The Evolution of Brachiopoda

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Abstract

Brachiopods are (perhaps all too) familiar to any geology student who has taken an invertebrate paleontology course; they may well be less familiar to biology students. Even though brachiopods are among the most significant components of the marine fossil record by virtue of their considerable diversity, abundance, and long evolutionary history, fewer than 500 species are extant. Reconciling the geological and biological perspectives is necessary in order to test hypotheses, not only about phylogenetic relationships among brachiopods but also about their spectacular decline in diversity in the end-Permian mass extinction, which permanently reset their evolutionary trajectory. Studying brachiopod ontogeny and development, population genetics, ecology, physiology, and biogeography, as well as molecular systematics and phylogenomics, enables us to better understand the context of evolutionary processes over the short term. Investigating brachiopod morphological, taxonomic, and stratigraphic records over the Phanerozoic Eon reveals historical patterns of long-term macroevolutionary change, patterns that are simply unknowable from a biological perspective alone.

1. INTRODUCTION

Brachiopods (from the Greek, meaning "arm-foot"), also known as lamp shells or the "other" bivalves, have played a central role in both geologists' and biologists' understanding of the history and evolution of life on Earth. They assert their importance quietly, by their near-ubiquitous presence in the rock and fossil record and their remarkable diversity throughout the Phanerozoic Eon, up to and including the Holocene. However, because their shells no longer litter our beaches worldwide, and they live largely hidden and unobtrusive, at great depths and in commonly inaccessible locations at low diversity and abundance, they have acquired a certain mystique in biology. In the process of untangling the evolutionary history of brachiopods, it is clear that geologists and biologists have approached the topic of brachiopod evolution differently. A comprehensive understanding of brachiopod evolutionary pattern and process will look somewhat different as the evidence and analysis of evolution differ, and I think this difference has generated, and unnecessarily perpetuated, a kind of dynamic tension between paleontologists and neontologists. This situation has, happily, improved markedly over the past decade. It is increasingly evident that paleontologists and neontologists, geologists and biologists, must to work together more effectively than we have in the past. Only by doing so can we reach a more complete understanding of the evolution of brachiopods, a clade of marine organisms with significant, if diminished, extant diversity, and a long, rich, and tremendously informative fossil record.

2. WHAT ARE BRACHIOPODS?

Brachiopods are bivalved lophophorates, recognized today by a distinctive combination of mineralized and nonmineralized morphological features (**Figure 1**). The current, most widely cited definition of Brachiopoda (Williams et al. 2000) presents something of a paradox: Of all the many features used to define the phylum, only the presence of a bivalved, bilaterally symmetrical organophosphatic or organocarbonate shell can be preserved with fidelity in the fossil record, which records fully 95% of brachiopod diversity. All other features can be verified only in the extant representatives of the group, which comprise fewer than 5% of the total number of named brachiopod species. Because brachiopods are known primarily as fossils, paleontologists, studying variation in shell morphological features, have largely put themselves in charge of the identification and recognition of species, as well as the establishment of higher taxa and the arrangement of those taxa in a scheme of classification. As for most other organisms over the past several centuries, the scheme used for brachiopods has been the Linnean hierarchy, and the structure of the hierarchy is widely assumed to convey some sense of their evolutionary history.

Despite the dominance of paleontologists in constructing our current worldview of brachiopod evolutionary history through classification, biologists first gave names to brachiopods. Dumeril (1806), a French zoologist, first used the term Brachiopodes to refer to an order of Mollusques, one of nine divisions into which he placed all animal life. Since the early 1800s, a dizzying number of classifications have been proposed, adopted, and abandoned (Muir-Wood 1955), based on the presumed homology of morphological features involving the form of the lophophore (Gray 1848), the nature and orientation of the pedicle in relation to the valves (Beecher 1891), and, most recently, the nature of articulation between the two valves (Huxley 1869, Williams & Rowell 1965), modified by valve mineralogy and microstructure (Williams et al. 2000) (see sidebar, Anatomical Terms).

Many evolutionary questions are raised by the current classification (Williams et al. 2000) (see sidebar, Phylogenetic Terms). Is phylum Brachiopoda a clade (a single system of common ancestry) or not? Are the relatively few extant species representative of the phylogenetic breadth
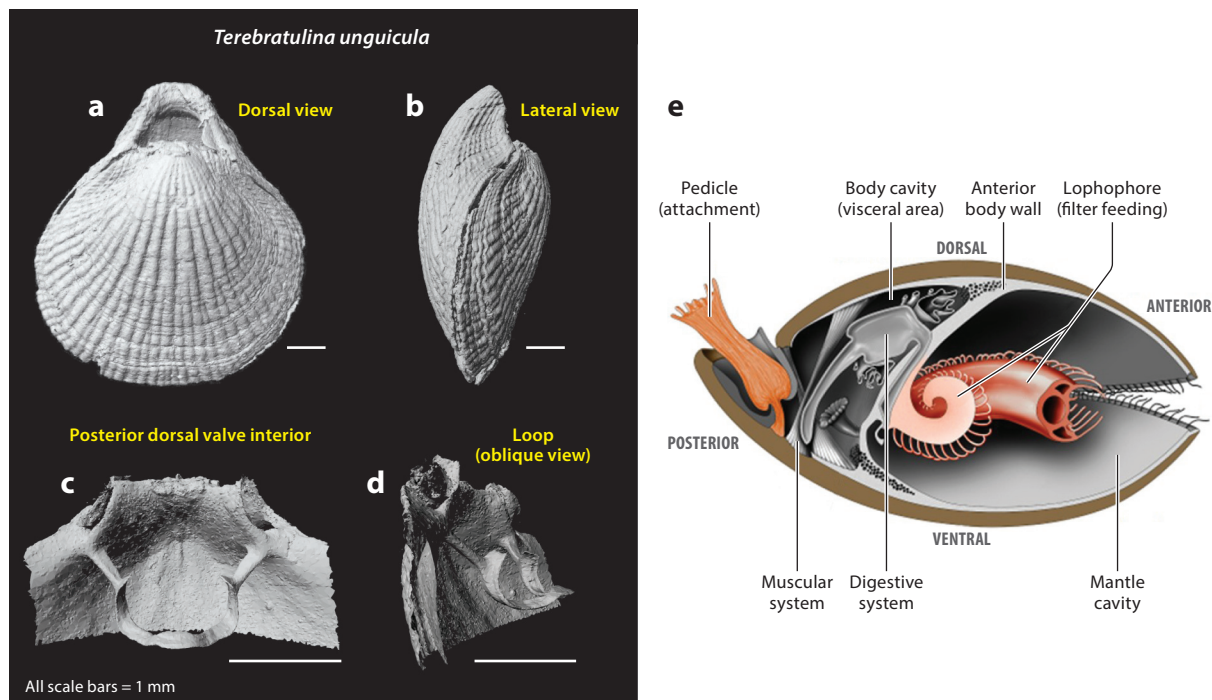
Figure 1

Three-dimensional models constructed from computed tomography scans of an older juvenile of *Terebratulina unguicula* (CAS183808; locality info: California, Cordell Bank National Marine Sanctuary, Cordell Bank); Terebratulida. (*a*) Dorsal view of articulated valves; pedicle opening visible near top of ventral valve. (*b*) Lateral view; ventral valve on left. (*c*) Partial view of posterior dorsal valve interior, showing sockets on either side of medial posteriormost diductor muscle attachment, crural processes, and incomplete (juvenile) short loop. (*d*) Oblique view of loop, illustrating its ventral projection into the mantle cavity. (*e*) Reconstruction of half of an articulated terebratulide brachiopod sectioned along the plane of symmetry to expose internal anatomy. Panel *e* reproduced with permission from L. Holmer, Uppsala University, Sweden.

ANATOMICAL TERMS

Lophophore: The lophophore is an organ of two arms that bear ciliated tentacles used for filter feeding and respiration (**Figures 1e** and **5**) in brachiopods. Cilia (minute hair-like structures) generate a unidirectional current of water through the mantle cavity, extracting oxygen and food particles and transporting them to the mouth. Gametes and waste products are expelled from the mantle cavity by the same process. Lophophorates are animals possessing a lophophore.

Pedicle: The pedicle is a stalk-like structure emerging between the two valves of most brachiopods, facilitating attachment to a hard substrate (**Figure 1e**). Lingulida are free-living brachiopods that burrow in soft substrates; their pedicle does not tether them to a hard substrate.

Strophic and astrophic: These are two end-member types of valve hinge lines. Strophic hinges are straight (**Figure 6a–c,e**). Astrophic hinges are curved (**Figures 1a** and **6d,f**).

of the entire group? How are extant and extinct species related to one another, and what can these inferences reveal about character evolution among brachiopods? How are brachiopods related to other metazoans: Are brachiopod lophophores homologous to phoronid and bryozoan lophophores or not? Does the classification reveal useful, testable patterns about brachiopod macroevolution?

3. WHAT DO WE KNOW ABOUT BRACHIOPOD EVOLUTION?

And how do we know it? On the basis of what evidence? What do we assume? Which assumptions have been tested? Evolution, described simply as change over time, has many dimensions that can be approached and studied in different ways.

3.1. The Geological Perspective

Because the vast majority of named brachiopod species are extinct, the geological perspective on brachiopod evolution has dominated our understanding. The traditional approach to studying brachiopod evolution examines macroevolutionary patterns of change in the stratigraphic ranges of named taxa over geological time, and in the morphological characters that define them. Classifications sort differences among organisms on the basis of their morphology, and for brachiopods, that means primarily features of shell morphology. Central to this approach is the assumption that morphological change adequately and accurately represents evolutionary change,

and that named taxa represent evolutionary entities (clades). All macroevolutionary hypotheses rely on this fundamental assumption. Because these assumptions are rarely tested, it is difficult to know how generally true they are; there is much room for uncertainty (Jablonski & Finarelli 2009a,b; Smith & O'Meara 2009; Bitner & Cohen 2015). It is critically important, therefore, that we seek to understand what classification represents with respect to phylogeny in order to study large-scale patterns and processes of evolution, and not merely artifacts of pattern resulting from nonphylogenetic classifications.

Brachiopods are morphologically and taxonomically diverse. The most current and complete classification, at the lowest taxonomic level (genus), is detailed in the six volumes of the *Treatise on Invertebrate Paleontology*, Part H (Revised): *Brachiopoda* (Kaesler & Selden 1997–2007) with contributions from 47 paleontologists from around the world; nearly 5,000 genera are described and classified morphologically into 26 orders and eight classes (**Figure 2**). After encouragement from R.C. Moore, the initial brachiopod *Treatise* volumes, published in 1965, were prepared and coordinated largely by Alwyn Williams and Bert Rowell. Philosophical disagreements led G. Arthur Cooper to leave the initial *Treatise* project, but he produced many outstanding contributions to brachiopod systematics (e.g., Cooper 1956, Cooper & Grant 1969–1976) that complement the *Treatise* compilation.

