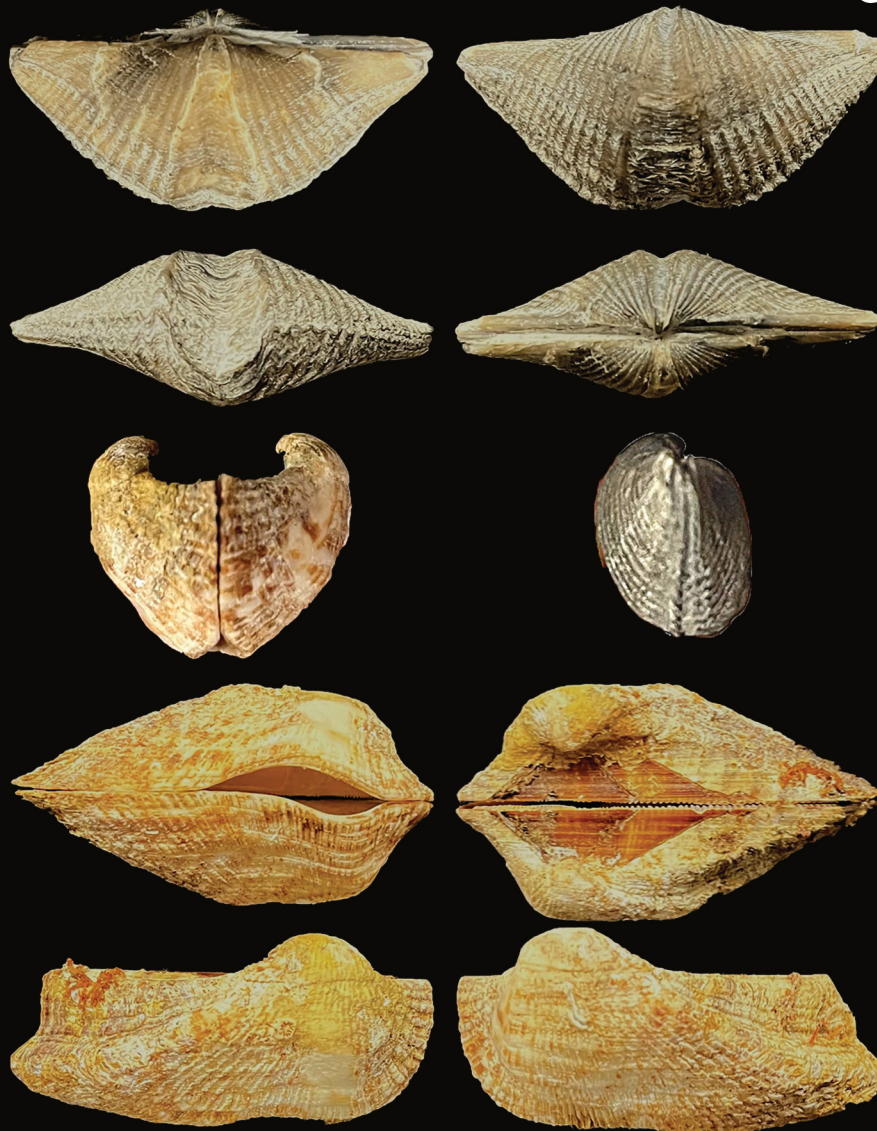


Evolution by valves: morphological constraints, environmental change, and the replacement of brachiopods by bivalves

Geerat J. VERMEIJ



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The Devonian brachiopod *Mucrospirifer mucronatus* (top and middle-right) and the Recent bivalve *Arca noae* (bottom and middle-left). Both in the Vermeij Collection.

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Evolution by valves: morphological constraints, environmental change, and the replacement of brachiopods by bivalves

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ABSTRACT

Brachiopoda and Bivalvia evolved the bivalved condition independently during the early Cambrian, but they have contrasting histories, with bivalves largely replacing brachiopods in warm, shallow, post-Paleozoic seas. Overlapping hypotheses have been proposed to explain this replacement, but it remains unclear how inherent constraints and evolutionary potentials of the bivalved form in the two groups interacted with environmental changes that favoured bivalves. Here I document the origins, fates, limitations, and versatility of 55 morphological and habitat traits, of which 13 are unique to brachiopods, 23 are unique to bivalves, and 19 evolved convergently in both. Only 6.3% of brachiopod traits are post-Paleozoic as compared with 24% of bivalve traits. Extinction affected 44% of brachiopod traits but only 2% of bivalve traits. Characteristics associated with post-Paleozoic bivalve proliferation evolved much earlier, including the early Cambrian origin of the extensible foot, hinge ligament, and morphological within-valve modularity, none of which evolved in brachiopods and all of which provided early versatility in bivalves. Constraints on form were already present in early Cambrian brachiopods and were never overcome. The full potential of bivalves was realized only when more intense biological activity made Mesozoic and Cenozoic seas more productive.

