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Evolution of left–right asymmetry in side-resting (pleurothetic) bivalves: a test of genes as leaders or followers

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ABSTRACT

Side-resting (pleurothetic) lifestyles evolved independently many times across the Bivalvia in free-lying, byssally attached and cementing lineages. Within some species individuals lie indifferently on either their right or left side (randomly pleurothetic), whereas in others they lie consistently on one side (left-pleurothetic or right-pleurothetic). Morphological differences between valves (asymmetries) typically accompany this behaviour, so it can be studied widely across living and fossil bivalves. Because direction of asymmetry is rarely inherited in cases of random asymmetry, any evolutionary transition from randomly pleurothetic to fixed (left or right) qualifies as a case of ‘genes as followers’. Origins of left-pleurothetic or right-pleurothetic taxa directly from upright (orthothetic) ancestors would represent examples of ‘genes as leaders’. I therefore surveyed pleurothetic lifestyles across the Bivalvia. By mapping pleurothetic states onto a comprehensive phylogenetic tree that included both living and fossil families, I assessed the prevalence of these alternate modes of evolution. Various lines of evidence were also used to hypothesize phylogenetic relations within the Chamidae—the only living bivalve family exhibiting all three pleurothetic states. Randomly pleurothetic forms (direction not inherited) arose from orthothetic ancestors about half as often as fixed pleurothetic forms (direction is inherited). Unlike many other animal groups, fixed pleurothetic forms rarely arose from randomly pleurothetic ancestors, suggesting a ‘genes as leaders’ mode of evolution was most prevalent. However, many fascinating examples of randomly pleurothetic forms among Upper Ordovician and Silurian bivalves suggest that evolutionary transitions from random to fixed may have been more common. Also, randomly pleurothetic forms were short-lived in some fossil lineages, which would reduce the likelihood of them being detected. Hopefully, this preliminary analysis will motivate further study of (1) phylogenetic relations of key groups like the Chamidae, and basal Limida, Ostreida and Pterioidea, and (2) morphological variation among early members of other pleurothetic bivalve groups.

INTRODUCTION

In the conventional view of evolution, new phenotypic variation is thought to arise primarily via mutation (Futuyma & Kirkpatrick, 2017), a ‘genes as leaders’ perspective (West-Eberhard, 2003). But developmentally plastic responses to differences in living conditions or behaviour can also yield phenotypic variation. If these plastic responses are adaptive and oft-repeated, randomly appearing genetic variation may eventually arise that enhances their expression, which can then accelerate the rate of evolution by natural selection, a ‘genes as followers’ perspective (West-Eberhard, 2003; sometimes also called genetic assimilation, Waddington, 1953; Palmer, 2012).

Conspicuous left–right asymmetries offer an attractive tool for studying whether genes are leaders or followers in evolution (Palmer, 2004, 2016). The logic is simple. First, in the vast majority of animal and plant species within which dextral (right-sided) and sinistral (left-sided) forms are equally frequent (random asymmetry), direction of asymmetry is not inherited. In other words, random asymmetry is a nearly unique morphological dimorphism where the difference between two discrete phenotypes is not heritable (e.g. determined by chance). Second, in species that are overwhelmingly left- or right-sided (fixed asymmetry), variants of the opposite chiral form typically *are* inherited (i.e. variation in direction of asymmetry is inherited). Third, if variation in direction of asymmetry is *not* inherited in randomly asymmetrical species, but *is* inherited in species with fixed asymmetry, then any evolutionary transition from random to fixed represents a case of 'genes-as-followers' (West-Eberhard, 2003), where phenotypic variation precedes genetic variation on evolutionary timescales.

Bivalves are an appealing group for studying the evolution of left–right asymmetry for several reasons. First, despite many exceptions, their body plan is fundamentally bilaterally symmetrical, with largely mirror-image right and left shell valves enclosing the body (Stanley, 1970). Second, pleurothetic forms—those that lie on, or are attached to the substratum by, one side—have evolved independently in many living and fossil groups (Nicol, 1958). Third, pleurothetic forms typically exhibit morphological differences between right and left valves that are easy to recognize and therefore score (e.g. Waller, 1978). Finally, and perhaps most importantly, left–right differences in shell form are easily identifiable in fossils, so both living taxa and the rich fossil record can be used to reconstruct the evolutionary history of pleurothetic lifestyles.

Pleurothetic bivalves fall into three broad categories (Seilacher, 1984): (1) unattached recliners or recessors that rest on one side, (2) byssally attached forms, where a tuft of tough byssal threads secreted by the foot anchors the animal to the surface and pulls it towards one side (attachment is facultative in some species) and (3) cemented forms, where the mantle secretes shell material directly onto the substratum (attachment is typically permanent, but is lost later in life in some groups that nonetheless remain pleurothetic, as in some gryphaeids, chamids and *Hinnites*). Fortunately, shells of pleurothetic bivalves may exhibit multiple differences between sides in (1) convexity, (2) sculpture, (3) features that accommodate the byssus, (4) site of cementation scar and (5) valve with most epibionts. These all indicate, or hint strongly at, which side is lowermost.

In principle, each asymmetrical shell trait associated with a pleurothetic lifestyle (e.g. cemented valve, side of greatest convexity and hinge asymmetry) could be used to reconstruct evolutionary relations among right-, left- and randomly pleurothetic forms. However, in this review, I will focus primarily on which side faces down because resting side, whether free, byssal, or cemented, can be scored across all pleurothetic Bivalvia. It also avoids problems of lack of independence (e.g. right-pleurothetic cemented pectinids nearly all arose from right-pleurothetic byssally attached forms; Seilacher, 1984).

Pleurothetic bivalves, particularly cemented ones, have been widely discussed (Nicol, 1958; Newell & Boyd, 1970; Yonge, 1979; Seilacher, 1984; Harper, 1991, 2006, 2012; Hautmann, 2001; Nevesskaja, 2003). So why another review? First, the significance of random asymmetry as an evolutionary precursor to the many groups that exhibit fixed asymmetries is not widely appreciated. Second, bivalve phylogenetic relations are increasingly well understood as more sequences and more taxa have been included (Sharma *et al.*, 2012; Bieler *et al.*, 2014; Combosch *et al.*, 2017; Lemer, Bieler & Giribet, 2019). Third, some new phylogenies, particularly the magisterial time-calibrated tree of Crouch *et al.* (2021), include both living and fossil taxa, so phylogenetic variation in shell asymmetry may be examined with much greater confidence across the vast sweep of bivalve diversity. Fourth, a consensus classification and tally of bivalve species that corrects for many synonyms and misclassifications now exists (World Register of Marine Species; WoRMS), which greatly reduces nomenclatorial confusion. Finally, I want to draw attention to the fascinating Chamidae, the only living bivalve family that includes clear examples of all three pleurothetic states—random, left and right—and whose phylogenetic relations therefore offer one of the strongest tests of genes as leaders or followers.

METHODS

First, a note on terminology (see Carter *et al.*, 2012). Most bivalves are considered orthothetic, where the commissural plane between the valves is oriented perpendicular to the substratum. In pleurothetic (side-resting) bivalves, the commissural plane leans towards one side (departs from perpendicular) and can be more or less parallel to the substratum, so one valve (either left or right) can be referred to as the lower valve. How far the commissural plane has to depart from vertical to be considered pleurothetic is somewhat arbitrary as even orthothetic bivalves may lean slightly to one side or the other. In species considered to be pleurothetic, the commissural plane usually departs significantly from vertical (e.g. by ≥30°). Within species the direction of the lean may be fixed to one side (e.g. right-pleurothetic or left-pleurothetic) or may vary indifferently to the right or left (randomly pleurothetic = amphi-pleurothetic).

Pleurothetic bivalve species, or higher taxa, were tallied from the literature. Of course, considering the tens of thousands of living and fossil species, my search was not exhaustive. Most significantly, with few exceptions I restricted my survey to families in the Crouch *et al.* (2021) tree, which excluded many fossil families. Consequently, some uncertainty remains in the final tallies and evolutionary patterns presented here. However, I did include a few extinct families that were critical to polarizing state changes in the Ostreida (e.g. left-pleurothetic Umburridae, Rhombopteriidae and Cassianellidae). I drew from the primary literature as much as possible, but was greatly aided by some key surveys or monographs (Nicol, 1958; Yonge, 1967, 1977,1979; Waller, 1978; Fürsich, 1982; Seilacher, 1984; Harper, 1991; Johnston, 1993; Newell & Boyd, 1995; Matsukuma, 1996; Carter, Campbell & Campbell, 2000; Graf & Cummings, 2006; Harper, Dreyer & Steiner, 2006; Oliver & Holmes, 2006; Temkin, 2006; Ujino & Matsukuma, 2010; Alejandrino, Puslednik & Serb, 2011; Hautmann & Hagdorn, 2013; Bieler *et al.*, 2014; Ros-Franch, Márquez-Aliaga & Damborenea, 2014; McCartney, 2021; Simone *et al.*, 2015; Hodges, 2022; Machado & Passos, 2022; Pinroth & Posenato, 2023) and the monumental survey of Phanerozoic bivalves by Nevesskaja (2003).