Cooper shared the opinion of Schuchert, not uncommon among invertebrate paleontologists of the early twentieth century, that paleontologists must first establish a classification based on patterns discerned in the fossil and rock (stratigraphic) record, then inductively address comparative anatomy, and finally attempt to discern relationships, or the how and why of evolution. Cooper's perspective was further bolstered by two additional concerns, homeomorphy (Schuchert & Cooper 1932) and incomplete sampling (Koch 1987), both of which could lead one astray in trying to discern phylogenetic relationships. Furthermore, any variation discernible in a fossil was thought to justifiably form the basis for naming a new species or genus, which led to a fair bit of splitting in taxonomy (Cooper 1956). This practice allowed for the possibility of increasingly smaller stratigraphic subdivisions to be distinguished by these different morphologies. Other paleontologists largely shared this perspective on the study of brachiopod evolution (Muir-Wood 1955, Muir-Wood & Cooper 1960, Boucot et al. 1964, Cooper & Grant 1969–1976), as did Davidson (1886–1888), Hall & Clarke (1892), and other much earlier paleontologists, whose collections and intellectual contributions provide a temporally and geographically rich empirical foundation for our understanding of brachiopod evolution today.

This view of classification and phylogeny is at odds with brachiopod biologists such as Beecher (1891) and Thomson (1927), as well as a number of vertebrate paleontologists, who were more directly concerned with understanding the process of evolution itself than with how it was ultimately revealed as a pattern in the fossil record. "Phylogeny must itself be determined before classification can be based on it" (Simpson 1945, p. 3). Williams, first with Rowell (1965) and then with many others (Williams et al. 1996, Kaesler & Selden 1997–2007), labored to produce a hybrid, both practically and philosophically, of these two extremes (Carlson 2001), advocating an empirical approach to elucidating evolution, a view shared by Rudwick (1970) and others.

Elements of these philosophical differences persist today largely unacknowledged and, until recently, have made closer collaborations difficult between brachiopod paleontologists and biologists. Some paleontologists wonder, How can studies of the only 5% of morphological diversity that is still extant be used to generalize evolutionary patterns and processes to the rest of the 95%? Some biologists wonder, How can evolution be understood when we lack a foundation of direct evidence about the relationships among morphology, genetics, and development and the ecological and environmental context within which brachiopods live today?
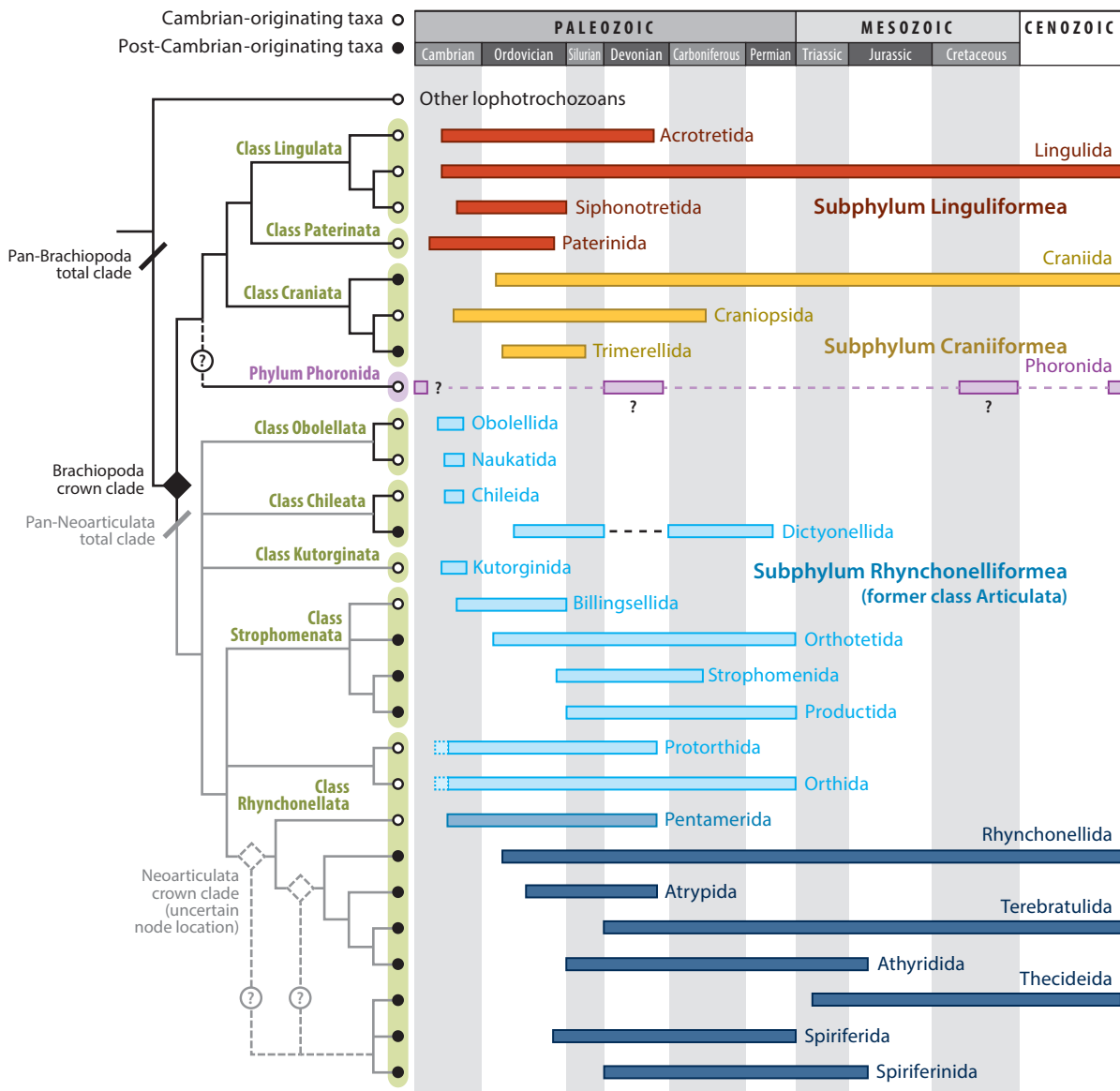
Figure 2

Consensus cladogram (*left*), illustrating a hypothesis of phylogenetic relationships among named orders of brachiopods; elongated green ellipses around terminal circles denote eight named brachiopod classes, plus Phoronida. Stratigraphic ranges (*right*) of named orders are illustrated from Cambrian to Recent. The uncertain position of Thecideida, Spiriferida, and Spiriferinida makes the position of the paraphyletic Pentamerida (*dark blue*) in the crown clade uncertain. Figure adapted with permission from Carlson (2007).

3.2. The Biological Perspective

Because so few named brachiopod species are living today, the biological perspective on brachiopod evolution has historically been more limited than the geological perspective. Comparative information in textbook compendia (Hyman 1959; Brusca & Brusca 1990, 2003) is often generalized to the entire phylum from a small number of species, in part because many brachiopods tend

to live today at great depths or in relatively inaccessible locations, and thus are difficult to collect and to study in situ.

The biological perspective on brachiopod evolution that has flourished more recently emphasizes phylogeny over stratigraphy and focuses on evolutionary transformations inferred over geological time based on patterns of internested taxa in a phylogenetic diagram, representing evolving combinations of shared derived characters (Carlson 1995, 2007) (**Figure 2**). Beginning with the development of polymerase chain reaction techniques in the 1980s, technological breakthroughs have revolutionized the field of molecular systematics and enabled sources of heritable information, beyond proteins, to be sequenced much faster and on a much larger sample of species than previously (Field et al. 1988). Determining patterns of divergence among ancient lineages became popular initially on the basis of comparisons of sequences of 18S rRNA, and later with additional genes and improved analytical techniques. The molecular systematic approach is now the standard for investigating phylogenetic relationships among extant taxa (Sperling et al. 2011, Cohen 2013, Giribet 2015). Most recently, next-generation sequencing techniques have allowed this field to take another major leap forward with technology that enables the rapid and relatively inexpensive reconstruction of evolutionary relationships among massive numbers of taxa using phylogenomic data (e.g., Hejnol et al. 2009, Nesnidal et al. 2013, Luo et al. 2015).

3.3. A Combined Perspective

Reconciling the biological and geological points of view is beginning to be accomplished (Giribet 2008, 2015; Valentine 2009; Slater et al. 2012; Hunt 2013), but only rather slowly among brachiopod workers, most of whom were trained from a geological perspective. Clearly, an approach combining geological and biological perspectives is the most productive, efficient, and informative way forward. This is a vastly more attainable goal now than it was a century ago, or even a decade ago, and it presents many compelling new research possibilities to brachiopod paleontologists and biologists who are committed to working together to solve evolutionary problems.

Progress is being made toward the goal of achieving a phylogenetic classification (de Queiroz & Gauthier 1990, de Queiroz et al. 2016). This approach, in my opinion, is the best way forward for two reasons: First, it establishes explicit testable hypotheses that acknowledge both extant and extinct species, and second, the process of developing phylogenetic definitions of taxa requires particularly careful, detailed examination of all available evidence. Both result in more thoughtfully considered and defensible phylogenetic hypotheses and classifications. Phylogenetic definitions of crown clades (i.e., groups that include all the descendants, extant and extinct, from a single common ancestor of all extant species) Brachiopoda and Neoarticulata and total clades Pan-Brachiopoda and Pan-Neoarticulata are currently in press (Carlson & Cohen 2016). One of the practical difficulties in adopting a fully phylogenetic approach to brachiopod classification, despite its philosophical advantages, is the fact that so few brachiopod species are extant, and relationships between the few extant and the many extinct species are not yet known in sufficient detail. Much more work at the species level is necessary.

4. BRACHIOPODS ARE MOST CLOSELY RELATED TO WHICH CLADE OF METAZOA?

Possession of a lophophore, a ring of ciliated tentacles that surrounds the mouth and excludes the anus, is a distinctive feature that has been used to support the close relationship of brachiopods, bryozoans, and phoronids (Emig 1984, Nesnidal et al. 2013). However, like wings purporting to

Protostome: In protostomes ("first mouth"), the oral end of the animal develops from the first opening to form in early development (e.g., in molluscs, annelids, and arthropods).

Deuterostome: In deuterostomes ("second mouth"), the oral end develops from a second opening forming in early development (e.g., in echinoderms and chordates).