KEY WORDS

Brachiopoda,
Bivalvia,
modularity,
ecological replacement,
evolutionary constraints.

RÉSUMÉ

L'évolution des mollusques bivalves : contraintes morphologiques, changements environnementaux et remplacement des brachiopodes par les bivalves.

Les brachiopodes et les bivalves ont développé indépendamment la structure bivalve au début du Cambrien, mais leurs histoires sont contrastées : les bivalves ont en grande partie remplacé les brachiopodes dans les mers chaudes et peu profondes après le Paléozoïque. Plusieurs hypothèses se recoupant ont été avancées pour expliquer ce remplacement, mais on ne sait toujours pas comment les contraintes inhérentes et les potentiels évolutifs de la forme bivalve chez ces deux groupes ont interagi avec les changements environnementaux qui ont favorisé les bivalves. Je présente ici les origines, les évolutions, les limites et la polyvalence de 55 caractères morphologiques et liés à l'habitat, dont 13 sont propres aux brachiopodes, 23 aux bivalves et 19 ont évolué de manière convergente chez les deux groupes. Seuls 6,3 % des caractères des brachiopodes sont post-paléozoïques, contre 24 % chez les bivalves.

MOTS CLÉS
Brachiopodes,
bivalves,
modularité,
remplacement écologique,
contraintes évolutives.

L'extinction a touché 44 % des traits des brachiopodes, mais seulement 2 % de ceux des bivalves. Les caractéristiques associées à la prolifération des bivalves post-paléozoïques ont évolué bien plus tôt, notamment l'origine, au Cambrien inférieur, du pied extensible, du ligament de charnière et de la modularité morphologique intra-valve ; aucune de ces caractéristiques n'a évolué chez les brachiopodes et toutes ont conféré une polyvalence précoce aux bivalves. Des contraintes morphologiques étaient déjà présentes chez les brachiopodes du Cambrien inférieur et n'ont jamais été surmontées. Le plein potentiel des bivalves ne s'est concrétisé que lorsque l'intensification de l'activité biologique a rendu les mers du Mésozoïque et du Cénozoïque plus productives.

INTRODUCTION

Brachiopods and bivalves are lophotrochozoan animals that independently evolved a two-part (bivalved) mineralized external shell, whose valves grow by accretion in a spiral direction. Despite their superficial similarity and comparable times of origin during the early Cambrian, brachiopods and bivalves have contrasting evolutionary histories. With more than 6000 genera and 12000 fossil species, brachiopods achieved spectacular diversity and abundance during the Paleozoic and the first half of the Mesozoic (Carlson 2016; D. A. T. Harper *et al.* 2017) and then declined to about 350 extant species. Bivalves diversified through most of their history and now greatly outnumber brachiopods in extant species (about 20000) and individuals.

Previous work suggested that brachiopods have lower metabolic rates (Steele-Petrovič 1975, 1979; Vermeij 1987; Payne *et al.* 2014), slower growth (Vermeij 2015), lower fecundity (Law & Thayer 1991), lower tolerance of anoxia and high CO₂ levels in tissues (Clapham & Bottjer 2007a, b; Knoll *et al.* 2007), less ability to adapt to increasing productivity (Vermeij 1987; Vörös 2010), greater vulnerability to increasing turbidity and bioturbation (Steele-Petrovič 1979; Manojlovic & Clapham 2021), inability to survive dislodgement by predators and grazers (Vermeij 1977; Thayer 1983, 1985; Bradley 2010), limited competitive ability (Thayer 1986), and higher magnitudes of extinction during the end-Permian and other crises (Gould & Calloway 1980; Liow *et al.* 2015; Hsieh *et al.* 2019). The replacement of brachiopods by bivalves began during the Late Devonian (Leighton *et al.* 2013; Balseiro *et al.* 2014) but affected some environments more than others (Clapham & Bottjer 2007a, b; Clapham 2015). Brachiopods recovered rapidly after the Permian and remained common and diverse through the first half of the Mesozoic (Fraiser & Bottjer 2007), but with the extinction of large warm-water species during the Early Cretaceous (E. M. Harper & Peck 2024) they became largely restricted to deep-water and cryptic reef environments, although small brachiopods were locally abundant in shallow seagrass habitats as late as the Miocene (Dulai 2025). These hypotheses and trends treated brachiopods and bivalves as internally homogeneous groups and did not link potential advantages and adaptive shortcomings of their bivalved body plan to adaptability in the face of long-term environmental change.