The present survey suffers from one big weakness: I often had to use data for one or a few species as exemplars for an entire genus or family (Supplementary Material Table S1 and Fig. S1). As much as possible, I tried to find data for multiple species to validate scoring for most genera and families.

To tally the vast diversity of bivalves, and avoid as much nomenclatorial mess as possible, I followed without question the impressively thorough listing and classification in the World Register of Marine Species (WoRMS, 2023, www.marinespecies.org, as drawn from MolluscaBase, www.molluscabase.org), despite still being incomplete, particularly for fossils. This listing offers the most broadly accepted higher classification and eliminates a great many synonyms and misnomers. When I encountered species reassigned to other genera or families, I adhered to the WoRMS classification (reassignments are indicated in Supplementary Material Table S1). When I encountered fossil taxa of interest not listed in the WoRMS database, I included them in my tally according to the taxonomic affinity suggested by the author of the source paper. Also, throughout this paper, I follow the WoRMS classification as closely as possible, despite some significant conflicts with other classifications (e.g. genera included in the superorder Nepiomorphia by Kříž, 2007).

For phylogenetic relations among bivalve families, I used the time-calibrated tree of Crouch *et al.* (2021), a composite topology derived from transcriptomic, DNA sequence, morphological data and the fossil record. This tree includes the vast majority of living families (97 of *c.* 110; Bouchet *et al.*, 2010). It also includes 30 phylogenetically significant fossil families, but these are only a fraction of the estimated 214 extinct families (Bouchet *et al.*, 2010). So, some key taxa with important asymmetric groups were not included (e.g. Chondrodontidae, Cyrtodontida, Lithiotidae,

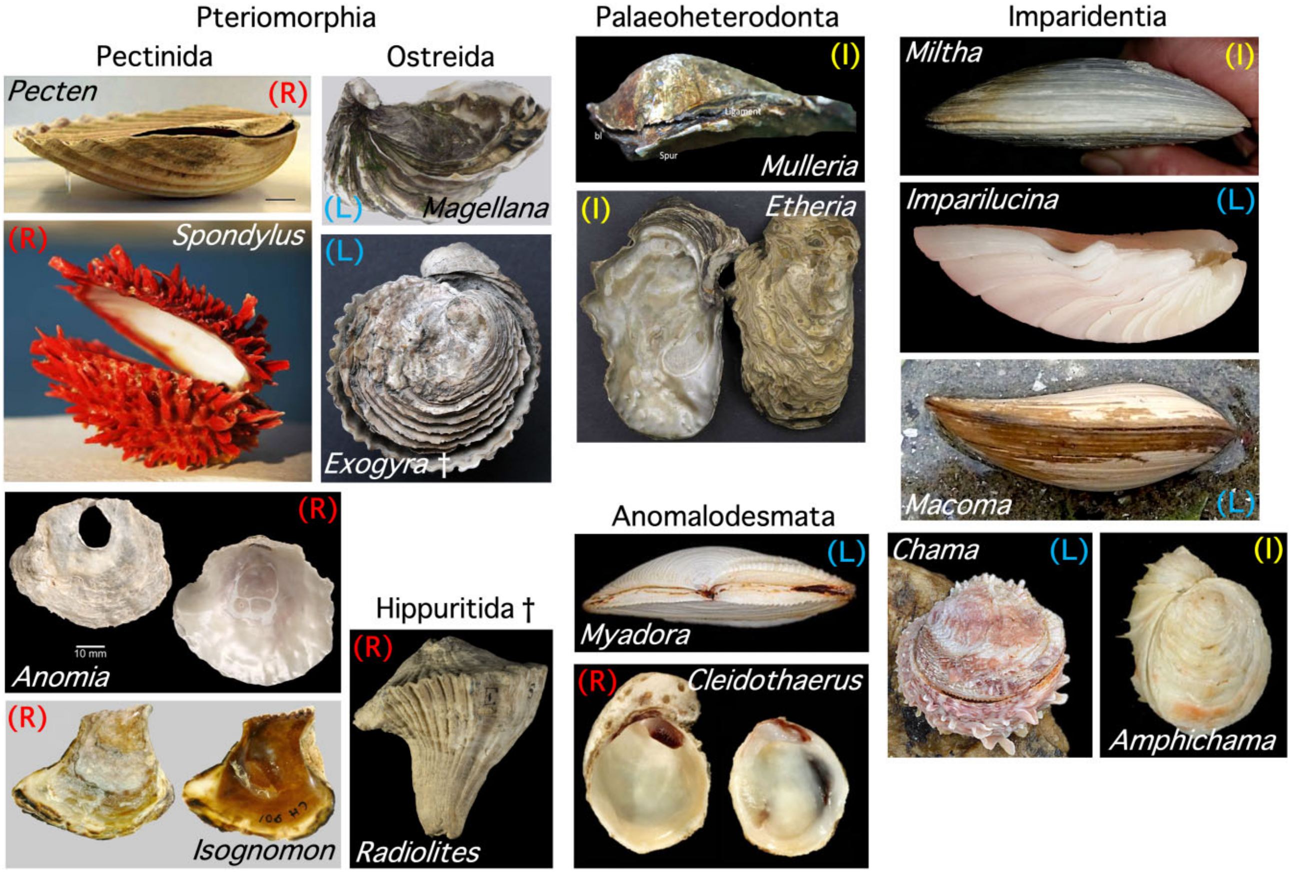

Figure 1. Selected examples of pleurothetic bivalves from all major bivalve groups that include pleurothetic cases. Abbreviations: I, indifferently (randomly) pleurothetic; L, left-pleurothetic; R, right-pleurothetic. Photo credits: *Imparilucina rosacea* (Lucinidae), J. Taylor; *Exogyra costata* (Gryphaeidae), R. Wolf; all other images from public sources.

Megalodontida, Myalinida and Hippuritida). For phylogenetic relations within families of interest, I used the most recent molecular phylogeny I could find. The shortage of intrafamilial phylogenies for many families greatly limited my inferences about the number of independent origins of different asymmetry types. For the Chamidae, I propose a phylogeny among all living genera, and within two genera (*Chama* and *Eopseuma*). The topology was inferred as best as possible from morphological differences (hinge dentition and asymmetry type), the fossil record and some limited molecular analyses.

Four character states for downward-facing = pleurothetic side—neither = orthothetic, random, left, right—were mapped onto a condensed version of the Crouch *et al.* (2021) tree (Crouch *et al.*, 2021: fig. 3; see Supplementary Material Fig. S1). To keep the bivalve-wide tree manageable, I condensed and pruned the Crouch *et al.* (2021) tree by merging families into higher taxa where pleurothetic state did not vary. Two groups worth examining more closely (Ostreida and Chamidae) were further analysed in separate, more detailed, trees. In the Bivalvia and Ostreida trees, I placed extinct families according to their order of bifurcation in the Crouch *et al.* (2021) tree, so I was unable to capture their paraphyletic status. Characters were mapped onto this condensed tree using simple parsimony (character states unordered; MacClade v. 4.08, Maddison & Maddison, 2005). For two major pteriomorph clades, I resolved basal branching relations by referring to recent molecular phylogenies (Combosch *et al.*, 2017; Lemer *et al.*, 2019): both support Mytilida as sister to Ostreida, and Arcida as sister to Pectinida. For relations among basal Ostreida (e.g. Rhombopteriodea and Pterineidae), I relied heavily on the interpretation of Johnston (1991).

RESULTS AND DISCUSSION

Higher-level patterns

The diversity of side-resting (pleurothetic) bivalves is almost bewildering (select examples in Fig. 1). For example, some are unattached recliners that simply rest on or just below the sediment surface; somewhat surprisingly, the more convex side can either face down (e.g. *Pecten*, *Imparilucina* and *Macoma*) or up (e.g. *Miltha* and *Myadora*). Some byssally attach near the hinge line, typically to hard surfaces, and lean towards one side even though the shells may not be very asymmetrical (e.g. various pterioids like *Isognomon*). Some byssally attached species adhere to surfaces so tightly they almost look cemented with the more convex valve facing up (e.g. *Anomia*). Some cement to hard surfaces, and the larger, more convex valve typically faces down (e.g. *Cleidothaerus*, *Exogyra*, *Ostrea*, *Spondylus*, various chamids and hippuritids). Impressively, some Cretaceous side-resting taxa are among the largest bivalves ever known. These include massive columnar hippuritids to 1 m in height (e.g. *Praebarrettia*; Johnson, 2002), and some bizzarely large, flattened inoceramids (e.g. *Platyceramus*, to 3 m in diameter; Kauffmann *et al.*, 2007). Which side faces downwards—right, left or random—depends on the group (Fig. 1; Supplementary Material Table S1).