Mesoderm: The mesoderm is the middle layer of the three primary germ layers in the very early embryo, between the endoderm and ectoderm.

Trochophore larvae: This type of planktonic larva swims by the action of bands of cilia beating in synchrony.

Lecithotrophic larvae: Lecithotrophic ("yolk-eating") larvae get their nutrition solely from yolk originally in the egg; they commonly live in the water column for a short period of time (days to weeks).

Planktotrophic larvae: Planktotrophic ("plankton-eating") larvae are capable of feeding and live in the water column for longer periods of time (weeks to months), increasing their dispersal capabilities.

Heterochrony: Heterochrony describes the evolutionary consequences of changes in developmental timing or rate. Paedomorphic taxa, as adults, appear similar to juveniles of their ancestors; neotenic taxa decrease rate of development, whereas progenetic taxa truncate development. Peramorphic taxa delay maturation and extend their development beyond the adults of their ancestors.

unite birds and bats, the monophyly of the lophophore has been questioned, particularly when evaluated in concert with other traits.

Where the mouth develops and how the mesoderm originates and develops during early development were considered to be highly conserved homologous characteristics indicating broad patterns of phylogenetic affinity among metazoans. Hyman (1959) noted that brachiopods represent a curious mosaic of both deuterostome and protostome characteristics and was reluctant to suggest a close relationship with either group. Over the next few decades, on the basis of additional embryological and morphological evidence, brachiopods were considered to be more closely related to the deuterostomes (Eernisse et al. 1992, Luter & Bartolomaeus 1997, Nielsen 2002) (see sidebar, Developmental Terms).

Appreciation of the broader significance of brachiopods in metazoan evolution was triggered by the Field et al. (1988) study that attempted to reconstruct the molecular phylogeny of the animal kingdom by comparing sequences of nucleotides from small-subunit (18S) rRNA—at the time, a lofty but tremendously exciting goal. Field et al. (1988) concluded, on the basis of the inclusion of *Lingula reevi* in their study, that brachiopods were more closely related to molluscs (a protostome group) than to hemichordates and other deuterostomes. If robust, this molecular analysis would indicate that numerous significant developmental characters had evolved in parallel between the brachiopods and the deuterostomes (Eernisse et al. 1992, Luter & Bartolomaeus 1997, Peterson & Eernisse 2001), which was unsettling to many. Many researchers subsequently sequenced additional species, attempting to test the conclusions of Field and colleagues and establish an ever more robust and defensible phylogeny of all animals. These studies included at least one, sometimes two or three, brachiopod species, in part because of their mosaic of features, articulated so clearly by Hyman (Giribet et al. 2000, Paps et al. 2009, Sperling et al. 2011). From these and other studies, the Lophotrochozoa (Halanych et al. 1995) emerged, a clade that includes, among others,
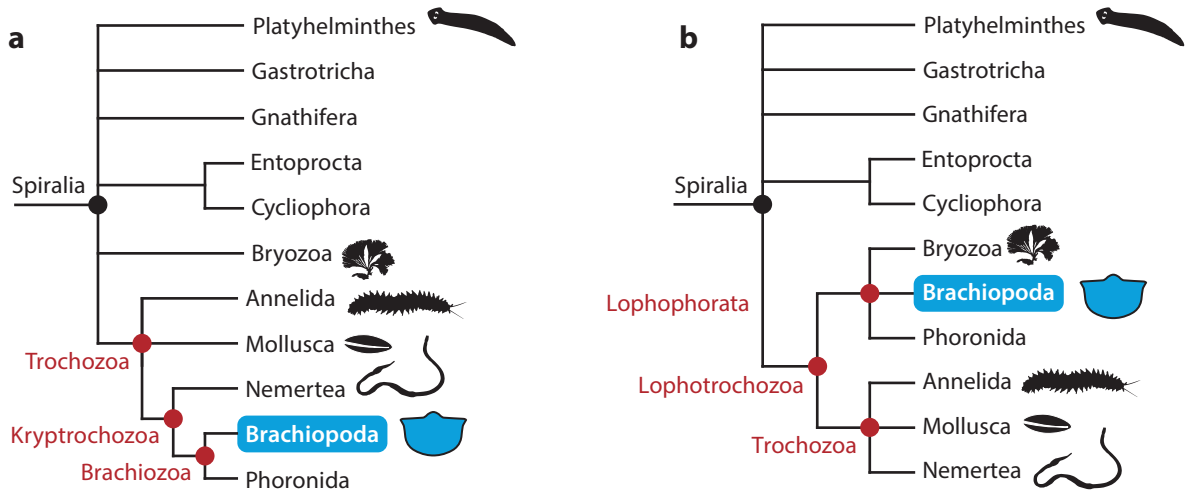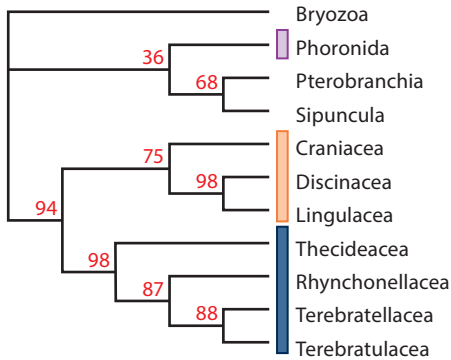
Figure 3

Hypotheses of phylogenetic relationship among Spiralia. Red dots indicate nodes with poor or conflicting support, and names that have been associated with those clades are in red; blue rectangles highlight the position of Brachiopoda. (*a*) Brachiopods and phoronids as sister taxa, with bryozoans more distantly related (from Hejnol et al. 2009). (*b*) Brachiopods and phoronids in a polytomy with bryozoans in Lophophorata (from Nesnidal et al. 2013). The organism silhouettes were illustrated by Noah Schlottman and submitted to PhyloPic (**http://www.phylopic.org**). They are available for reuse under the Creative Commons Attribution-ShareAlike 3.0 Unported license. Figure adapted from Dunn et al. (2014) with permission from Annual Reviews.

molluscs, annelids, bryozoans, phoronids, and brachiopods, deriving its name from morphological features of the lophophore and trochophore larvae.

Relationships among the lophotrochozoans have been difficult to establish (Giribet 2008), but until recently a consensus was beginning to emerge in which brachiopods and phoronids would form a clade more closely related either to molluscs (Mallatt & Winchell 2002, Paps et al. 2009, Luo et al. 2015) or to annelids (Dunn et al. 2008, Podsiadlowski et al. 2009), with bryozoans more distantly related, near the base of the lophotrochozoan clade (Nielsen 1995, 2002; Hejnol et al. 2009; Paps et al. 2009) (**Figure 3***a*). More recent phylogenomic studies, however, have recovered a monophyletic Lophophorata (Nesnidal et al. 2013) (**Figure 3***b*), which supports a hypothesis proposed initially by Emig (1984) on the basis of morphology. Relationships among phoronids and brachiopods remain contentious: Are they separate clades (**Figure 4***a,b*) or internested clades (**Figure 4***c*)? Cohen (2000) proposed the hypothesis that phoronids are brachiopods that have secondarily lost the bivalved shell, along with other morphological modifications. Despite the fact that this hypothesis nests one phylum inside another, which can be difficult for those with a static taxic view of the world to accept, this hypothesis is relatively easy to reconcile phylogenetically. It also has obvious implications for hypotheses about the evolution of the bivalved shell in brachiopods (Section 5.4). Later analyses have recovered the more traditional view that brachiopods and phoronids could be sister clades (Giribet et al. 2000, Sperling et al. 2011). Ongoing research (E.A. Sperling, personal communication) on the phylogenomics of brachiopods and phoronids utilizing next-generation sequencing techniques will hopefully resolve this disagreement definitively in the near future.

From the geological perspective, Conway Morris & Peel (1995) were the first to suggest that brachiopods might trace their origin to an unusual and poorly understood extinct group, the halkieriids, which possess multiple skeletal elements of unknown original mineralogy. However,

a Parsimony analysis of morphological and embryological characters

b Bayesian analysis of housekeeping genes and ribosomal subunits
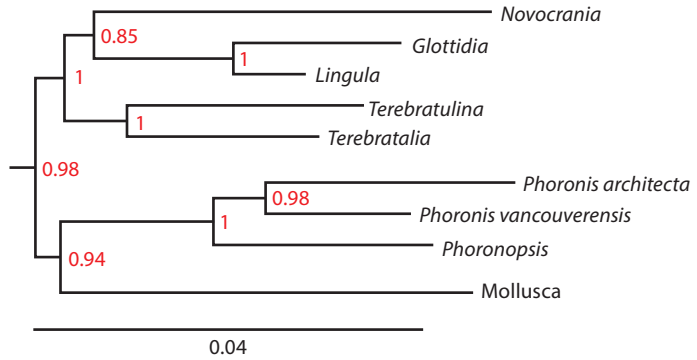
c Bayesian analysis of rDNA subunits

Phoronida

Brachiopoda (Inarticulata)