From a preliminary survey of functionally important traits, I developed the hypothesis that bivalves have always had greater evolutionary potential to expand and modify the bivalved body plan, and that this potential was not fully realized until more intense biological activity in marine ecosystems created conditions that only bivalves were in a position to exploit. Here I test this hypothesis by documenting the functions, evolutionary potential, origins, and fates of variations on the bivalved theme. I distinguish among traits that are unique to brachiopods, unique to bivalves, or convergently evolved in both groups, and ask how and when these traits evolved and affected the brachiopod-bivalve replacement.

METHODS

From a deep reading of the literature and extensive observations on the morphology of living and fossil brachiopods and bivalves, I compiled a list of 55 morphological and ecological traits, some of which are unique to either brachiopods or bivalves and some are convergent in the two groups. For each trait I determined the published times of first and last appearance in each group at the period level. These data were drawn directly from fossils rather than from phylogenetic inferences, and thus reflect a literal reading of the fossil record. Most traits evolved multiple times independently, but only their first and last occurrences were considered. Statistical differences in the distribution of first appearances of phenotypes in the two groups were assessed with chi-square tests against expectations that no differences exist.

In order to assess differences in evolutionary potential between brachiopods and bivalves, I analyzed morphological modularity (or differentiation) within and between valves by identifying how many parts of the shell can vary semi-independently. This was done by examining adult valves for anteroposterior, dorsoventral, and left-right differentiation in shape, sculpture, relative size, and hinge dentition.

The focus on individual-level shell morphology, evolutionary potential, and habits contrasts with collective measures such as disparity, or morphospace occupation, in the two groups. Collective morphospace is a descriptive clade-wide summary that does not incorporate evolutionary potential or take into account many adaptive features relevant to the lives