This side-resting (pleurothetic) lifestyle evolved surprisingly early in bivalve history—mid-Ordovician in both the Limida and Ostreida (Crouch *et al.*, 2021)—and multiple times afterwards across the Bivalvia (Fig. 2; Supplementary Material Fig. S1). Unfortunately, convergence of form is rampant in two groups with many pleurothetic forms—Ostreida and Pectinida (Seilacher, 1984; Alejandrino *et al.*, 2011; Hautmann & Hagdorn, 2013)—which

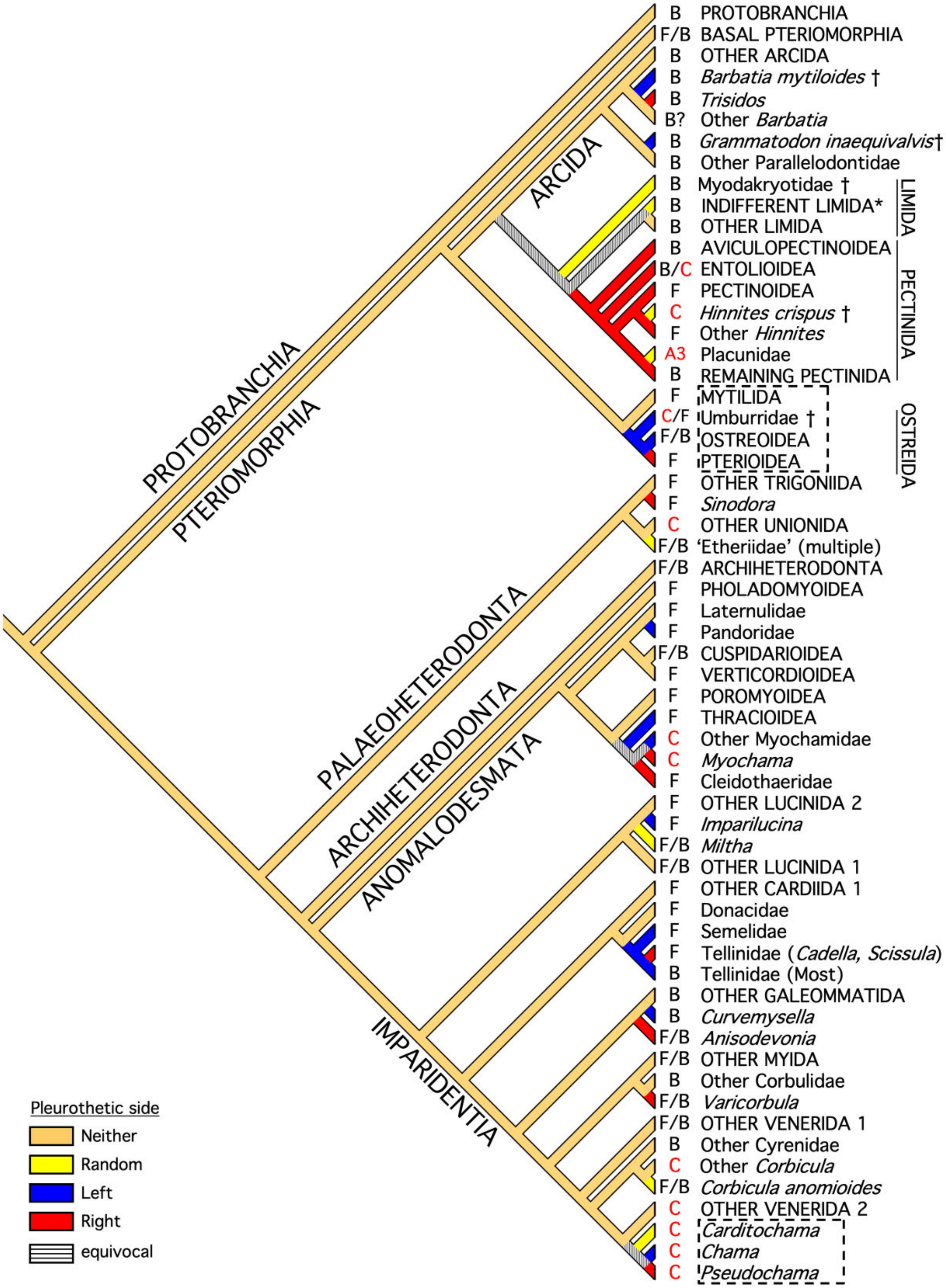

Figure 2. Evolutionary history of pleurothetic (lower) side in Bivalvia. The tree is a pruned version of figure 3 of Crouch *et al.* (2021). Character states for pleurothetic side (neither = orthothetic, random, left, right) were unordered, character mapping was by parsimony. Letters by branch tips indicate whether, or how, shells were attached to the substratum: F, free (shells not attached); B, shells byssally attached; C, one valve cemented; A3, all three attachment states occur within that group (details and references for all groups in Supplementary Material Table S1). Red font highlights taxa that include cemented species. Whether taxa are orthothetic (upright) or pleurothetic (side resting) is indicated by the colour of the branch tip as noted in the legend. Dashed boxes indicate groups for which a more detailed tree is presented (Ostreida, Fig. 3; Chamidae, Fig. 4). *Potentially indifferent Limida include genera like *Ctenostreon*?, *Limea*?, *Palaeolima* and *Pseudolimea*?.

Table 1. Number of bivalve families* that include at least some taxa that are pleurothetic (side-resting) as adults.

	Pleurothetic side						
Taxon	Neither†	Random	Left	Right	Total pleurothetic‡	Total families*	Percent of families*
Protobranchia	7	0	0	0	0	7	0%
Pteriomorphia	8	5	8	24	30	38	79%
Palaeoheterodonta	10	1	0	1	2	12	17%
Archiheterodonta	4	0	0	0	0	4	0%
Anomalodesmata	15	0	4	2	5	20	25%
Imparidentia	38	3	5	4	7	45	16%
Totals	82	9	17	31	44	126	35%

*Of families included in the Crouch *et al*. (2021) tree, which omits many fossil groups.
†'Neither' means orthothetic (i.e. commissural plane is vertical).
‡Total of pleurothetic families is less than the sum of all pleurothetic types because some families contained more than one pleurothetic type.

greatly complicates the classification of early fossil bivalves and renders tentative some of my results and conclusions.

Overall, 35% of all families listed by Crouch *et al.* (2021) include pleurothetic taxa (Table 1, Supplementary Material Fig. S1; for complete list see Supplementary Material Table S1). Families with pleurothetic species are absent from two higher taxa (Protobranchia and Archiheterodonta) and infrequent in three others (16–25% of families in Palaeoheterodonta, Anomalodesmata and Imparidentia). As noted by Harper (2012), the absence of pleurothetic taxa among the Protobranchia is not surprising, because they must move through sediment to deposit feed with their labial palps. The absence of pleurothetic forms in the Archiheterodonta is also not that surprising, given how few families it includes. Strikingly, nearly 80% of pteriomorph families in the Crouch *et al.* (2021) tree contain pleurothetic taxa, including all families of Pectinida, Ostreida and Limida (see Supplementary Material Fig. S1). Only the two families in Mytilida and six of eight families of Arcida appear to lack pleurothetic taxa.

Across all Bivalvia, many more families had right-pleurothetic taxa (31) than left- or randomly pleurothetic (17 and 9, respectively; Table 1). However, this class-level right-side bias was due almost entirely to the Pteriomorphia, where right-pleurothetic cases outnumber the other two types nearly three to one. Among non-pteriomorph taxa, families with randomly pleurothetic, left-pleurothetic and right-pleurothetic taxa were more comparable (4, 9 and 7 taxa, respectively).

Given the large number of families with pleurothetic taxa, the relatively small number of independent evolutionary origins across all Bivalvia (<20) seems surprising (Fig. 2). A pleurothetic lifestyle appears to have arisen from orthothetic ancestors at least six times in the Pteriomorphia (three times in Arcida, once or twice in Limida, once in Pectinida and once in Ostreida), perhaps four times in the Palaeoheterodonta (if all three genera typically placed in 'Ethereiidae' represent independent origins; see Harper, 2012), at least twice in the Anomalodesmata and at least eight times in the Imparidentia (twice in Lucinida, once in Cardiida, twice in Galeommatida, once in Myida and twice in Venerida).

As more is learned about pleurothetic fossil taxa and their relations to modern groups, the number of independent evolutionary origins will likely increase. For example, many pleurothetic types occur among extinct Myalinida, including (1) indifferently pleurothetic forms like *Maminka* in Lunulacardiidae (Kříž, 2001), (2) right-pleurothetic forms [some *Myalina* (Stanley, 1972) and derived species of *Maminka* (Kříž, 2001)] and (3) left-pleurothetic forms in the Inoceramoidea and Prokopievskioidea (Supplementary Material Table S1). Inequivalved (torted) and semi-pleurothetic forms were also apparently common among the Nepiomorphia of Kříž (2007) (P.A. Johnston, personal communication). And, of course, the remarkable rudists (Hippuritida) famously include one left-pleurothetic clade (Requieniidina) and a large right-pleurothetic clade (Hippuritidina) (Skelton, 2018). The evolutionary origins of the Hippuritida remain obscure (Skelton, 2018), so their precursors may or may not have been randomly pleurothetic. So far, the massively thick-shelled, equivalved, epibenthic but orthothetic recliner *Pachyrisma grande* remains the closest ancestor to rudists (Schneider, 2017). *Pachyrisma grande* (Bathonian stage, *c.* 167 Ma) occurred *c.* 5 Ma earlier than the earliest rudists (Oxfordian stage, *c.* 161 Ma; Schneider, 2017), so if a randomly pleurothetic ancestor to the rudists exists, it should occur during this narrow time window. Curiously, orthothetic descendents appear to have arisen multiple times from pleurothetic ancestors in the Pterioidea (e.g. some Malleidae, Isognomidae, Vulsellidae and Margaritidae), and perhaps additional times in other basal lineages of the Ostreida (Fig. 3). So, the evolutionary path to a pleurothetic lifestyle does not appear to be one-way.