Brachiopoda (Articulata)
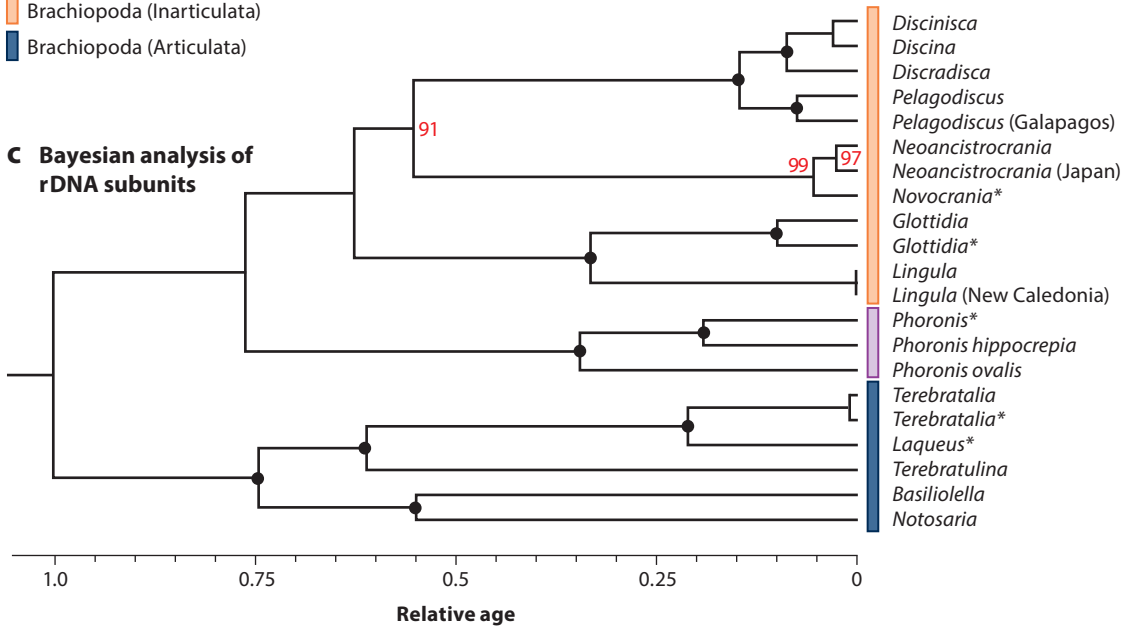
Figure 4

Three hypotheses of relationship among extant brachiopods and phoronids. (*a*) Parsimony analysis of 112 morphological and embryological characters distributed among exemplar taxa from each extant superfamily; red numbers indicate bootstrap support for each node. Panel adapted with permission from Carlson (1995). (*b*) Bayesian analysis of seven housekeeping genes and 18S, 28S, and 5.8S ribosomal subunits, analyzed under mixed models; red numbers at nodes indicate posterior probabilities. Panel adapted from Sperling et al. (2011) with permission from J. Wiley & Sons. (*c*) Bayesian analysis of ribosomal DNA (rDNA) subunits rooted by relaxed-clock methods. Black dots indicate 100% support; the 91% node should be considered to be collapsed, forming an inarticulated polytomy. The numbers are posterior probabilities, but written as percentages rather than as decimals. Asterisks denote sequences used by Sperling et al. (2011). Panel adapted from Cohen (2013) with permission from J. Wiley & Sons.

Vinther & Nielsen (2005) concluded that halkieriids were likely to have been calcareous, and very likely to be more closely related to molluscs than to brachiopods. The study by Conway Morris & Peel (1995) triggered a host of other papers on a variety of rather poorly known Lower Cambrian phosphatic fossils referred to generally as tommotiids because of their first appearance in the Tommotian Stage of the Early Cambrian. One genus of tommotiid, *Micrina*, previously argued to be a halkieriid (Holmer et al. 2002), was claimed to represent a stem group brachiopod, largely because of microstructural features of the phosphatic sclerites (Williams & Holmer 2002, Skovsted et al. 2014). Several other Lower Cambrian fossils have also been considered as possible stem group brachiopods, including *Mickwitzia* (Skovsted & Holmer 2003), *Tannuolina* (Skovsted et al. 2014), *Paterimitra* (Larsson et al. 2014), and *Heliomedusa* (Zhang et al. 2009). The latter studies argue that the brachiopod ancestor closely resembled one of the many different Lower Cambrian fossils and possessed either a multielement phosphatic or agglutinated skeleton, or was soft-bodied (Balthasar & Butterfield 2009).

The term stem group has a specific meaning. It refers to a paraphyletic group basal to a crown clade, within a total clade (see sidebar, Phylogenetic Terms). In order to establish the boundaries of a stem group, a crown clade and a total clade must first be established. Yet neither had been established before the proliferation of papers that asserted, without phylogenetic analysis, putative stem groups or stem fossils (Skovsted et al. 2008). Most speculation on stem groups was untested (Skovsted et al. 2009, 2011). A more explicit phylogenetic analysis of many of these putative brachiopod stem groups (Carlson & Cohen 2009) suggests a range of hypotheses that are all equally plausible given the limited evidence in hand; if anything, these analyses point to a possible stem-linguliform relationship (S.J. Carlson, in preparation). Later studies (Murdock et al. 2012, 2014) recommended that a robust phylogenetic analysis was needed to test, with data, the various stem group hypotheses. Coupled with the establishment of phylogenetic definitions of Brachiopoda and Pan-Brachiopoda (Carlson & Cohen 2016) (**Figure 2**), which define the brachiopod crown and total clades, more such analyses will enable the many stem group hypotheses to be tested rigorously.

5. WHAT ARE SOME OF THE DIMENSIONS OF EVOLUTIONARY CHANGE WITHIN BRACHIOPODA?

5.1. Populations and Species: Microevolution

The process of microevolution involves the interactions among individuals in populations, and among populations in species, causing changes in allele frequencies over time. We know relatively little about populational variation today and microevolutionary change over time in many species of extant brachiopods, on the basis of either morphology or genetics, albeit with several notable exceptions (Foster 1974, Tunnicliffe & Wilson 1988, Cohen et al. 1993, Endo et al. 2001, Baumgarten et al. 2014). Size-frequency distributions have been used in the past as proxies to discern population structure (Thayer 1975). Bivariate plots of valve length and width from samples of individuals thought to represent populations have traditionally provided support for the identity and recognition of species (Cooper 1983). Multivariate studies of morphological variation facilitating species discrimination are becoming somewhat more common among paleontologists (Huang & Harper 2013), but the relationship between changes in allele frequency and changes in morphology in brachiopods is still not well known.

Early attempts to determine the extent of genetic variation in extant populations (Valentine & Ayala 1975) found a high degree of variation in *Frieleia halli*, in otherwise environmentally stable deep-sea habitats, but very low variability in Antarctic subtidal *Liothyrella notorcadensis*, making

cross-phylum generalizations about genetic and morphological variation difficult. Studies of variation in extant *Terebratulina* species, using mtDNA, allozyme data, and limited morphometric analysis, concluded that named species could be distinguished both morphologically and genetically (Cohen et al. 1993). Other studies have identified major conflicts between molecular and morphological phylogenetic analyses of extant brachiopod species (Saito et al. 2001, Bitner & Cohen 2015). Genomic (Stechmann & Schlegel 1999, Helfenbein et al. 2001, Endo et al. 2005, Adachi et al. 2013, Luo et al. 2015) and, more recently, proteomic (Immel et al. 2015, Jackson et al. 2015) studies, as well as studies of gene expression in brachiopod species, are now being tackled, with exciting, compelling results (Altenburger et al. 2011, Passamaneck et al. 2015). Establishing relationships between genetic variation, gene expression, and morphology is the next frontier in linking geological and biological approaches to the study of brachiopod evolution.

Fossil species are still identified and distinguished from one another on the basis of shell morphological variation, with the assumption that morphological distinction is a proxy for reproductive or genetic distinction. Because morphological variation among individuals in populations of extant species is rarely compared quantitatively with morphological variation among individuals in congeneric fossil species, it is not clear whether named fossil species correspond in the degree and nature of variability to named extant species (N. Lopez Carranza, in preparation). The general lack of comparison of morphological and genetic variability in extant species, and morphological variability in extant and extinct species, has led to a practice referred to as generification (Hendricks et al. 2014), or the paleobiological analysis of genera, under the assumption that genera serve as meaningful proxies for species. Fossil brachiopod species based on morphology alone may well have been oversplit (Cooper 1956) and are more susceptible to sampling biases than genera (Raup 1979). Thus, genera are used more frequently than species as terminal taxa in phylogenetic studies involving fossils, although this practice is beginning to change (Wright & Stigall 2013). Having a more comprehensive understanding of brachiopod species delimitation and intraspecific variability, from multiple sources, is clearly a desirable, essential element in understanding brachiopod evolution.

5.2. Phylogeny

Phylogenetic hypotheses illustrate patterns of internested clades that signify relative recency of common ancestry; they hypothesize patterns of evolutionary change over time based on the distribution of characters: morphological, molecular, or both. Because of reticence on the part of many early brachiopod paleontologists to make specific predictions about phylogenetic relationships (Cooper 1956), very few hypotheses of relationship among groups of brachiopods existed at the time (Rudwick 1970, Wright 1979, Rowell 1982), beyond those that linked named higher taxa by dashed lines on a stratigraphic range chart or in a massive basal polytomy (Williams & Rowell 1965). Morphological phylogenetic analyses (Carlson 1995) of the seven superfamilies with extant genera, coded for over 100 characters and using phoronids, bryozoans, a protostome (sipunculids), and a deuterostome (pterobranchs) as outgroups, concluded that brachiopods, inarticulate brachiopods, and articulate brachiopods are each clades, but with rather weak support for the inarticulate clade (**Figure 4a**). This extant-only morphological analysis provided welcome support for brachiopod monophyly (Rowell 1982), as well as for the two-class system of Inarticulata and Articulata widely in use at the time (Williams & Rowell 1965).

Despite the good news that crown clades in these three higher taxa are each monophyletic, attempts to incorporate extinct taxa (>95% of named genera) at lower taxonomic levels (e.g., genera in families or superfamilies; superfamilies in orders) to test total clade monophyly produced less than optimistic results (Carlson 1991b, Williams et al. 1996, Carlson & Leighton 2001).

Several named orders (Pentamerida, Rhynchonellida, Athyridida, and most likely Spiriferida and Spiriferinida as well as other orders not yet investigated in detail), represented by genera in superfamilies, appeared to be paraphyletic or polyphyletic (see **Figure 2**). This was not a particularly surprising result among brachiopod paleontologists, as numerous higher taxa had been thought (although never tested) to represent grade-level taxa, and not clades, making researchers understandably cautious about drawing evolutionary inferences from taxa having uncertain evolutionary identities. However, it became common practice for named taxa at several ranks to be referred to as clades (Gould et al. 1977) with no attempt made to test their status as clades; each taxon was assumed to be monophyletic (representing a single system of common ancestry). This untested assumption resulted in the grouping together of unlike evolutionary entities in attempts to quantify diversity over time, a practice that can lead to misleading interpretations of evolution (Patterson & Smith 1987). The uncritical assertion that taxa are clades has become an unfortunate point of contention among some specimen-based brachiopod paleontologists, and some taxon-based macroevolutionary paleobiologists.

Identifying paraphyletic stem groups (e.g., the light blue group in **Figure 2**) reveals combinations of features that characterize the basal members of a total clade (e.g., Pan-Neoarticulata) that lack features of the crown clade (e.g., Neoarticulata, in dark blue in **Figure 2**) members. Paraphyletic groups can only be recognized and understood once crown clades and total clades are identified. The crown and total clades of Brachiopoda appear to be coincident with one another, with all extinct brachiopods nesting among the extant brachiopods (**Figure 2**). The crown and total clades of the former Inarticulata, which is now divided into two taxa, Craniiformea and Linguliformea (Williams et al. 1996), which may or may not be clades, might be coincident. Crown and total clades of the former Articulata (**Figure 2**) are not coincident, with many extinct articulated brachiopods lying outside the crown clade, in a large, diverse, and rather poorly resolved paraphyletic stem group (in light blue in **Figure 2**). The crown clade of articulated brachiopods has been recently named Neoarticulata (Carlson & Cohen 2016) for the first time, with Pan-Neoarticulata as its associated total clade (Carlson & Cohen 2016) in accordance with phylogenetic nomenclature. Results of molecular analyses support not only the monophyly of the crown clades of Brachiopoda, Inarticulata, and Neoarticulata (**Figure 4**) but also the monophyly of crown clade Terebratulida, Thecideida, and Rhynchonellida, and within Terebratulida, the monophyly of crown clade Terebratellidina and Terebratulidina (Cohen & Gawthrop 1997; Cohen 2000, 2007, 2013; Cohen & Weydmann 2005). Total clade monophyly has not been established for most of these groups, however.