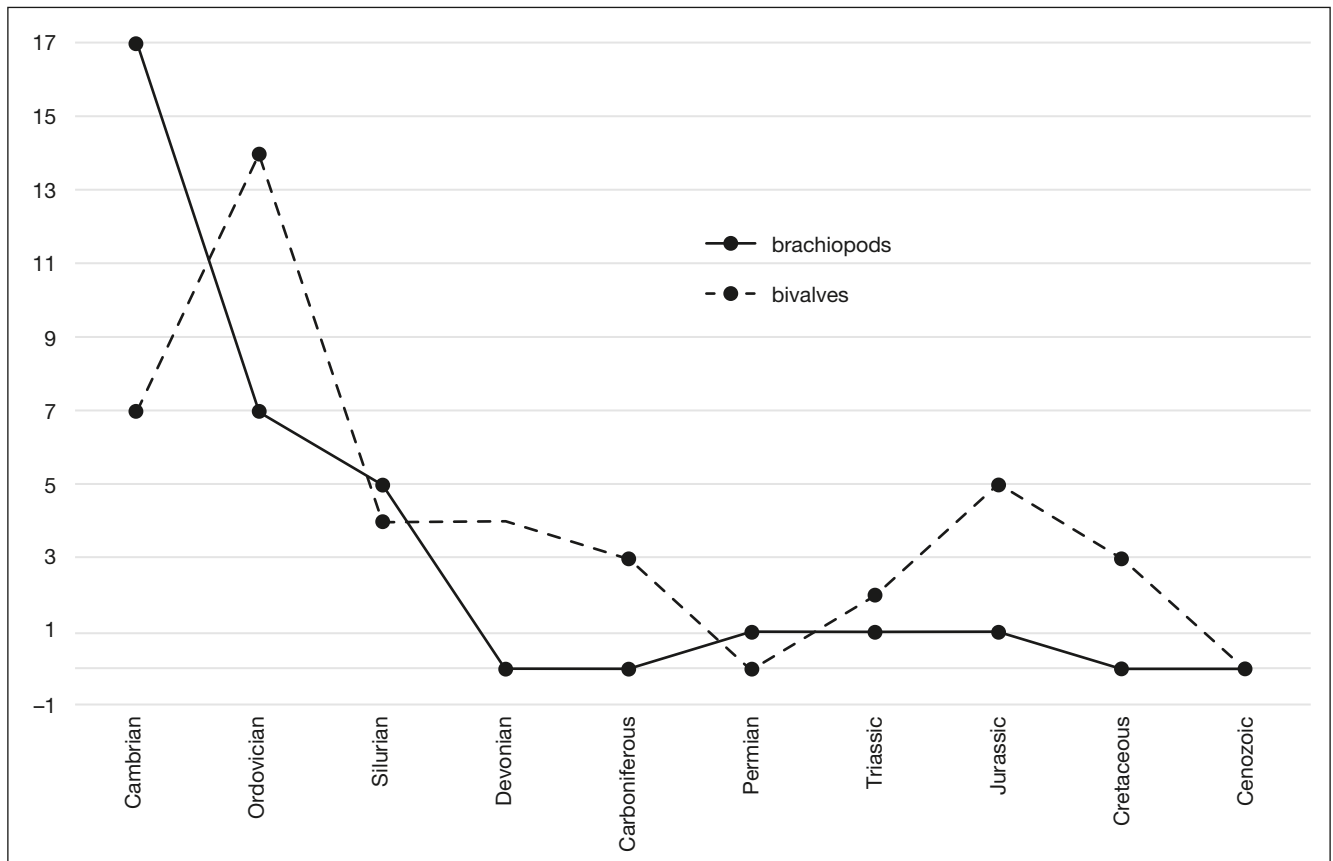


FIG. 1. — Number of brachiopod and bivalve trait origins per geological time interval.

TABLE 1. — Temporal ranges of brachiopod-only characteristics

Trait	Time range
Plane of symmetry perpendicular to commissure	early Cambrian to Recent
Single left-right valve module	early Cambrian to Recent
Body-wall musculature absent (Rhynchonelliformia)	early Cambrian to Recent
Attachment of mantle to whole inner valve surface	early Cambrian to Recent
Hydraulic opening of shell (Linguliformea, Craniiformea)	early Cambrian to Recent
Movable setae	early Cambrian to Recent
Loss of lower valve (Craniiformea)	Early Ordovician to Recent
Mineralized lophophore	Early Ordovician to Recent
Pedicle as part of animal for attachment to substrate	early Cambrian to Recent
Shell not in contact with substrate when attached by pedicle	middle Cambrian to Recent
Anchoring spines on lower valve	Late Ordovician to Triassic
Hinge dentition growing with continual resorption	Early Ordovician to Recent
Perforated valves (Pygopides)	Late Jurassic to Early Cretaceous

and interactions of individuals. My phenotypic approach also makes clear that large clades like Brachiopoda and Bivalvia are not internally homogeneous.

RESULTS

Of the 55 habitat and morphological traits examined, 13 (23.6%) are unique to brachiopods, 23 (41.8%) are unique to bivalves, and 19 (34.5%) evolved convergently in the two

groups (Tables 1-3). Of the 32 phenotypes of brachiopods, 24 (75%) appeared during the first 96 million years of the Phanerozoic (Cambrian and Ordovician); for bivalves this number is 21 (50% of 42; Fig. 1). Among the 19 convergent phenotypes, three evolved at about the same time during the early Cambrian in the two groups, 15 evolved earlier in brachiopods than in bivalves, and one evolved earlier in bivalves. Given the expectation that half of the convergent traits would have evolved earlier in brachiopods and half earlier in bivalves, this latter result is in favour of brachiopods