Pteriomorphia: Arcida, Limida and Pectinida

The earliest Pteriomorphia appear to have been epibyssal, orthothetic, equivalve forms (e.g. Mytilida and most Arcida; Fig. 2, Supplementary Material Fig. S1 and Table S1). With very few exceptions [e.g. *Leiosolenus* and *Stavelia*, which are both weakly inequivalve (Nicol, 1958) and a few twisted forms like *Modiolus americanus* (Savazzi, 1989)], most Mytilida remain this way, although some may lean slightly towards one side as in *Mysidioptera* (Newton *et al.*, 1987).

Within the Arcida, however, multiple lineages independently invaded soft-sediments (Audino, Serb & Marian, 2019), and among these a pleurothetic lifestyle evolved in at least three different genera: *Barbatia*, *Trisidos* and *Grammatodon* (Fig. 2; Supplementary Material Table S1). Among living arcids, *Trisidos* nests within a clade of *Barbatia* species (e.g. *Barbatia trapezina*, *Barbatia virescens*, *Barbatia foliata* and *Barbatia lima*; Feng, Li. & Kong, 2015, Combosch & Giribet, 2016; Audino *et al.*, 2019). However, the much older genus '*Barbatia*' (back to Triassic) ends up as polyphyletic in most analyses. Therefore, within the Arcida, the Pliocene left-pleurothetic *Barbatia mytiloides* and Eocene right-pleurothetic *Trisidos* are most likely independent origins from orthothetic ancestors (Savazzi, 1981: fig. 6; Savazzi & Yao, 1992), as is the Lower Jurassic left-pleurothetic *Grammatodon inaequivalvis* (Etter, 2010) (Fig. 2).

Phylogenetic relations among closely related pteriomorph groups hint at a randomly pleurothetic origin for the Pectinida (Fig. 2). The Arcida (likely sister to Limida + Pectinida; Combosch *et al.*, 2017; Lemer *et al.*, 2019) are almost universally orthothetic and byssally attached except for the few derived forms noted above. The mostly byssally attached and orthothetic Limida are widely accepted as sister to the Pectinida (Crouch *et al.*, 2021, and references

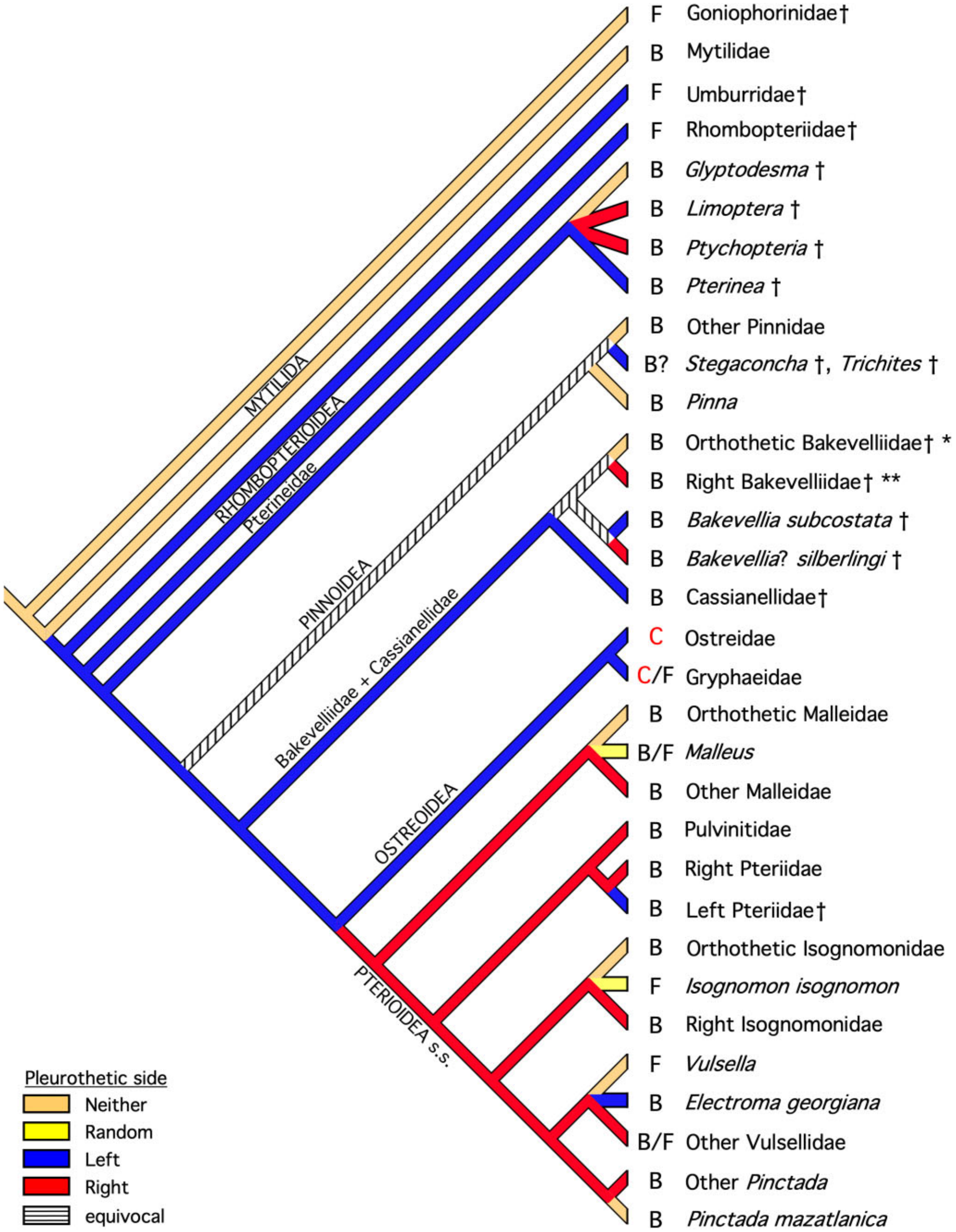

Figure 3. Evolutionary history of pleurothetic (lower) side in oyster-like bivalves (Ostreida). The tree is a moderately expanded version of this clade in figure 3 of Crouch *et al.* (2021). Several subtaxa were added to family branches to show cases that depart from the family-level pattern. Also, three extinct families not in Crouch *et al.* (2021) (Umburridae, Rhombopteriidae and Cassianellidae) were added because they provided crucial information about character polarity of some deep branches in the tree (see justification in the 'Methods' section). Letters by branch tips are as in the legend of Figure 2. In orthothetic taxa, the commissural plane is more or less perpendicular to the substratum, not leaning towards one side. *Orthothetic Bakevelliidae include genera like *Aguilerella*, *Bervillella* and *Gervillia*. **Right-pleurothetic Bakevelliidae include genera like *Cassiavellia* and *Kobayashites*.

therein). Significantly, three extinct limid genera appear to include randomly pleurothetic taxa: the Upper Carboniferous *Palaeolima retifera* (Carter *et al.*, 2000), the Late Triassic *Ctenostreon philocles* (see Yin & McRoberts, 2006: table 5) and the Upper Jurassic *Pseudolimea* cf. *arctica* (Fürsich, 1982). In addition, an even older unranked pteriomorphian, the Upper Ordovician *Myodakryotus deigryn* (Myodakryotidae), lay on either valve indifferently even though retaining a byssal notch in the right valve (Carter *et al.*, 2000). Lal (1996) argued that species of *Plicatula* (Plicatulidae) were indifferently attached, but most others insist all plicatulids were right-cemented (Waller, 1978; Harper, 1991; Marquez-Aliaga *et al.*, 2005). A survey of other fossil limid, myodakryotid and basal pectinid groups (e.g. Aviculpectinoidea) would provide a strong test of whether the earliest Pectinida were randomly pleurothetic. Unfortunately, given the uncertainty about relations among fossil limid and myodakryotid groups, no strong conclusion is possible about the pleurothetic state of the earliest Pectinida.