These results are encouraging, to be sure. But in a clade like Brachiopoda, in which so many of well over 10,000 named species are extinct, it is a difficult task to determine crown and total clade relationships with confidence for each named higher taxon. And yet, doing so is critically important because it will enable us to test the monophyly of these named higher taxa, which is essential in establishing their evolutionary role in macroevolutionary studies. The results of morphological analyses (Carlson 1991b, 1995; Williams et al. 1996; Holmer & Popov 2000; Popov et al. 2000; Carlson & Leighton 2001), together with molecular systematic analyses (Cohen & Gawthrop 1997; Cohen 2007, 2013; Sperling et al. 2011) of representative species of the fewer than 5% extant, made it possible to construct a composite cladogram (**Figure 2**) that represents the most likely pattern of relationships among named orders, given our knowledge at this time. Future analyses will test the stability of this hypothesis. Of course, such a diagram, with orders as terminal taxa, implies the monophyly of each order, which we know does not obtain for many orders. For some orders (Rhynchonellida), the degree of incongruity of morphological results (Schreiber et al. 2013) and molecular results (Cohen & Bitner 2013), even among only the few species extant, is worrisome. For others (Terebratulida), the agreement appears to be greater

(Cohen 2007; S.J. Carlson, in preparation; however, see Saito et al. 2001, Bitner & Cohen 2015). Overall, the morphological and molecular disagreement among brachiopods tends to increase as we descend the taxonomic hierarchy from orders to species (Carlson et al. 2014). I suspect that as more genomic and combined morphological and molecular analyses (Wiens 2009, Giribet 2010, Reeder et al. 2015) are conducted, past results that appeared to be in conflict will be better resolved. Phylogenomic studies (Kocot et al. 2013, Nesnidal et al. 2013, Jackson et al. 2015, Lemer et al. 2015, Luo et al. 2015) will also help clarify these disagreements, and allow us to interpret results with greater confidence than is possible at this time.

Technological advances in the analysis of molecular sequence data have easily surpassed those in the analysis of morphological data, often at an astonishingly dizzying pace. However, certain molecular analyses, particularly those of single genes, can suffer from the problem of long branch attraction (Felsenstein 1978), in which distantly related species share more similarities by homoplasy, and thus appear to be closely related by virtue of the longer time each has had to accumulate changes. One of several major advantages of adding extinct taxa to analyses that include only extant species is that they can break up long branches, because fossils possess unique character combinations that expose the false similarity in distantly related extant species (Patterson 1981, Slater et al. 2012). It is significant to note that some molecular systematists are firmly in support of the value of morphology in elucidating evolutionary history and are willing to say so with confidence (Giribet 2015).

5.3. Ontogeny and Development

The relationship between evolution and development has long been a focus of attention among brachiopod workers, from Beecher (1891) to Atkins (1959) to Jaecks & Carlson (2001). The evolutionary consequences of changes in developmental rate and timing, referred to as heterochrony (Haeckel 1875, Alberch et al. 1979), can result in paedomorphic or peramorphic patterns of evolutionary change. Because of their relatively simple external shape and relatively large adult body size, terebratulide brachiopods have been claimed to be neotenic (A. Williams, personal communication); tiny thecideides may be progenetic (Jaecks & Carlson 2001). Very small adult body size, observed in all thecideide and a number of extant terebratulide and rhynchonellide brachiopod species (Motchurova-Dekova et al. 2002), determines many aspects of life history: Brooders are often small as adults and produce fewer gametes over their life span than do free-spawners; small adults may have shorter life spans, or grow at slower rates, and reach sexual maturity earlier than large adults; small adults interact with their ambient fluid environment differently than do large adults. Because body size increases over ontogeny, and because body size is such a biologically important feature of an organism, it is easy to see why heterochronic processes that affect adult body size have the potential to effect significant evolutionary change. More studies that attempt to relate ontogeny, developmental genetics, morphology, and evolutionary change in brachiopods are much needed.

Thecideide brachiopods provide a useful example to illustrate the differences between a biological and a paleontological approach to the study of evolution and development. Thecideides are very small-bodied brachiopods, and they live cemented to hard substrates, often in cryptic environments like caves (Jackson et al. 1971). They are the last brachiopod order to appear in the fossil record (**Figure 2**), and there has been much debate regarding their origin and phylogenetic relationships. Mainly because of their small size, paleontologists have argued that they are paedomorphic (small as a secondary innovation) (Elliott 1953), which requires a hypothesis of ancestor-descendent or sister-group relationships despite the fact that their phylogenetic affinities were not agreed upon. Elliott (1953) and Rudwick (1970) followed Beecher (1891) in claiming that

thecideides were most closely related to extinct strophomenates, as extant survivors, based on certain morphological features that resemble those found in productide brachiopods. Williams (1973) took exception to this conclusion and argued, largely on the basis of shell microstructure, that thecideides were paedomorphic descendants of one group of extinct, spire-bearing brachiopods (spiriferides), rather than strophomenates. In meticulous investigations of morphology and ontogeny, Baker (1990) concluded that thecideides were more closely related to a different group of extinct spire-bearers. Regardless of which group shares closest common ancestry with thecideides, adults of all candidate species are large-bodied and extinct, which further supports the hypothesis that thecideides are paedomorphic, or secondarily small-bodied as adults.

Examining only the extant brachiopods, however, a very different evolutionary interpretation presents itself. Thecideides appear to be the most basal of the major extant articulated groups (**Figures 2** and **4a**), which suggests that small body size among adults is primitive, rather than a secondarily derived state (Carlson 1995, 2007), and that the direction of phylogenetic change mirrors that of ontogenetic change. This is yet another indication that inferring patterns of evolution from only the extant 5% of brachiopod taxa, lacking the perspective from extinct taxa preserved in the fossil record, could result in a completely different conclusion about the direction of character change in evolution. The complex brachial ridges that support the thecideide lophophore strongly suggest a peramorphic, not paedomorphic, pattern as well. Rather than characterizing entire clades as paedomorphic or peramorphic, it is more informative to focus on suites of individual characters and the mosaic of heterochronic patterns they exhibit (Jaecks & Carlson 2001).

Embryological and larval studies have revealed extremely useful information relevant to brachiopod evolution as well (James et al. 1992, Freeman 1993, Chuang 1996). For example, the relative sizes of embryonic and larval shells that can be preserved in adult shells through the process of accretionary growth can indicate the larval ecology of extinct species. Comparing patterns of the first-formed shell size in a phylogenetic context, studies by Freeman & Lundelius (1999) concluded that, rather than indicating homology due to common ancestry, lecithotrophy evolved independently twice in brachiopods from planktotrophy, in craniides and in rhynchonellates. These data can play a critically important role in testing hypotheses of homology, and thus the inference of evolutionary patterns.

5.4. Morphological Character Suites

Tracing evolutionary transformations in suites of morphological characters is another way to approach macroevolutionary questions, distinct from tracing evolution from patterns of taxonomic diversity over time. Five interrelated character suites, only three of which (valve mineralogy, valve articulation, and mineralized lophophore supports) can be preserved unambiguously in fossils, have played a particularly important role in the study of brachiopod evolution.

5.4.1. Articulation between two mineralized valves. Huxley (1869) established the presence (Articulata) or absence (Inarticulata) of articulation between the valves as a single, key character separating brachiopods into two orders. The clade status of Articulata was confirmed (Carlson 1995), but lingering uncertainty over the clade status of Inarticulata led to the naming of two new subphyla, Craniiformea and Linguliformea (Williams et al. 1996), to accommodate the possibility that these two taxa might not be sister clades. Later analyses support the hypothesis that they are sister clades (**Figure 4a,b**).

The evolution of valve articulation is complex and complicated by uncertainty in the relationship of brachiopods to various multielement fossils purported to be stem brachiopods. Articulation appears to involve several steps in various patterns of succession (Williams & Carlson 2007), from

the presence of a hinge axis but no hinge line (e.g., linguloids) to valve-to-valve contact along a hinge line (e.g., craniides) to a hinge line coincident with a hinge axis (e.g., paterinates), all of which are without articulatory structures (teeth and sockets). Teeth and sockets of uncertain homology with later types of articulation evolved in a rudimentary fashion in some early brachiopods (e.g., kutorginates), first as noninterlocking (deltidiodont) and then as interlocking (cyrtomatodont; Jaanusson 1971) structures. All neoarticulates possess interlocking hinge structures.

Several different types of unusual Cambrian fossils (chileides, naukatides, and others; **Figure 2**) have been discovered in the past few decades (Popov 1992, Bassett et al. 2001). They are brachiopods but with poorly developed kinds of articulation (Carlson 1995, 2007), and the homology of these various articulatory structures to one another and to those in crown clade neoarticulates has not been determined with confidence and may never be so determined. This uncertainty has made it difficult to produce a character-based definition of the current subphylum Rhynchonelliformea (Williams et al. 1996); thus, Pan-Neoarticulata (Carlson & Cohen 2016) was defined as the total clade that includes all brachiopods more closely related to crown clade Neoarticulata than to any other crown clade in Brachiopoda.

5.4.2. Mineralization. Phosphatic valve mineralogy was long considered to be primitive for Brachiopoda because of stratigraphic polarity (Williams & Rowell 1965). However, calcareous brachiopods have now been identified deeper in the Lower Cambrian (Cooper 1976, Holmer 2001), and stratigraphic polarity can no longer be used to definitively distinguish primitive from derived mineralogy. Examining the pattern of mineralogy across metazoans, and assuming that mineralogy can be reliably homologous at such a broad level of comparison [an assumption that might well be incorrect (Wright 1979, Runnegar 1989, Luo et al. 2015; see also Ushatinskaya 2014)], the ability to mineralize is basal for animals, with the exception of Ctenophora (Dunn et al. 2014), which may have secondarily lost the ability to mineralize. Molecular (Sperling et al. 2011, Cohen 2013) and morphological (Carlson 1995) analyses confirm that a calcitic valve mineralogy is likely to be homologous among all brachiopods (Balthasar et al. 2009), but as a primitive, not a derived, state. Mineralization has been lost numerous times among metazoans (Dunn et al. 2014), with phosphatic mineralogy having evolved independently in chordates (from mesoderm) and in linguliform brachiopods (from ectoderm) (Luo et al. 2015). Calcitic mineralogy may have evolved independently multiple times among metazoans, or perhaps even among brachiopods, but this possibility has not yet been tested in a comprehensive fashion.