TABLE 2. — Temporal ranges of bivalve-only characteristics

Trait	Time range
Deposit-feeding	Early Ordovician to Recent
Burrowing without attachment structures	Early Ordovician to Recent
Endolithic habits	middle Silurian to Recent
Freshwater habits	Middle Devonian to Recent
Swimming habit	Late Devonian to Recent
Micropredation	Triassic to Recent
Parasitism/commensalism	?
Plane of symmetry coincident with commissure	early Cambrian to Recent
Each valve comprising two or three modules	early Cambrian to Recent
Overlapping valves at growing margin	Devonian to Recent
Secondary shell/crypt	Late Jurassic to Recent
Mobile extensible foot	early Cambrian to Recent
Elastic ligament	early Cambrian to Recent
Mantle retraction from shell margins	Ordovician to Recent
Single adductor muscle	Middle Ordovician to Recent
Byssus for attachment close to substrate	Early Ordovician to Recent
Crenulated inner valve margins	Ordovician to Recent
Serrated valve margins	Mesozoic to Recent
Permanently gaping valves	Ordovician to Recent
Valves rocking around vertical axis	?Ordovician to Recent
Inhalant/exhalant siphons and mantle fusion	Late Ordovician to Recent
Partial or complete envelopment of both valves by mantle	Late Jurassic to Recent
Sexual dimorphism	Early Jurassic to Recent
Bimineralic shell	Ordovician to Recent
Chalky deposits	Early Jurassic to Recent
Thick periostracum	?
Mineralized periostracum	Ordovician to Recent
Remote biomineralization	?

TABLE 3. — Temporal ranges of characteristics convergent in brachiopods and bivalves

Characteristic	Brachiopoda	Bivalvia
Suspension-feeding	early Cambrian to Recent	Early Ordovician to Recent
Photosymbiosis	Late Ordovician to Permian	early Silurian to Recent
Chemosynthetic habits	Silurian to Miocene	Early Ordovician to Recent
Shell pores/punctae	early Cambrian to Recent	Early Ordovician to Recent
Each valve asymmetrical	early Cambrian to Miocene	early Cambrian to Recent
Each valve twisted	Silurian to Miocene	Middle Devonian to Recent
Accessory shell plates	Late Triassic	Late Jurassic to Recent
Adductors to close shell	early Cambrian to Recent	early Cambrian to Recent
Diductors to open shell	early Cambrian to Recent	Carboniferous to Recent
Burrowing-enhancing sculpture	late Cambrian to Early Ordovician	Triassic to Recent
Protective spines	Silurian to Recent	early Carboniferous to Recent
Upper valve enveloped by mantle	Permian	Late Cretaceous
Cementation to substrate	early Cambrian to Recent	late Carboniferous to Recent
Clasping spines	Silurian to Permian	Middle Cretaceous to Recent (rare)
Passive weighting	Late Ordovician to Pliocene	early Silurian to Recent
Strophic hinge	early Cambrian to Triassic	early Cambrian to Recent
Astrophic hinge	late Cambrian to Recent	Middle Ordovician to Recent
Plicated valves	Middle Ordovician to Jurassic	Silurian to Recent
Zigzag valve margins	Silurian to Jurassic	mid-Cretaceous to Recent

is highly significant ($p < 0.001$, chi-square test). Only two brachiopod traits (6.3% of 32) originate during the post-Paleozoic as compared with 10 bivalve traits (24% of 42).

The post-Paleozoic brachiopod innovations discussed by Guo and colleagues (2024) did not include the two features identified here (the Late Triassic cooperculum, a supernumerary plate in labalid spiriferinides, and the perforated valves of Late Jurassic to Early Cretaceous pygopid terebratulides). Instead, the innovations seen in Mesozoic brachiopods all converge on traits and features of Paleozoic brachiopod

lineages, including protective and rootlike spines, plicated valves, valve cementation, concavo-convex shell form, asymmetrical valves, and chemosynthetic habits.

As might be expected from the precipitous decline of brachiopods, a large number of brachiopod phenotypes (14 of 32, 44%) are extinct and not represented in the extant fauna, including 12 that converge with bivalve phenotypes. Only one of 42 bivalve phenotypes (2.4%) is extinct. This difference in phenotype extinction between brachiopods and bivalves is highly significant ($p < 0.01$, contingency test).