With two fascinating exceptions, the Pectinida appear to be entirely right-pleurothetic, regardless of whether unattached and reclining on one side, byssally attached, or cemented (Fig. 2; Supplementary Material Fig. S1 and Table S1). Curiously, the more convex valve may face up [e.g. the earliest scallop, *Pleuronectites*

(Hautmann, 2010), and other early Pectinida] or down (e.g. most Pectininae and many others; Supplementary Material Table S1). The ancestral state appears to be byssally attached, but numerous transitions occurred to a free-resting, recessing or swimming lifestyle (Waller, 2006; Alejandrino *et al.*, 2011). A cemented lifestyle also evolved at least 12 times in the Pectinida (Harper, 1991, 2012), always with the right side attached, including seven times in Pectinidae, once each in Spondylidae, Prospondylidae, Plicatulidae and Dimyidae, and likely multiple times in the extinct Pseudomonotidae (Newell & Boyd, 1970: 230) and other fossil groups not included here (Lithiotidae and Chondrontontidae) (Harper, 2012). The numerous transitions from byssally attached to cemented are not surprising. Byssal attachment in some juvenile pectinids was so tight that the lower (right) valve developed an imprint of distinctive substratum (e.g. ammonoid umbilicus), even though they did not appear to be cemented (e.g. *Crittendenia kummeli*, Newell & Boyd, 1995: 54).

The two interesting pectinid exceptions are *Placuna placenta* and *Hinnites crispus* (Fig. 2). *Placuna placenta* rests on the surface indifferently on either the right or left side based on the distribution of epibionts (Yonge, 1977: 503). Some have argued that the Placunidae are derived from byssally attached anomioidians (Yonge, 1977), but their older age (Crouch *et al.*, 2021) suggests the reverse order. A survey of epibionts in other *Placuna* species, and in fossil free-resting or recessing pteriomorphians, may reveal other examples of randomly pleurothetic taxa. The Pliocene *Hinnites crispus* also rests indifferently on the right or left side, but was likely derived from a cemented *Hinnites* ancestor (Seilacher, 1984). Therefore, both interesting exceptions among the almost entirely right-pleurothetic Pectinida were transitions from right-pleurothetic to randomly pleurothetic, one each from byssally attached or cemented ancestors.

Pteriomorphia: Ostreida

The classification of the Ostreida remains contentious, particularly for fossil groups (Johnston, 1993; Temkin, 2006; Bouchet *et al.*, 2010; Carter *et al.*, 2011). Except for two families, I followed the classification of Ostreida in the WoRMS database. The Bakevelliidae are sister to the crown Ostreida (Ostreoidea + Pterioidea *s.s.*; Crouch *et al.*, 2021), and the Cassianellidae diverge early from the Bakevelliidae before the split between Ostreoidea and Pterioidea (Temkin, 2006: fig. 5). So, I excluded both the Bakevelliidae and Cassianellidae as a clade separate from the Pterioidea, and refer to the remaining pterioid families as Pterioidea *s.s.*

Unlike the almost universally right-pleurothetic Pectinida, the Ostreida exhibit all three pleurothetic states, although randomly pleurothetic are rare (Fig. 3, Supplementary Material Fig. S1 and Table S1). Nonetheless, within Ostreida a left-pleurothetic lifestyle appears to have evolved quite early. It first appears in the late Early Ordovician or early Middle Ordovician *Umburra*-like precursors to all remaining Ostreida (Johnston, 1991: 314). Furthermore, it persisted in primitive members of both the Rhombopteriidae and Pterineidae (Johnston, 1993; Temkin, 2006). Therefore, orthothetic pterineids like *Glyptodesma* and subequivalve *Leptodesma* are likely derived from left-pleurothetic ancestors, as are right-pleurothetic *Limoptera* and *Ptychopteria* (Johnston, 1991, 1993) (Fig. 3). Within the Pinnoidea, the extinct, weakly left-pleurothetic *Stegaconcha* and *Trichites* might suggest that the largely orthothetic living Pinnidae were derived from left-pleurothetic ancestors. However, both are stratigraphically younger than early orthothetic *Pinna*, so Seilacher (1984) argues strongly that these are derived from an orthothetic *Pinna*-like ancestor. Finally, the complex Bakevelliidae include left-pleurothetic, right-pleurothetic and orthothetic forms. However, the left-pleurothetic Cassianellidae, which branch off early from the basal bakevelliid lineage (Temkin, 2006), implies that early bakevelliids were left-pleurothetic. All of this suggests that transitions between orthothetic and pleurothetic lifestyles, and between pleurothetic sides, were widespread among early Ostreida.

Among the crown Ostreida (Ostreoidea + Pterioidea *s.s.*), the cemented Ostreoidea (Ostreidae + Gryphaeidae) almost all are left-pleurothetic (Fig. 3). A significant switch to right-pleurothetic orientation occurred at the base of the Pterioidea *s.s.* Although they are overwhelmingly right-pleurothetic, and in contrast to the more stable Ostreoidea, numerous changes in pleurothetic state occurred in the Pterioidea: to orthothetic (some Malleidae, some Isognomonidae, *Vulsella* and some *Pinctada*), to left-pleurothetic (*Electroma* and some *Pteriidae*), and to randomly pleurothetic (*Malleus* and *Isognomon isognomon*; Fig. 3). At least within the Ostreida, the pleurothetic side of byssally attached lineages appears to be more labile than in cemented lineages.

Numerous fossil families not included in the Ostreida phylogeny of Crouch *et al.* (2021) are also pleurothetic, which could alter the conclusions above. During the Early Jurassic, a remarkable diversity of difficult-to-classify gregarious bivalves—the '*Lithiotis* facies'—was widespread in tropical environments. They included enigmatic 'lithiotid' and dubious 'isognomonid' and 'pteriid' genera all recently re-assigned to the ostreid family Plicatostylidae based on a distinctive, shared shell microstructure (Posenato & Crippa, 2023). Curiously, both subfamilies in the Plicatostylidae include both left-pleurothetic genera (*Gervilleioperna* in Pachygervilliinae and *Cochlearites* in Plicatostylinae) and right-pleurothetic genera (*Pachyperna* in Pachygervilliinae; *Lithiotis* in Plicatostylinae, where right-pleurothetic juveniles transition to orthothetic adults; Loriga & Posenato, 1996) (Supplementary Material Table S1). In addition, Pachygervilliinae includes one genus that is effectively orthothetic (*Pachygervillia*) and another with highly variable orientation ranging from orthothetic to pleurothetic in either direction (*Lithioperna*) (Posenato & Crippa, 2023). Until more is known about relations among plicatostylid genera, not much can be said about the evolutionary origin of pleurothetic forms, but both left- and right-pleurothetic types may have evolved twice in the Plicatostylidae.

One other important fossil group not in the Crouch *et al.* (2021) tree, the problematic Posidonioidea, may also hold implications for the evolutionary history of pleurothetic forms in the Ostreida. Genera in two families, Daonellidae (*Daonella*) and Posidoniidae (*Posidonia* and *Posidonotis*) include right-pleurothetic species (Supplementary Material Table S1). The Posidoniidae are known as far back as the Lower Carboniferous (Waller & Stanley, 2005), before the split between Ostreoidea and Pectinoidea *s.s.* (Fig. 3). So, this could imply as many as two transitions from left-pleurothetic to right-pleurothetic forms.

Anomalodesmata

The Anomalodesmata includes a bewildering diversity of lifestyles (burrowing, byssally attached, cemented, endolithic, suspension feeding and predatory; Harper, Taylor & Crame, 2000; Machado & Passos, 2022), and some exceedingly weird forms like the watering pot shells (Clavagelloidea; Morton & Machado, 2021). Curiously, all four families with unattached pleurothetic examples are left-resting: a few species in the Pandoridae, nearly all species in the Thracioidea (Periplomatidae + Thraciidae) and all three non-cemented genera in the Myochamidae (*Hunkydora*, *Myadora* and *Myadoropsis*) (Fig. 2, Supplementary Material Fig. S1 and Table S1). In contrast, both families with cemented taxa attach by the right valve (*Myochama* in the Myochamidae, and all Cleidothaeridae). Right-attached forms appear to have evolved twice in the Myochamoidea, once in Myochamidae (where three other genera are not attached) and once in Cleidotheridae (where all species are cemented). In the bizarre Clavagelloidea, either one (the left, Clavagellidae) or both (Penicillidae) valves become incorporated into a massive, vertically oriented adventitious tube, but they are technically not cemented (Harper, 1991) or pleurothetic, so I treat them as free and orthothetic. The clavagellids that incorporate only the left valve appear to have derived from free-living, non-pleurothetic and equivalved Laternulidae (Harper *et al.*, 2000) and so could be considered an independent origin of left-sidedness.

The relation of cemented forms to free-living or byssally attached pleurothetic Anomalodesmata is not obvious (Fig. 2, Supplementary Material Fig. S1). Most of the 20 families are free-living, but three include a few byssally attached representatives (Lyonsiidae, Verticordiidae and the basal Sanguinolitidae) and four include left-pleurothetic taxa (Supplementary Material Table S1). Strangely, the right-attached *Myochama* lies within a family (Myochamidae) where the three other genera are free-living but left-pleurothetic (Harper *et al.*, 2006), as are the closely related Periplomatidae. Even odder, two of these left-pleurothetic genera are strongly inequivalve (*Hunkydora* and *Myadora*), with the lower left valve flat and the upper right valve convex (Harper, 1991), which makes it hard to understand how right-attached *Myochama*, with more convex upper left valves, arose. This contrasts starkly with the Pectinida, where right-pleurothetic, byssally attached forms gave rise to right-cemented forms in many groups (see the 'Pteriomorphia: Arcida, Limida and Pectinida' subsection).