5.4.3. Lophophore. A true lophophore is a ciliated tentacular organ that encloses the mouth and excludes the anus. The lophophore is homologous among all brachiopods, and it may (Emig 1984, Nesnidal et al. 2013) or may not (Nielsen 1995, Dunn et al. 2014) be homologous among lophotrochozoans. It could have evolved once, and then been lost multiple times in all lophotrochozoans lacking lophophores (**Figure 3b**). Alternatively, it may have evolved independently twice, once in brachiopods and phoronids and once again in bryozoans. Lophophores (**Figure 5**) are only rarely preserved in the fossil record, but they can often be inferred from their mineralized supports (**Figures 6** and **7b**) and from phylogenetic congruence with other morphological features (**Figure 7c**). There is no doubt that the spirolophe lophophore is basal for brachiopods (**Figures 5** and **7**) and was the most diverse type of lophophore through much of the Paleozoic. The appearance of brachial ridges (**Figure 6b**) preserved on the interior surface of the dorsal valves of adult productides and some other strophomenates (Muir-Wood & Cooper 1960, Brunton et al. 1995) suggests that these relatively flat or convexo-concave brachiopods possessed schizolophe (or possibly planar spirolophe) lophophores in a range of sizes, a geometry that is a developmental precursor
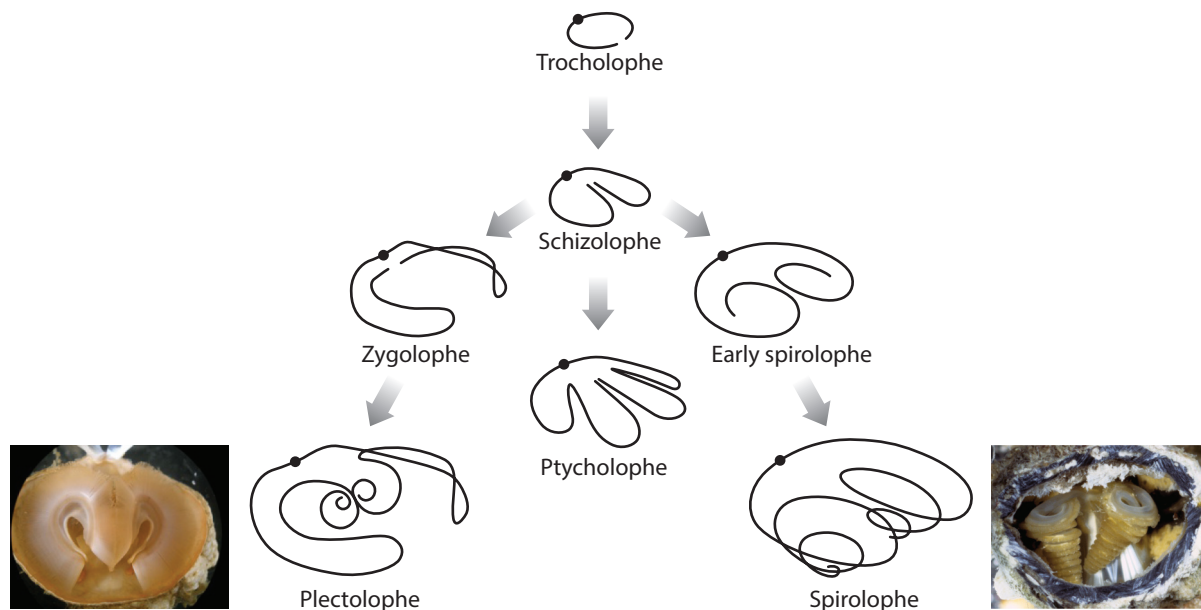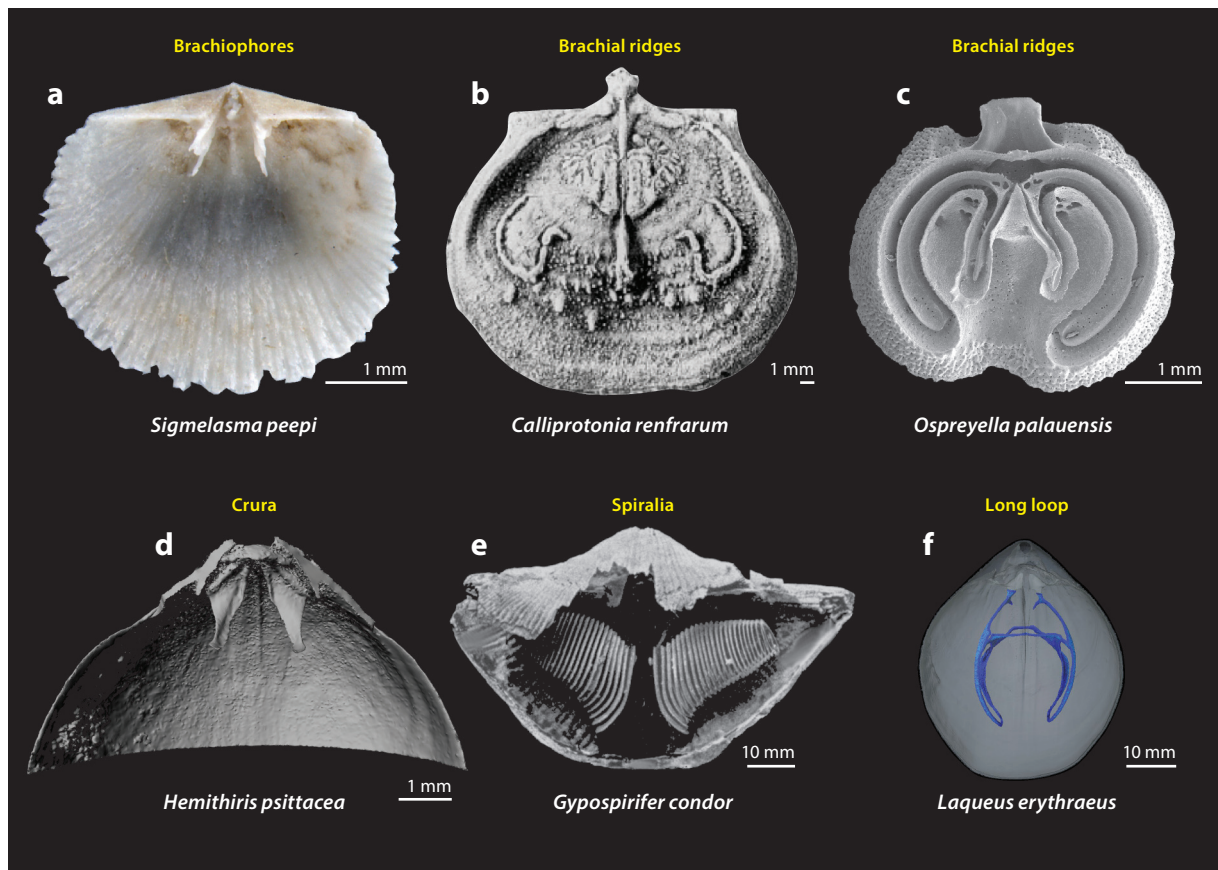
Figure 5

Three-dimensional geometry of the base of the two brachiopod lophophore arms (tentacles/filaments absent). Black dots indicate the posterior position of the mouth between the two arms. Arrows indicate ontogenetic transformations in geometry as body size increases; the three configurations at the bottom represent the adult lophophore geometries in the three extant articulated groups (**Figure 2**): Terebratulida (plectolophe), Thecideida (ptycholophe), and Rhynchonellida (spirolophe). Figure adapted from Rudwick (1970). Plectolophe (*Terebratalia transversa*, filaments relaxed and extended) photo reproduced with permission from J. Vinther; spirolophe (*Hemithiris psittacea*, filaments contracted) original photo by author.

to all three adult lophophore types observed in extant brachiopods: spirolophe, plectolophe, and ptycholophe (Rudwick 1970) (**Figure 5**).