DISCUSSION

Was post-Paleozoic predominance of bivalves correlated with or causally linked to the continued proliferation and persistence of bivalve innovations and the near absence of novelty in brachiopods? The answer is a qualified no. Post-Paleozoic innovations in bivalves hardly contributed to bivalve-wide diversification but instead mostly affected small radiations: micropredation (mostly in deep-water Propeamussiidae and septibranchs; Morton 1981; Waller 2006), secondary shell tube/crypt (in some endolithic or slow-burrowing Gastrochaenoidea and Clavagelloidea; Morton 1985; Savazzi 2005; Sigwart *et al.* 2025), mantle envelopment of the upper valve (some Late Cretaceous Hippuritoidea; Skelton & Wright 1987; Schumann 2010) or both valves (in some Galeommatoidea and partially in some Gastrochaenoidea; Morton 1980; Goto *et al.* 2012), sexual dimorphism associated with larval incubation but not mate choice (in some members of five clades; Heaslip 1969; Turner & Yakovlev 1983; Lützen & Nielsen 2005; Barnhart *et al.* 2008; Yoshimura *et al.* 2019; Karapınar *et al.* 2021; Pérez & Soto 2021), chalky deposits associated with rapid shell growth (in some Ostreoida and some Mesozoic Pterioidea; Chinzei 2013; Banker & Sumner 2020; Checa *et al.* 2020; Posenato *et al.* 2022; Posenato & Crippa 2023), accessory shell plates (endolithic Pholadoidea; Purchon 1955; Monari 2009), zigzag valve margins (some Ostreoida, Anomioidea, and tridacnine Cardiidae Carter 1968), and clasping spines around narrow objects (Carter 1968). Only burrowing-enhancing ratcheted sculpture, during the Triassic (Hautmann 2001), is widespread in mainly post-Mesozoic infaunal bivalves (Checa & Jiménez-Jiménez 2003; Vermeij & Thomson 2026).

Morphologies and habitat traits that eventually led to post-Paleozoic bivalve proliferation all originated during the early and middle Paleozoic. These include infaunal burrowing and adaptations to it such as siphons formed by mantle fusion (Stanley 1968, 1970), permanent anterior and posterior shell gaps (Stanley 1970; Runnegar 1974), and valves rocking on a vertical axis (Savazzi 1990; Checa & Cadée 1997); only serrations with asymmetrical projections on the posterior sector of the valves of some shallow-water burrowers are of Mesozoic origin (Vermeij 2013a). Early origins and greatly delayed radiations apply to swimming bivalves (Stanley 1970; Hayami 1991), chemosymbiotic bivalves (Taylor & Glover 2010; Stanley 2014), photosymbiotic bivalves (Vermeij 2013b), bivalves with protective spines (E. M. Harper & Skelton 1993), valves overlapping at growing margins (Vermeij 2013a), crenulated inner valve margins (Vermeij 2013a), and plicated valves (E. M. Harper & Skelton 1993). Endolithic bivalves that bore into hard substrates are known from the Silurian onward but radiated only after the Paleozoic (Vermeij 1987).

Guo and colleagues (2024) likewise correctly noted that new or re-emerging traits in post-Paleozoic brachiopods did not contribute to diversification. All these traits evolved in, and were restricted to, very small clades, most of which are no longer represented in the extant fauna.

An important and unexplored difference between brachiopods and bivalves resides in the morphological differentiation within the shell. Although each valve is rigid and would therefore seem to comprise a single morphological module, as reflected in the common usage of the term “generating curve” to refer to the shape of the valve outline, inspection of bivalved shells indicates that sculptural expression in the anterior, median, and posterior sectors of the valve differs in many species (Vermeij 2013a; Vermeij & Thomson 2026). These sectors, which are often demarcated by a radial rib, keel, or change in curvature, must reflect differentiation of the mantle edge where shell deposition in the spiral direction takes place. The fully calcified shell margin is thus indeed rigid, but rigidity does not mean that the margin is to be interpreted as unitary. Note that marginal modularity is independent of any anatomical differentiation that is reflected on the shell’s inner surface as indicated by muscle impressions or, in the case of brachiopods, muscle platforms and lophophore supports.

Greater morphological modularity in the shell provided bivalves with a broader range of adaptive possibilities than was achievable in brachiopods. The valves, on either side of the plane of symmetry coinciding with the commissure, are never identical, differing in hinge dentition and, in many derived lineages, in size, convexity, and sculpture (Palmer 2024). They thus constitute two distinct modules (Roopnarine & Goodwin 2024). In addition, each valve comprises two or three morphologically distinct sectors from anterior to posterior (Vermeij 2013a; Vermeij & Thomson 2026), a trait already evident in the earliest bivalves (Cope 1996). Differentiation of the hinge dentition may further divide both the anterior and posterior sectors of the valves. There are thus at least eight degrees of freedom (semi-independent modules) in the bivalve shell.