Cemented freshwater bivalves

Bivalves independently radiated into freshwater at least three times: Unionida (six families), Sphaeriidae and Cyrenidae (Graf, 2013; Crouch *et al.*, 2021). Among these three clades, cemented pleurothetic forms evolved in two (Harper, 2012): the 'Etheriidae' (three monotypic genera, *Etheria*, *Mulleria* and *Pseudomulleria*; Yonge, 1978) within the otherwise equivalve and unattached Unionida, and *Corbicula anomioides* (previously *Posostrea*; Bogan & Bouchet, 1998) in the otherwise equivalve and unattached Cyrenidae (Venerida) (Fig. 2; Supplementary Material Table S1). Somewhat remarkably, in both groups the attached side is random (Harper, 1991; Bogan & Bouchet, 1998). This implies two independent origins of randomly attached taxa from unattached, equivalve ancestors.

Unfortunately, phylogenetic relations among etheriid genera remain controversial (Bogan & Hoeh, 2000; Hoeh *et al.*, 2009; Graf & Cummings, 2010, 2021), so cemented, randomly attached forms might have evolved two or even three times within 'Etheriidae'. The issue is complex because, the three monotypic cemented genera each occur on separate continents, Africa (*Etheria*), South America (*Mulleria*) and India (*Pseudomulleria*) (Harper, 1991), and the oldest (*Etheria*) is known as far back as the early Miocene (Crouch *et al.*, 2021). Their anatomical similarities suggest monophyly (Yonge, 1978; Graf & Cummings, 2010). But some analyses that include molecular data suggest polyphyly (Graf & Cummings, 2006; Hoeh *et al.*, 2009), a result annoyingly confounded by a problematical cytochrome *c* oxidase subunit I (COI) sequence for *Pseudomulleria* (Graf & Cummings, 2010). Also, in a tree based on COI sequence data, each 'etheriid' genus places more closely to species from the same continent rather than to other 'etheriids' (D. Campbell, personal communication). Finally, the fourth enigmatic etheriid genus *Bartlettia*, which nestles in crevices but is not cemented, has yet to be included in any phylogenetic analyses. So, a robust phylogenetic analysis that includes all four etheriid genera could reveal as many as four independent origins of randomly pleurothetic taxa among freshwater bivalves, three in 'Etheriidae' and one in Cyrenidae.

Imparidentia: other

Despite the great diversity of lifestyles and habitats, pleurothetic taxa are uncommon in the Imparidentia (present in 16% of 45 families; Table 1; Supplementary Material Table S1). Pleurothetic lifestyles evolved in three unattached families (Lucinidae, Tellinidae and Semelidae), two byssally attached families (Corbulidae and Lasaeidae) and two families that include cemented species (Cyrenidae and Chamidae) (Fig. 2, Supplementary Material Fig. S1).

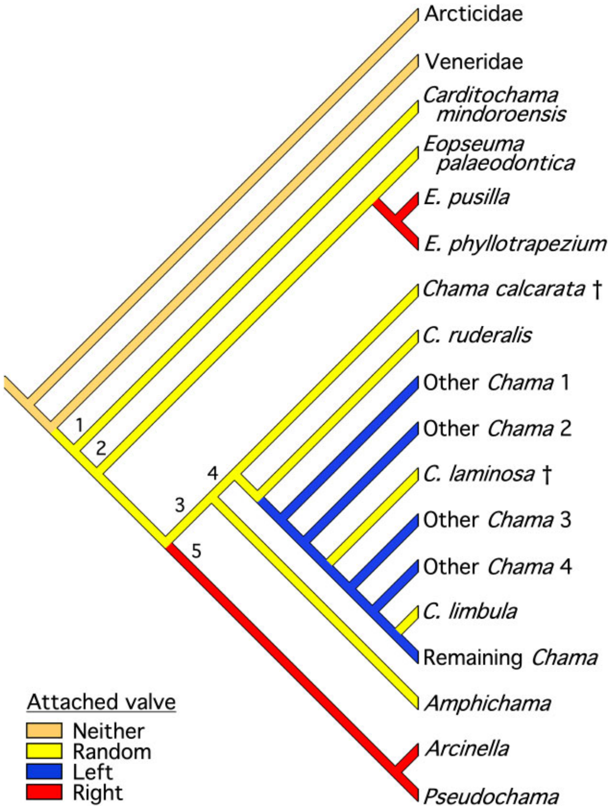

Figure 4. Hypothesis of relations among genera and select species of Chamidae. See text (*Imparidentia: Chamoidea*) for justifications for numbered branches.

In the ancient, chemosymbiotic, overwhelmingly orthothetic (strangely, dorsal upwards) Lucinida (Taylor & Glover, 2021), pleurothetic forms evolved in two unrelated genera out of nearly 100 (Fig. 2). Both living and fossil *Miltha* are randomly pleurothetic (Vokes, 1969) whereas the monotypic *Imparilucina rosacea* is left-reclining (Taylor & Glover, 2021). Both are likely surface dwellers or shallow burrowers that lie on one side. In the even more diverse Tellinoidea, two families are predominantly left-reclining shallow burrowers (Semelidae and Tellinidae) (Ujino & Matsukuma, 2010). Curiously, within the Tellinidae, two genera (*Cadella* and *Scissula*) are right-reclining (Ujino & Matsukuma, 2010), so a behavioural left-reclining asymmetry appears to have inverted to right-reclining twice. Within Corbulidae, two genera are strongly inequivalve (*Varicorbula* and *Corbula*). Little seems to be known about corbulid life orientation, but in the byssally attached *Varicorbula gibba* 82% of epibionts were on the flatter left valve, suggesting a right-pleurothetic orientation (Mikkelsen & Bieler, 2001). Within the Cyrenidae, among the great many *Corbicula*, one peculiar freshwater species (*Corbicula anomioides*) cements to the substratum in a randomly pleurothetic manner (Bogan & Bouchet, 1998). And finally, species of Chamidae are all cemented by one side (next section).

Imparidentia: Chamoidea

The Chamoidea, or jewel box shells, offer a particularly interesting study in the evolution of pleurothetic forms. Its sole family, Chamidae, is the *only* living family of bivalves in which all three pleurothetic states—random, left and right—are well represented by different genera and species (Fig. 4, Supplementary Material Table S1). The oldest and largest genus (*Chama*) is typically left-attached, three genera are typically right-attached (*Arcinella*, *Eopseuma* and *Pseudochama*) and two are indifferently (randomly) attached (*Amphichama* and *Carditochama*). Significantly,

Table 2. Living Chamidae of particular phylogenetic interest*.

Species	Attached side	Fossil age	Question of interest
Carditochama	Random	?	Is *Carditochama* sister to remaining Chamidae?
Eopseuma palaeodontica	Random	?	Was the first *Eopseuma* randomly attached?
Chama ruderalis	Random	Late Miocene	Were the earliest *Chama* randomly attached?
Chama limbula	Random	Late Pliocene	Is *Chama limbula* a reversal from left-attached to random?
Chama congregata	Left-attached	Early Miocene	Were the earliest *Chama* left-attached?
Chama gryphoides	Left-attached	Early Miocene	Were the earliest *Chama* left-attached?
Chama macerophylla	Left-attached	Middle Miocene	Were the earliest *Chama* left-attached?
Chama pulchella	Mostly left-attached	?	Are left-attached species with many right-attached specimens basal or derived within *Chama*?
Chama asperella	Mostly left-attached	Early Miocene	Are left-attached species with many right-attached specimens basal or derived within *Chama*?

*Sources for attached side and fossil ages are in Supplementary Material Table S1. ?Fossil age not known.

two genera typified as left- or right-attached nonetheless include some randomly attached species (*Chama* and *Eopseuma*). The family also has a decent fossil record extending back at least as far as the late Cretaceous (Sepkoski, 2002). This wide diversity of forms therefore allows robust tests of the evolutionary sequence of pleurothetic side within the Chamidae.

Unfortunately, phylogenetic relations among chamid genera are poorly known. Even placement of the family within Bivalvia has long been problematic (Lemer *et al.*, 2019). Chamids do appear in large-scale bivalve molecular phylogenies, but are typically only represented by the genus *Chama* and often the same species (Taylor *et al.*, 2007; Bieler *et al.*, 2014; Combosch *et al.*, 2017; Lemer *et al.*, 2019; Wang *et al.*, 2023). In addition, chamids emerge as having unusually long branch lengths in some analyses (Taylor *et al.*, 2007; Bieler *et al.*, 2014; Combosch *et al.*, 2017; Lemer *et al.*, 2019), which limits the ability to resolve their placement more precisely (Crouch *et al.*, 2021). To make matters worse, misidentified, misclassified or uncertain chamid species outnumber valid species by more than two to one (211 *vs* 96; WoRMS). Therefore, many *names* of Chamidae that occur in papers may be incorrect or invalid. And finally, the one molecular phylogeny on multiple chamid species revealed that the common *Chama congregata* may include multiple cryptic species (Campbell *et al.*, 2004).