5.4.4. Mineralized lophophore supports. The stratigraphically earliest (**Figure 7a**) and phylogenetically most basal (**Figure 7c**) brachiopods lack any type of mineralized support for the lophophore, which is supported hydrostatically. Derived articulated brachiopods possess a range of types of mineralized supports (**Figure 6**) that may be preserved in the fossil record: spiralia and loops, both preceded in ontogeny by crura; brachial ridges on the dorsal valve interior; and brachiophores, extensions of the socket ridges that may or may not have served to support the base of the lophophore. In order to explore in greater detail the evolution of these supports, I tallied each genus in the *Treatise*, Part H (Revised) (Kaesler & Selden 1997–2007), based on its generic description, by the particular type of mineralized lophophore support it possessed, per time period (**Figure 7a**). Four waves of innovation in lophophore supports can be clearly discerned based on peaks in generic diversity: absence of mineralized supports in the Cambrian and Ordovician (with brachiophores possibly providing limited support); dominance of crura and spiralia in the Silurian and Devonian; brachial ridges in the Carboniferous and Permian; and crura and loops in the post-Paleozoic, with the Triassic as a transition period (Carlson et al. 2014; S.J. Carlson, H.A. Schreiber & D.W. Bapst, in preparation). The particular developmental (MacKinnon & Lee 2006) and/or environmental (Holland & Sclafani 2015, Veizer & Prokoph 2015) impetus for the successive peaks in diversity is not yet clear but is under investigation. By inferring the
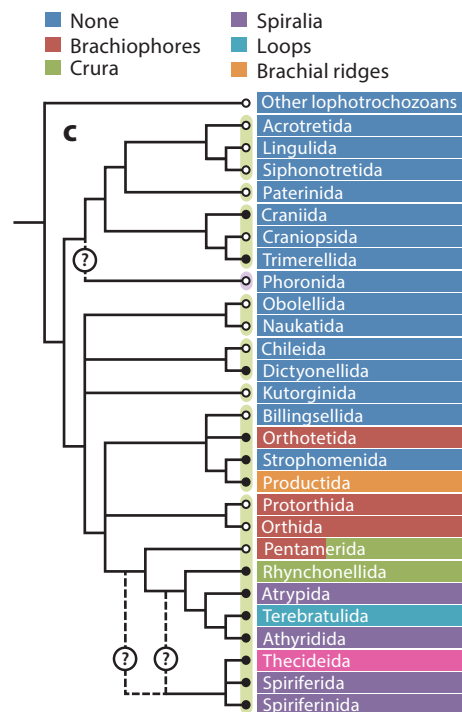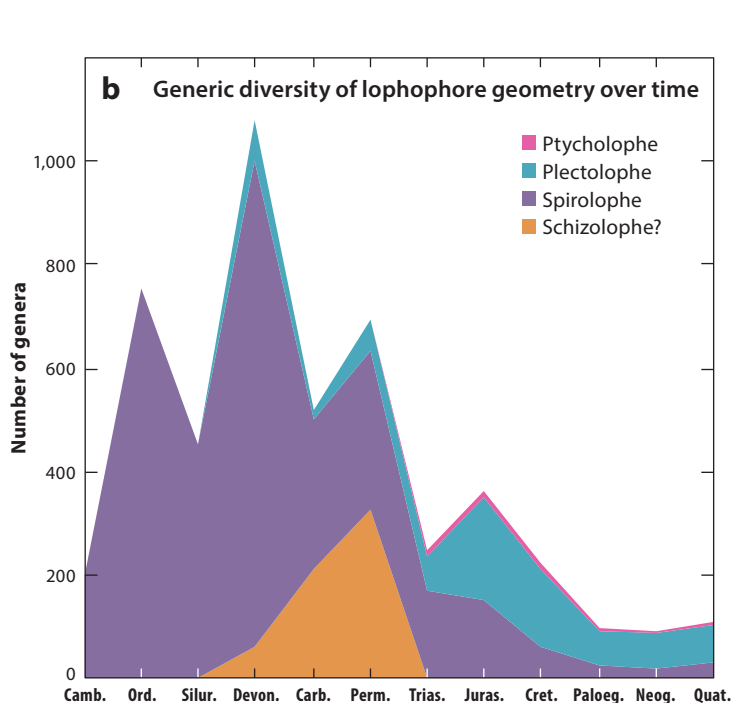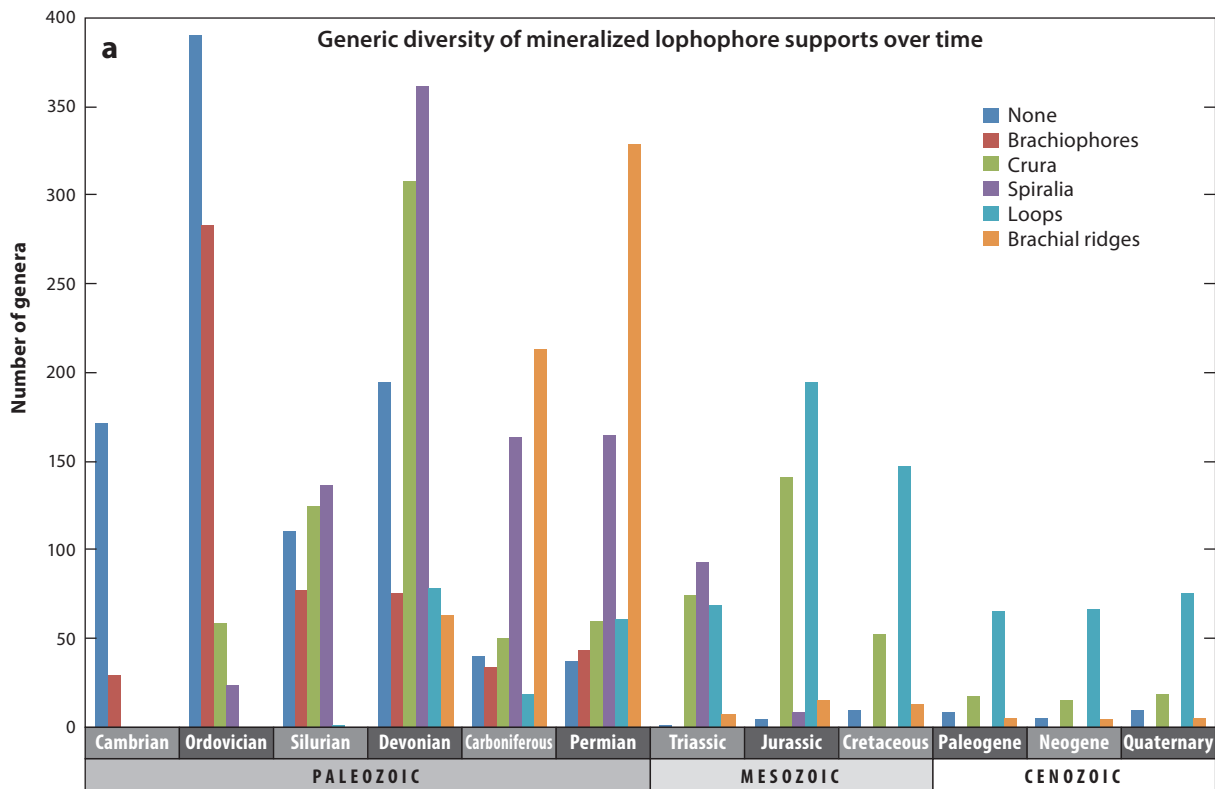
Figure 6

Articulated brachiopod dorsal valve interiors illustrating mineralized lophophore supports tallied in **Figure 7**. (*a*) Brachiophores: paired projections visible just below strophic hinge line, whose function as lophophore supports is unclear (Hints 2012, figure 3C-1; specimen GIT 626-16, Institute of Geology at Tallinn University of Technology; image from the Estonian geocollections database, **http:// geocollections.info/specimen/150907**). (*b*) Brachial ridges: two U-shaped ridges symmetrically located on either side of the plane of symmetry, possibly supporting a schizolophe lophophore (Muir-Wood & Cooper 1960, figure plate 81, figure 13). (*c*) Brachial ridges (also referred to as brachial lobes and grooves): occupy most of the surface of the valve and support a ptycholophe lophophore (Logan 2008, figure 5-3). (*d*) Crura: paired prong-like projections at valve posterior that support the posterior base of a spirolophe lophophore (see **Figure 5**) (original image by H. Schreiber). (*e*) Spiralia: two laterally projecting cones symmetrically located; support the entire spirolophe lophophore (Mancenido & Gourvennec 2008, figure 6*b*). (*f*) Long loop: extension of crura projecting anteriorly, then turning dorsally to close the loop posteriorly that supports a plectolophe lophophore (**Figure 5**) (original image by N. Lopez Carranza). Images reproduced with permission from the indicated sources.

Figure 7

(*a*) Histogram of the number of genera per Phanerozoic time period possessing one of five different types of mineralized lophophore supports or no mineralized support at all, counted (S.J. Carlson, unpublished data) from each generic description in the six-volume *Treatise on Invertebrate Paleontology*, Part H (Revised): *Brachiopoda* (Kaesler & Selden 1997–2007). (*b*) Number of genera with one of four different adult lophophore geometries, inferred from mineralized lophophore supports. (*c*) Cladogram from **Figure 2**, with ordinal names color-coded by lophophore support, mineralized or none (hydrostatic), according to the key in panel *a*.

a Generic diversity of mineralized lophophore supports over time

Legend:
- None
- Brachiophores
- Crura
- Spiralia
- Loops
- Brachial ridges

b Generic diversity of lophophore geometry over time

Legend:
- Ptycholophe
- Plectolophe
- Spirolophe
- Schizolophe?

c

Legend:
- None
- Brachiophores
- Crura
- Spiralia
- Loops
- Brachial ridges

Cladogram tips:
- Other lophotrochozoans
- Acrotretida
- Lingulida
- Siphonotretida
- Paterinida
- Craniida
- Craniopsida
- Trimerellida
- Phoronida
- Obolellida
- Naukatida
- Chileida
- Dictyonellida
- Kutorginida
- Billingsellida
- Orthotetida
- Strophomenida
- Productida
- Protorthida
- Orthida
- Pentamerida
- Rhynchonellida
- Atrypida
- Terebratulida
- Athyridida
- Thecideida
- Spiriferida
- Spiriferinida

geometry of the lophophore in extinct forms from their mineralized supports, it can be deduced that the lower Paleozoic was dominated by spirolophes, the upper Paleozoic by schizolophes and spirolophes, and the post-Paleozoic by plectolophes, albeit at lower overall diversity. The plectolophe geometry requires three-dimensional mineralized support; it is impossible to attain by internal hydrostatic pressure in the lophophore alone. One could conclude from these successive waves of peak diversity that the plectolophe is the most successful lophophore configuration, in the parlance of an evolutionary arms race, among extant brachiopods.

5.4.5. Pedicle. This stalk-like structure is unique to brachiopods, but it is unmineralized and thus only very rarely preserved directly in the fossil record. Its distribution among extant brachiopods is interesting: A pedicle develops from an outgrowth of the posterior body wall in Linguliformea; it develops from a larval rudiment in Rhynchonellida and Terebratulida; and it is absent entirely in Craniiformea and Thecideida, both of which are cemented to a hard substrate. Because the development of the pedicle is quite different in extant inarticulated and articulated brachiopods, the pedicles in these two groups are not considered to be homologous (Williams & Rowell 1965, Carlson 1995, Williams & Carlson 2007). This structure appears to have evolved independently twice in Brachiopoda, and was lost at least twice as well (**Figures 2** and **4***c*), although a compelling case could be made for the lack of a pedicle as the basal condition in brachiopods (**Figure 4***a*).

Perhaps the most useful aspect of adopting a phylogenetic rather than a strictly taxonomic perspective on brachiopod evolution is the demonstration that not all morphological similarities are necessarily both shared (homologous) and derived. The presence of two valves appears to be a derived feature shared among all brachiopods as a result of common ancestry (even if they may have been secondarily lost in phoronids). Some traits, such as a calcitic valve mineralogy, may be shared and primitive, whereas others are not shared (not homologous) at all, like pedicles in inarticulated and articulated brachiopods. Seeking to construct a more defensible argument about trait homology and the direction of trait change in evolution is obviously preferable to simply making assertions on the basis of overall similarity.