In brachiopods, the plane of symmetry separates the right and left sides of each valve. There is internal morphological differentiation along the anteroposterior axis of each valve and between the upper and lower valves, but very rarely between the right and left sectors of each valve. Early Cambrian stenothecoid stem brachiopods and several lineages of Silurian to Miocene rhynchonelliforms have asymmetrical valves (Fürsich & Palmer 1984; Gaspard & Charbonnier 2020; Johnston & Streng 2021), but the two halves differ primarily in size and in the orientation of the commissure, and the asymmetry develops late in ontogeny. Each valve thus has a single left-right module, implying a total of five (not eight) semi-independent degrees of freedom in brachiopod shells. This characterization is consistent with genetic evidence. The morphologically upper and lower valves correspond to two developmental domains, which in early stages of development are anatomically anterior and posterior (Altenburger *et al.* 2017) that become dorsal and ventral as the result of body folding (Cohen *et al.* 2003; Plandin & Temereva 2023; Kuzmina & Malakhov 2025). This development is consistent with the absence of a hinge and of hinge dentition in the earliest brachiopods and in linguloids, and with these structures being derived within Brachiopoda (Carlson 2016). Within-valve modularity has not been genetically investigated in either brachiopods or bivalves.

Additional early bivalve-only features provide versatility by affecting movement and attachment. The muscular foot, inherited from univalved conchiferans, enabled locomotion, first on the sediment surface (Peel 2023) and later adapted for burrowing beginning in the Early Ordovician (Stanley 1970). Glands in the larval foot extrude the fibrous byssus for attachment, which beginning in the Early Ordovician was adopted by adults of numerous lineages as a means of flexible attachment to substrates while also allowing for some locomotion and for recovery from dislodgement (Stanley 1972). The elastic ligament, already present in the earliest bivalves, opens the shell quickly upon relaxation of the adductor muscles that shut the valves (Waller 1990; Ubukata 2000). Movement of the mantle margin relative to the shell is enabled by muscles connecting the mantle and shell at the pallial line just inside the valve margins. In some pteriomorphians the mantle can be withdrawn far into the shell, whereas in many heterodont bivalves the mantle can extend over the valve margins (Vermeij 2013a).

The full range of bivalve-only traits is realized in warm shallow seas, in deep marine, cold, or fresh waters. This is notably the case with crenulated and serrated valve margins, ratcheted sculpture, enveloped valves, and chalky deposits. Most other bivalve-only morphologies are known in at least some freshwater bivalves, either by inheritance from marine ancestors or by independent evolution in freshwater lineages, as with protective spines, gaping valves, and sexual dimorphism. Despite the limited morphological diversity of freshwater as compared with marine bivalves, and the early (Middle Devonian) origin of freshwater bivalves, many lineages colonized lakes and streams and, like their marine counterparts, achieved very high extant diversity, especially in Unionoidea, Cyrenoidea, and Shaerioidea. No brachiopods are known to have colonized fresh water.

The versatility of the bivalve shell is not matched in brachiopods. There is no mobile foot in brachiopods, and the mantle is attached to the whole of the valve interiors, precluding mantle extension and retraction (Vinn *et al.* 2025). Attachment to the substrate is typically by the pedicle, a posterior extension of the animal that in rhynchonelliforms allows some reorientation but not locomotion (LaBarbera 1978); the pedicle cannot reattach after dislodgement (Thayer 1983), although in *Lingula* Bruguière, 1791 the pedicle tip can autotomize and regenerate (Emig 1983). Lingulide burrowing is slow, always aided by the pedicle (Savazzi 1986). With the possible exception of some Permian lytoniid productides (Seilacher 1998), there is no ligament in brachiopods, and shell opening is slow, accomplished either hydraulically by pushing the valve apart as tissues swell with water (in linguliforms and craniiforms; Plandin & Temereva 2025), or by diductor muscle contraction (in rhynchonelliforms; Rudwick 1970; Carlson 1989). Some semi-infaunal pinnid and endolithic pholadid bivalves also open the shell with diductors (Yonge 1953; Purchon 1955).