Despite these limitations, evidence from hinge dentition (Matsukuma, 1996; Campbell *et al.*, 2004), the fossil record (Glibert & van der Poel, 1966; Kennedy, Morris & Taylor, 1970; Healy, Lamprell & Stanisic, 1993) and a preliminary mitochondrial 16S ribosomal RNA (16S rRNA) phylogeny (Campbell *et al.*, 2004) can be used to advance a hypothesis of phylogenetic relations among and within chamid genera that would be worth testing with molecular data (Fig. 4). First, the Chamidae are clearly nested within the Venerida, so Arcticidae and Veneridae—two older, nearby families—are natural, orthothetic, unattached outgroups (Crouch *et al.*, 2021). Second, several lines of evidence support the numbered branches in the tree. (1) *Carditochama* has the most primitive-looking lucinid-like hinge teeth of any chamid (cardinal and lateral teeth retained; Matsukuma, 1996). (2) *Eopseuma* also has traces of primitive-looking cyrenid-like hinge teeth (Matsukuma, 1996); *E. palaeodontica* is hypothesized to be sister to remaining *Eopseuma* because it is the only *Eopseuma* indifferently attached by either the right or left valve (the primitive state in the Chamidae) (Matsukuma, 1996). (Curiously, both *Carditochama* and *Eopseuma* also appear to be relict taxa in the Indo-Pacific; Matsukuma, 1996.) (3) *Amphichama* is hypothesized to be sister to *Chama* because a preliminary mitochondrial 16S rRNA phylogeny placed *Amphichama inezae* within the genus *Chama* (Campbell *et al.*, 2004). (4) Within the genus *Chama*, the randomly attached *Chama calcarata* is one of the oldest fossil species (Eocene; Glibert & van de Poel, 1966) and has primitive 'carditid-like' hinge dentition (Kennedy *et al.*, 1970), so it is a natural sister taxon to the remaining *Chama*; *Chama ruderalis* is a living randomly attached *Chama* that extends the furthest back in the fossil record (Upper Miocene; Beu, 2006); the Late Miocene to Early Pliocene *Chama laminosa* (right-attached common) and the nearly random Late Pliocene to recent *Chama limbula* (Healy *et al.*, 1993) are likely both reversals from among the many remaining, almost entirely left-attached *Chama*. (5) *Arcinella* and *Pseudochama* are widely recognized as closely related (Nicol, 1952; Gibson-Smith, 1979; Matsukuma, 1996); Nicol (1952) goes so far as to suggest that *Arcinella* (restricted to Central America; Bernard, 1976) is derived from the more cosmopolitan *Pseudochama*.

If this hypothesis for relations is correct, it would strongly support a genes-as-followers mode of evolution within the Chamidae (Fig. 4): (1) the ancestral state in Chamidae was indifferently (randomly) attached, (2) right-attached taxa arose twice, in the *Eopseuma* and *Pseudochama*/*Arcinella* clades (note that *Arcinella* species are weirdly only attached as juveniles and become detached and considerably less inequivalve as adults; Campbell *et al.*, 2004), (3) left-attached taxa arose only once (within basal *Chama*), (4) two or more reversions to randomly attached may have occurred within *Chama*, (5) the species sister to all other species within two 'fixed'-sided taxa (*Eopseuma* and *Chama*) was likely indifferently (randomly) attached and (6) the loss of attachment in adult *Arcinella* is derived.

Clearly, a molecular phylogenetic analysis that includes all six living genera is sorely needed to test the hypothesis proposed here (Fig. 4). However, this hypothesis does help identify which living *Eopseuma* and *Chama* would be particularly valuable to include in any future molecular analyses (Table 2) to answer key questions: Is *Carditochama* sister to the remaining Chamidae? Were basally branching *Chama* and *Eopseuma* randomly attached, left-attached (*Chama*) or right-attached (*Eopseuma*)? Are any randomly attached *Chama*, or right-attached species, reversals from left-attached ancestors?

Ontogeny of shell asymmetry in pleurothetic bivalves

The time when valves become asymmetrical during ontogeny varies greatly among bivalve groups. The early larval stage (prodissoconch 1) in all bivalve groups has symmetrical valves (Malchus & Sartori, 2013). Therefore, during ontogeny, one valve must diverge in form from the other to yield a bilaterally asymmetrical adult shell. Asymmetrical valves appear early (e.g. prodissoconch 2) in most Ostreoidea and Anomiidae, where the larval shell asymmetry is conspicuous, and in pterioid and bakevelliid bivalves, where larvae are at most only weakly inequivalve (Malchus & Sartori, 2013). In contrast, shell asymmetry arises quite late in oyster-like freshwater *Etheria* (Unionida) and the rock scallop *Hinnites* (Pectinida), where post-larval and early juvenile stages are equivalve before becoming

Table 3. Number of inferred evolutionary transitions among pleurothetic states inferred from Figures 2, 3 and 4*.

Ancestral pleurothetic side	Derived pleurothetic side	Number of transitions	Ancestral taxon	Derived taxon
Origins				
(A) Neither*	Random	5–8	Basal Pteriomorphia	Myodakryotidae†?
			Other Limida	*Palaeolima*†?
			Other Unionida	'Etheridae' (up to 3)
			Other Lucinida	*Miltha*
			Other Corbicula	*Corbicula anomioides*
			Other Venerida	Basal Chamidae?
(B) Neither*	Left	8–10	Other Arcida	*Barbatia*
			Other Parallelodontidae	*Grammatodon*†
			Basal Mytilida	Basal Ostreida
			Other Pinnoidea	*Stegaconcha*†?
			Other Pinnoidea	*Trichites*†?
			Laternulidae	Pandoridae
			Basal Anomalodesmata	Thracioidea?
			Basal Anomalodesmata	Myochamoidea?
			Other Lucinida	*Imparilucina*
			Other Cardiida	Tellinoidea
			Other Galeommatida	*Curvemysella*
(C) Neither	Right	4–6	Other Arcida	*Trisidos*
			Basal Pteriomorphia	Basal Pectinida?
			Other Trigonida	*Sinodora*†
			Basal Anomalodesmata	Myochamoidea?
			Other Galeommatida	*Anisodevonia*
			Other Corbulidae	*Varicorbula*
(D) Random	Left	0–1	Basal Chama	Derived *Chama*?
(E) Random	Right	0–3	Basal Limida	Basal Pectinida?
			Basal Chamidae	Some *Eopseuma*?
			Basal Chamidae	*Arcinella* + *Pseudochama*?
Reversals or inversions				
(F) Random	Neither**	0		
(G) Left	Neither**	3	Basal Pterineidae	*Glyptodesma*†
			Basal Ostreida	Basal Pinnoidea?
			Basal Bakevelliidae†	Orthothetic Bakevelliidae†
(H) Left	Random	0–2	Other *Chama*	*Chama laminosa*†?
			Other *Chama*	*Chama limbula?*
(I) Left	Right	5–7	Other Pterineidae	*Ptychopteria*†?
			Other Pterineidae	*Limoptera*†?
			Basal Bakevelliidae†	Right Bakevelliidae†
			Basal Bakevellia†	*Bakevellia silberlingi*†
			Basal Ostreida	Pterioidea *s.s.*
			Tellinidae	*Cadella*
			Tellinidae	*Scissula*
(J) Right	Neither**	4	Other Malleidae	Orthothetic Malleidae
			Other Isognomonidae	Orthothetic Isognomidae
			Other Vulsellidae	*Vulsella*
			Other Magaritidae	Orthothetic *Pinctada*
(K) Right	Random	4	Other Pectinida	*Placuna*
			Other *Hinnites*	*Hinnites crispus*†
			Other Malleidae	*Malleus*
			Other Isognomonidae	*Isognomon*
(L) Right	Left	2	Other Pteriidae	Left Pteriidae†
			Other Vulsellidae	*Electroma georgiana*

*Row 'A' represents origins of presumably non-heritable variation in pleurothetic side; rows 'B' and 'C' represent 'genes as leaders'; rows 'D' and 'E' represent 'genes as followers'. Question marks by derived taxa indicate uncertain transitions.
†Extinct taxon. **'Neither' means orthothetic (i.e. commissural plane is vertical).