5.5. Macroevolution

A paleontological perspective on macroevolution has traditionally involved analysis of patterns of taxonomic diversity over the Phanerozoic Eon (Sepkoski et al. 1981), focusing on the significance of mass extinctions (Bambach 2006) and originations (Harper et al. 2015), as well as abundance of individuals (Olszewski & Erwin 2004) and macroecology and the environmental context of macroevolutionary change (Powell et al. 2015). The generic diversity of brachiopods, tallied per order and by time period, is illustrated in **Figure 8**; three general time periods can be distinguished based on taxonomic composition, largely corresponding to those discussed with respect to lophophore geometry: early, mid-late, and post-Paleozoic, with the Cambrian, Silurian, and Triassic periods transitional in composition. Through the Paleozoic, each time period is marked, beginning and end, by notable diversification and extinction; the post-Paleozoic is marked by much lower and very gradually declining diversity. The relationship to inferences about lophophore geometry is not surprising, given the fundamental importance of the lophophore to all essential biological functions of brachiopods: respiration, excretion, food gathering, and reproduction. Allowing for stochastic effects (Raup 1979), focusing on the essential biological requirements of individual brachiopods provides some indication of deterministic explanations for patterns of diversity over time and should help to illuminate the extrinsic environmental or ecological causes of evolutionary change (Clapham 2015, Holland & Sclafani 2015, Powell et al. 2015), as well as the intrinsic developmental and physiological causes (Knoll et al. 2007, Finnegan & Droser
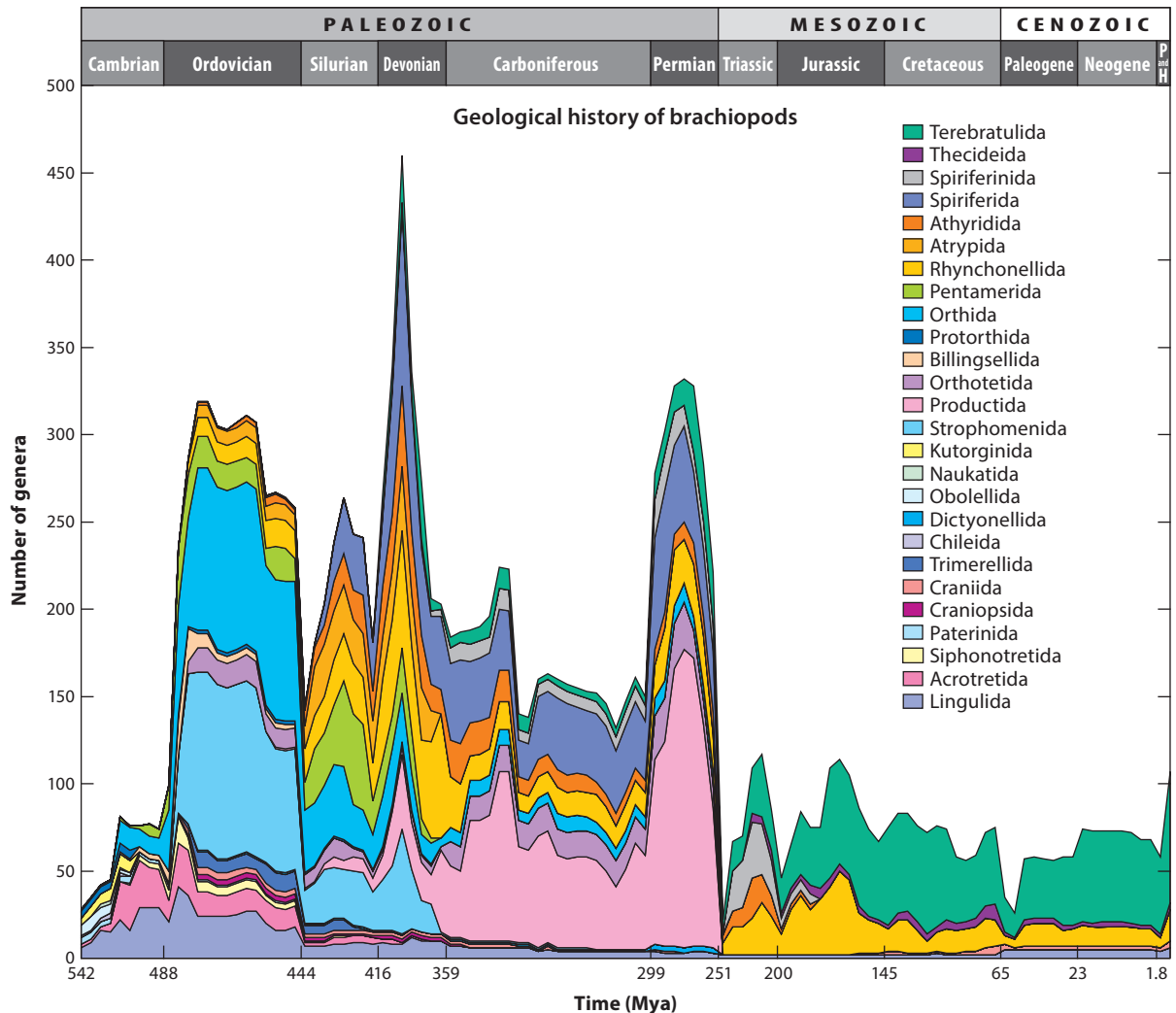
Figure 8

Generic diversity per geological stage in the Phanerozoic Eon, color-coded by ordinal affiliation. Adapted from Curry & Brunton (2007), with permission from G. Curry.

2008). Many paleontological studies have proposed explanations for the causes of diversification or extinction events (Rong & Shen 2002, Chen et al. 2005, Erwin 2005, Erwin & Tweedt 2012, Harper et al. 2015). Many attribute cause to extrinsic environmental factors: changes in primary productivity, hypercapnia due to increased CO_2 in the atmosphere, anoxia, bolide impact, volcanism, onset of cooling and glaciations or of warming, changes in continental shelf area or in sea level, and so on.

Brachiopods, articulated brachiopods in particular, represent the quintessential example of the power of extinction to effect macroevolutionary change (Stanley 1979). The end-Permian extinction reset brachiopod taxonomic (Curry & Brunton 2007), morphological (Carlson 1991a), and functional and ecological (Thayer 1979) diversity permanently. The end-Permian (**Figure 2**)

marked the near (Chen et al. 2005) extinction of the highly diverse Productida and Orthotetida (with pseudopunctate shell structure, most lacking pedicles as adults, and with brachiophores or brachial ridges supporting the lophophore), the impunctate Spiriferida (with spiralia and pedicle foramina), and the last of the Orthida (those with punctate shell structure and brachiophores). All had calcareous shells with strophic hinge lines, and most had noninterlocking (deltidiodont) articulation (Carlson 1991a). The pattern of extinction is consistent with Thayer's (1979) biological bulldozing hypothesis, which proposes that immobile suspension feeders (brachiopods) living on soft substrates declined because of disruption from infaunalization and bioturbation. Except for the very low-diversity inarticulated brachiopods and thecideides, brachiopods thriving today have astrophic hinge lines, are attached by a pedicle to hard substrates, and have some type of mineralized lophophore support (**Figures 6** and **7**).

I have unfortunately given short shrift in this review to too many dimensions of macroevolutionary change in brachiopods, particularly regarding adult and larval ecology, biogeography, physiology, and biomineralization and biogeochemistry. However, two particular examples require mention: competition with bivalved molluscs and body size evolution. Because both bivalves and brachiopods have two valves, they are often assumed to occupy the same ecological niche, but in fact they do not now and have never really done so (although see Liow et al. 2015). Some overlap exists, but bivalves are much more diverse in their feeding behavior and mode of life, and although it might be possible to argue that brachiopods are therefore inferior competitors, no competition for food or space in a particular location or habitat has been clearly documented. High brachiopod Paleozoic diversity was thought to have been gradually replaced by high bivalve post-Paleozoic diversity, implying superior competitive ability of bivalves, as far back as Agassiz (1859). The now classic study of "ships that pass in the night" by Gould & Calloway (1980) counted the diversity of brachiopods and bivalve molluscs and concluded that each actually tracked the other in diversity in the Paleozoic and post-Paleozoic, and that it was the Permian extinction event that reset the initial diversities, reversing the dominance before and after; competition over food or space was unlikely to have played a role in generating this macroevolutionary pattern. Compared biologically, the two groups have very different internal anatomy, physiology, and patterns of development, which leads them to interact with their environment in different ways, so this was not a very surprising conclusion. The recent study by Payne et al. (2015) came as a welcome quantification and explanation of this pattern; they determined that metabolic activity of bivalves has been higher than that of brachiopods since the Ordovician, not only since the Triassic, which is consistent with the different physiological observations on the two groups today. Focusing on patterns of taxonomic diversity and abundance, rather than on biological processes themselves, can lead to plausible but ultimately misleading conclusions about macroevolutionary history.

Body size trends over the Phanerozoic have been the focus of great interest recently, again because of the many different biological processes that are directly related to the size of adults and the pattern of size increase over ontogeny (He et al. 2007, Novack-Gottshall & Lanier 2008, Payne & Clapham 2012, Heim et al. 2015). Zhang et al. (2015) compiled size data on more than 3,400 brachiopod genera and discovered two distinct modes, in the Paleozoic (size increase) and post-Paleozoic (indistinguishable from a random walk), consistent with the complete reset of macroevolutionary pattern by the action of the end-Permian extinction event. The next stage of macroevolutionary analysis of brachiopod body size could be the examination of body size evolution on a clade by clade basis; I predict that different clades would exhibit quite different and more complex patterns of body size evolution, one clade from another, and from the pattern observed among all genera together.

Finally, an impressive spate of important publications on several different aspects of brachiopod evolution has recently appeared, but space constraints unfortunately prevent me from discussing

them here. The central importance of a phylogenetic perspective to answer a host of long-standing evolutionary questions is becoming fully realized and signals an exciting and productive new phase in the coordinated efforts of biological and geological approaches to the study of brachiopod evolution.

FUTURE ISSUES

1. We must learn more about extant brachiopods, in much greater detail than our current understanding, for a larger number of species. Our knowledge of their physiology, life history, ecology, biogeography, and the like is far too general, and makes it dangerously possible to overgeneralize to the entire phylum on the basis of information from a small number of species. Establishing the nature and degree of variation among extant species is critical to be able to generate and test informed hypotheses about extinct species.

2. We need to develop a deeper and more detailed understanding of the relationship between morphology, development, and genetics, as well as genomics and proteomics. How do brachiopod morphological features develop, what are the developmental genetics regulating the expression of morphology, and how do they relate to the phylogenetic patterns of morphological characters that we can generate? It is vitally important that we reach a better understanding of the processes governing morphology in such a paleontologically important group in which well over 95% of species are extinct.

3. We need more paleontologists and neontologists to work on questions of brachiopod evolution. Very fortunately, more and more intelligent, creative, and enthusiastic younger scientists over the past decade have become intrigued by brachiopods and the fascinating interdisciplinary questions our current knowledge of their evolution raises. I sincerely hope this trend continues; our future knowledge of brachiopod evolution requires their diligence and their scientific passion.

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