Brachiopod-only features impose constraints that do not apply to bivalves. Besides limited shell modularity, slow shell opening, vulnerability of the pedicle, and mobility-limiting attachment of the mantle to the entire shell interior discussed

above, a major internal constraint on brachiopods is that the lophophore supports, which became mineralized in several lineages beginning in the Early Ordovician (Carlson 2016; Kuzmina *et al.* 2021), takes up a large fraction of internal shell volume. In extant brachiopods the mineralized lophophore supports account for 60 to 75% of internal volume (Peck 1992), which together with the diductor muscles leaves little room for other organs. Bivalve ctenidia, which function in respiration and suspension-feeding and which are not mineralized, take up 20% or less of shell volume (Peck 1992). The shell-opening mechanism in bivalves is external to the body.

In many productide and some other rhynchonelliforms without a pedicle, anchorage on soft bottoms is by spines growing through the lower valve (Grant 1980; Pérez-Huerta 2012). These anchoring spines are last seen in the Late Triassic (Cowen & Rudwick 1970), reflecting their increased ineffectiveness in post-Triassic environments where sedimentation rates are high (Seilacher 2005). Limited sedimentation also made possible the unusual extinct condition of having both sides perforated to allow passage of a tube that conveyed water and particulate matter from the sediment to the lophophore (Vörös 2023). This morphology was restricted to Late Jurassic and Early Cretaceous pygopide rhynchonelliforms. Also extinct are 11 brachiopod traits that converge on bivalve phenotypes. These include photosymbiosis and its attendant specializations such as an enveloped and recessed upper valve (Cowen 1970; Angiolini *et al.* 2019), chemosymbiotic habits (Kiel & Peckmann 2019), accessory shell plates (in a Late Triassic laballid spiriferoid of the genus *Sondylospira*; Hoover 1983), burrowing-enhancing ratcheted sculpture (Savazzi 1986), valve asymmetry (Lee 1980; Fürsich & Palmer 1984), clasping spines (Pérez-Huerta 2012), passively weighted valves in soft substrates (MacKinnon 1987; Chen *et al.* 2023), strophic hinges in which the hinge line coincides with the axis of valve rotation (Rudwick 1959), plicated valves and zigzag margins (Rudwick 1964), and twisted valves (Lee 1980; Gaspard & Charbonnier 2020).

CONCLUSIONS

Data on the times of appearance, fates, and functions of morphological and habitat characteristics show that, although brachiopods evolved many traits earlier than bivalves, including traits that independently evolved also among bivalves, these early innovations did not provide an initial evolutionary advantage. To the contrary, the inherently greater versatility of bivalves than of brachiopods was evident during the early Cambrian when both groups originated. Why, then, did it take so long for bivalves to become the predominant animals in the sea and the only ones in fresh water?

The answer, already hinted at in previous hypotheses listed in the introduction, is that the conditions of life changed, particularly after the Triassic, in ways that bivalves were in a better position to accommodate. These include intensifying predation, grazing, turbidity, bioturbation, and both planktonic and benthic productivity (Vermeij 1977, 1987;

Tarhan *et al.* 2025; Singh *et al.* 2025). Brachiopod traits are on the whole more suitable for slower and more passive modes of life, whereas bivalves are and likely always were higher-powered animals (Payne *et al.* 2014). Even sedentary epifaunal bivalves grow faster and to a larger size than their brachiopod counterparts. It is therefore not key innovations that spurred bivalve predominance after the Triassic, but changing conditions of life, especially those in warm, shallow, productive seas; nor are the contrasting fates of brachiopods and bivalves the result of chance or of mass extinctions as Gould & Calloway (1980) thought. That said, both the Brachiopoda and Bivalvia are adaptively heterogeneous clades. There were some fast-growing Paleozoic brachiopods, and many bivalves inhabit cold or nutrient-poor settings where passivity is the norm. The bivalve body plan is simply more versatile and better predisposed to adapt to a wider range of environments than that of brachiopods.

The phenotypic approach adopted here is applicable to other cases of partial replacement over time, including stalked echinoderms by mobile ones, shell-bearing cephalopods by more squid-like or octopus-like coleoids, and spore-bearing plants by seed plants. More complex cases, such as the long-term coexistence of the two great branches of tetrapods (diapsids and therapsids), which do not involve partial replacement, would also be highly instructive. The key is to consider individual-level adaptive traits, together with traits that either inhibit or expand evolutionary versatility, in relation to ecosystem-wide changes that the animals themselves helped bring about.

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