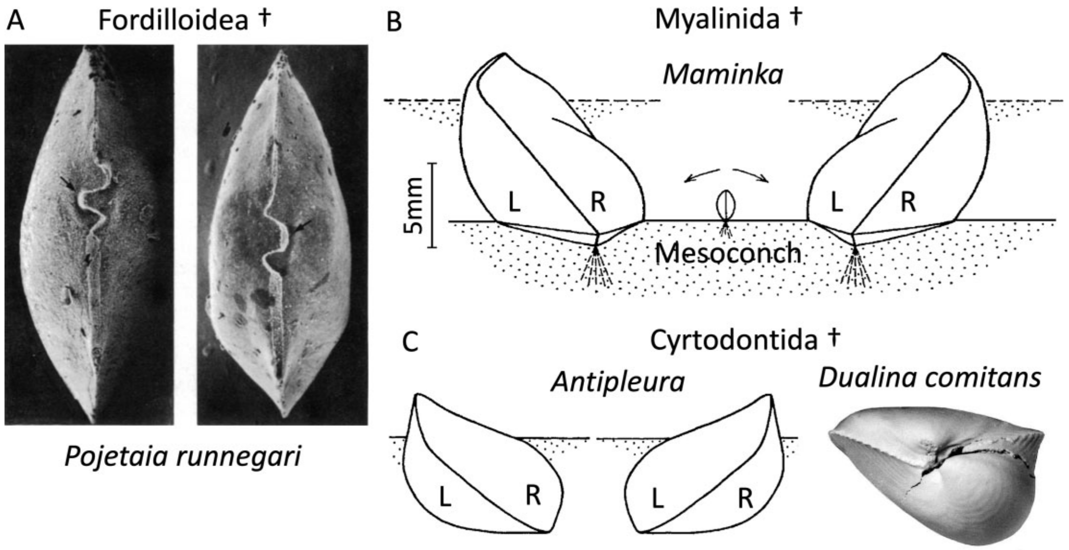

Figure 5. Examples of randomly asymmetrical, lower Paleozoic bivalves. **A.** Indifferent hinge-teeth asymmetry in *Pojetaia runnegari*, one of the earliest known bivalves from the Lower Cambrian (from Runnegar & Bentley, 1983). **B.** Indifferently pleurothetic forms in Silurian Myalinida (*Maminka*). **C.** Indifferently pleurothetic forms in Silurian (*Dualina*) and Lower Devonian (*Antipleura*) Cyrtodontida (**B** and **C** from Kříž, 2001).

cemented and asymmetrical (Yonge, 1978). Similarly, in the typically highly asymmetrical jewel-box shells (Chamidae), the larvae and early juvenile stages are equivalve up to sizes of 1.5–2.5 mm (Kennedy *et al.*, 1970; Matsukuma, 1996), a pattern also seen in extinct enantiomorphic genera from two different orders, *Maminka* (Myalinida) and *Antipleura* (Cyrtodontida; Kříž, 2007).

Genes as leaders or followers: the evolutionary significance of random asymmetry

The present survey offers a preliminary estimate of how often genes are leaders or followers in the evolution of pleurothetic lifestyles in the Bivalvia (Table 3). Crucially, recall that variation in 'direction of asymmetry' *is not* heritable in cases of random asymmetry but *is* heritable in species where one chiral form predominates (fixed asymmetry; Palmer, 2004). Therefore, any evolutionary transition from randomly pleurothetic to either left- or right-pleurothetic may be considered a case of genes as followers (Palmer, 2004, 2016). Unfortunately, at several key points in the tree, inferred ancestral states are equivocal (Figs 2, 3), and many fossil taxa were not included in the Crouch *et al.* (2021) tree. So, more taxa or better resolved topologies are needed for greater confidence in these results.

Across the Bivalvia, randomly pleurothetic lifestyles evolved from orthothetic ancestors about half as often (5–8 cases; Table 3A) as fixed pleurothetic forms (left or right, 12–16 cases; Table 3B, C). Also, rather few left-pleurothetic or right-pleurothetic forms evolved from randomly pleurothetic ancestors (0–4 cases; Table 3D, E), and most of these were in the Chamidae (Fig. 4). Multiple inversions occurred between left-pleurothetic and right-pleurothetic forms (7–9 cases; Table 3I, L), as did reversals to orthothetic from pleurothetic forms (7 cases; Table 3F, G, J), and reversals to random from fixed (4–6 cases; Table 3H, K). Therefore, the evidence for genes as followers among pleurothetic bivalves is weak to modest. On the one hand, new pleurothetic taxa were about one-third as likely to arise as randomly oriented (direction not inherited) rather than fixed. However, fixed pleurothetic forms were far less likely to arise from random ancestors (genes as followers) than from orthothetic ancestors (genes as leaders), and most of these putative cases depend on the as yet confirmed topology of the Chamidae tree (Fig. 4).

Unfortunately, at two key points in the Bivalve tree, inferred ancestral states are equivocal, so uncertainty remains about whether randomly pleurothetic was ancestral or not (Fig. 2). First, both families in Limida (Myodakryotidae and Limidae) either exhibit, or include, randomly plurothetic lifestyles. Because Limida is both older than, and sister to, Pectinida (Crouch *et al.*, 2021), randomly pleurothetic forms might have preceded the evolutionary split between them. Second, although the earliest Chamidae may have been randomly pleurothetic (see the 'Imparidentia: Chamoidea' subsection, Fig. 4), a more robust phylogeny of living Chamidae, particularly those in Table 2, is required to confirm this.

Evolutionary stability of pleurothetic side (not counting independent origins) did not appear to be strongly influenced by pleurothetic mode (free-lying, byssally attached or cemented) among the Crouch *et al.* (2021) families in this analysis. For example, among cemented groups, I encountered no compelling evidence of changes in pleurothetic side in either of the two families of Ostreoidea (Fig. 3; Supplementary Material Table S1), yet four possible side changes occurred in the Chamidae (Fig. 4) and one in the genus *Hinnites* (Fig. 2). Only two side changes were noted among the 10 free-lying pleurothetic clades (Table 3), and both were in the Tellinidae (*Cadella* and *Scissula* out of 61 total genera in the Tellininae; Fig. 2, Supplementary Material Table S1). Overall, side reversals or reversions to an orthothetic lifestyle were more common within the Pterioidea *s.s.* (5–8 cases) compared to Ostreoidea (no cases; Fig. 3), but this result is somewhat biased because Pterioidea *s.s.* includes three times as many pleurothetic families as Ostreoidea [six *vs* two of the Crouch *et al.* (2021) families; Fig. 3]. So pleurothetic side may have been somewhat more labile evolutionarily in byssally attached groups. But most groups with pleurothetic taxa across the Bivalvia are/were byssally attached (Figs 2, 3), so it is hard to say whether byssally attached forms were proportionally more labile.

Intriguingly, evidence from other fossil groups also suggests that randomly oriented forms may have been much more widespread among early bivalves. For example, two families in the extinct Ambonychioidea (Myalinida)—the Ambonychiidae (Newell & Boyd, 1970) and Lunulacardiidae (Kříž, 2001)—included randomly oriented, byssally attached groups (Fig. 5, Supplementary Material Table S1). Also, in the extinct Dualinoidea (Cyrtodontida), four families have some randomly oriented taxa (Antipleuridae, Dualinidae, Spanilidae and Stolidotidae;

Kříž, 2001, 2007; Fig. 5, Supplementary Material Table S1). Both orders date back to the late Ordovician or early Silurian, a time when most major extant bivalve groups originated (Crouch *et al.*, 2021). Finally, and perhaps most significantly, Kříž (2001: 312) notes that within-genera transitions from random to fixed pleurothetic occurred "very quickly during phylogeny" in families from two different orders: Myalinida (right-pleurothetic *Maminka arachne* in the Lunulacardiidae) and Cyrtodontida (left-pleurothetic *Dualina major* in the Dualinidae) (classification as in the WoRMS database, which unfortunately conflicts with the Nepiomorphia classification of Kříž, 2007). Clearly, a hunt for more Ordovician or Siluran pleurothetic bivalves, to test whether they are random or fixed, would be worthwhile.

Perhaps most surprising of all, the very earliest Paleozoic bivalves showed clear evidence of random asymmetry (Fig. 5A). Despite being rare among living and post-Cambrian bivalves, hinge-tooth transposition was common in both *Fordilla* and *Pojetaia* (Runnegar & Bentley, 1983: 83). From this, Runnegar & Bentley (1983) concluded: "This again indicates less precise genetic control on the formation of the skeleton than is usual for younger molluscs". Perhaps the same applies to pleurothetic lifestyles.

These observations by Kříž (2001) and Runnegar & Bentley (1983) raise an important caveat: the apparent rarity of randomly pleurothetic forms among fossil and living bivalve taxa reported here may be an illusion. If, as Kříž (2001) observed, randomly pleurothetic forms are evolutionarily short-lived, then they are less likely—perhaps significantly so—to be preserved or detected in the fossil record. They may therefore be greatly underrepresented in a survey like this one.

Bivalves offer a superb opportunity to test the prevalence of genes-as-leaders *vs* genes-as-followers modes of evolution because of their great diversity, the many independent evolutionary origins of a pleurothetic (side-resting and therefore asymmetric) lifestyle, their impressive fossil record and an increasingly well-resolved phylogenetic tree (Crouch *et al.*, 2021). Let the hunt for randomly pleurothetic living and fossil bivalves continue!

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Molluscan Studies* online.

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CONFLICT OF INTEREST

I declare no conflicts of interest.

DATA AVAILABILITY

All data extracted from the literature and used for this paper, along with source references, are in Supplementary Material Table S1.

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