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From symmetry to asymmetry: Phylogenetic patterns of asymmetry variation in animals and their evolutionary significance

(morphology/development/handedness/vertebrate/invertebrate)

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ABSTRACT Phylogenetic analyses of asymmetry variation offer a powerful tool for exploring the interplay between ontogeny and evolution because (i) conspicuous asymmetries exist in many higher metazoans with widely varying modes of development, (ii) patterns of bilateral variation within species may identify genetically and environmentally triggered asymmetries, and (iii) asymmetries arising at different times during development may be more sensitive to internal cytoplasmic inhomogeneities compared to external environmental stimuli. Using four broadly comparable asymmetry states (symmetry, antisymmetry, dextral, and sinistral), and two stages at which asymmetry appears developmentally (larval and postlarval), I evaluated relations between ontogenetic and phylogenetic patterns of asymmetry variation. Among 140 inferred phylogenetic transitions between asymmetry states, recorded from 11 classes in five phyla, directional asymmetry (dextral or sinistral) evolved directly from symmetrical ancestors proportionally more frequently among larval asymmetries. In contrast, antisymmetry, either as an end state or as a transitional stage preceding directional asymmetry, was confined primarily to postlarval asymmetries. The ontogenetic origin of asymmetry thus significantly influences its subsequent evolution. Furthermore, because antisymmetry typically signals an environmentally triggered asymmetry, the phylogenetic transition from antisymmetry to directional asymmetry suggests that many cases of laterally fixed asymmetries evolved via genetic assimilation.

Introduction

Patterns of Asymmetry Variation. Among higher metazoans, bilateral symmetry appears to have evolved only once (1). Because of this solitary origin, and because it happened so long ago, the evolution of bilateral symmetry is difficult to study. Fortunately, asymmetrical forms evolved many times among higher Metazoa (2, 3). These multiple independent origins permit hypotheses to be tested about developmental mechanisms or environmental conditions that promote the phylogenetic “breaking” of bilateral symmetry.

Conspicuously asymmetrical forms in animals generally fall into one of two broad categories: within a single species, “handedness” is either fixed [most individuals asymmetrical towards the same side, directional asymmetry (DA)] or it is random [“right-handed” and “left-handed” individuals equally frequent, antisymmetry (5)]. Wolpert emphasized a crucial difference between these categories nearly two decades ago: “There is no problem in making the two sides different; the problem is to define consistently a left side as opposed to a right side. For, unlike the antero-posterior axis and the dorsal-ventral axis, left-right asymmetry is a quite different property” (6). Because these categories imply fundamentally different developmental triggers, the evo-

lution of lateral bias (DA) must be recognized as distinct from the evolution of sometimes large but nonetheless random differences between sides [antisymmetry (AS)] (7).

Genetic and Developmental Aspects. For a trait to evolve, phenotypic variation must be heritable. However, herein lies a great puzzle (8). Unlike variation in virtually all other traits, deviations from bilateral symmetry in a particular direction have not responded to artificial selection. In contrast, the size of the difference between sides in traits exhibiting AS has responded to artificial selection. Therefore, although heritable variation does exist in mechanisms allowing opposite sides to diverge ontogenetically, bias toward a particular side appears quite refractory to selection. So how do fixed (directional) asymmetries evolve?

Whether the larger side in an individual is “genetically” versus “environmentally” determined is more vexatious than such a simple dichotomy might suggest (9). Nonetheless, intraspecific patterns of asymmetry variation do imply different developmental mechanisms (unpublished work). AS typically signals that a random, external environmental trigger induced one side to develop differently. DA, however, implies that internal, preexisting positional information influences the initial trigger, except where an external stimulus preferentially effects one side (see below).

Because the ontogenetic causes of bilateral differences are unknown for most groups, a substitute criterion is needed to assess the relative impact of genetic versus environmental factors on the evolution of asymmetry. The time during development at which bilateral differences first appear seems like a useful one because (i) it may be readily scored, and (ii) associations between ontogenetic and phylogenetic patterns may be identified without assumptions about underlying cause.

In addition, differences in developmental timing do imply different ontogenetic triggers (Table 1). Asymmetries determined early (larval) imply a greater impact of internal cytotenetic factors, whereas those determined late (postlarval) may be influenced more by external environmental factors. For example, spindle orientation relative to the plane of first cleavage determines the direction of shell coiling in gastropod molluscs (11), and thus represents a clear example of larval asymmetry. It also has a simple cytotenetic basis (12). In contrast, claw asymmetry in lobsters does not appear until after the fourth postlarval stage (13), and is thus a postlarval asymmetry. Significantly, the side that becomes larger is determined entirely by differential use (13). Therefore, although the distinction between developmental stages is sometimes arbitrary given the continuous nature of development, the dichotomy between larval and postlarval appearance of asymmetry allows a preliminary analysis of the impact of ontogenetic timing on phylogenetic patterns.

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Abbreviations: SYM, symmetry; AS, antisymmetry; DA, directional asymmetry.

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Table 1. Relations between observed ontogenetic origin and predicted phylogenetic pattern of conspicuous bilateral asymmetries

Ontogenetic origin of asymmetry		Predicted phylogenetic pattern	
Timing*	Presumed initial stimulus in asymmetrical ancestor†	Temporal sequence	Persistence of AS through cladogenesis
Larval	Internal, largely cytotenetic‡	SYM → DA	Absent or rare
Postlarval	External environment§	SYM → AS → DA	Common

SYM, symmetry; AS, antisymmetry; DA, directional asymmetry.

*Asymmetry first appears before or after birth, hatching, or metamorphosis.

†Primary stimulus inducing differential gene expression on one side of the plane of symmetry. Earlier appearance during development implies a greater cytotenetic influence, whereas later appearance implies a greater impact of external environmental stimuli.

‡Factors that affect the susceptibility of one side to differential gene expression, including: (i) cytoplasmic (invariant asymmetries present in the cytoplasm due to maternal effects from oogenesis or to molecular asymmetries in cytoskeletal elements), or (ii) genetic (a specific gene product in which mutations alter differential bilateral susceptibility).

§Random environmental stimuli arising entirely outside the organism and independent of preexisting internal asymmetries.

Predicted Phylogenetic Patterns. Different ontogenetic origins of asymmetry imply different patterns of phylogenetic precedence (Table 1). If early-developing (larval) asymmetry signals a predominantly internal cytotenetic trigger of the larger side, then fixed (DA) asymmetry may evolve more readily from a symmetrical progenitor because an underlying lateral biasing system already exists and selection may act on mutations affecting it. Alternatively, if late-developing (postlarval) AS signals a predominantly external environmental trigger, then the ancestor of an asymmetrical clade should exhibit AS because, although one side may inhibit the development of the other (7), the underlying bilateral biasing system upon which selection might act is weak or absent. Within these clades, fixed asymmetry (DA), if it evolves at all, should arise from an antisymmetrical ancestor.

Although not dealt with here, if the side that becomes larger is environmentally triggered, AS should persist more readily through speciation events than if it were determined genetically (Table 1). Therefore, where asymmetry is late-developing (postlarval), clades of exclusively AS species should be proportionally more common. Similarly, if the evolution of lateral biasing mechanisms represents a major hurdle (14), AS should be widespread either at present or at the time when fixed asymmetry (DA) first evolved.

Methods

To avoid Kinsbourne's despair that "one might tally up hundreds more instances for right and for left before losing heart about the enterprise altogether (as this contributor did)" (15), I restricted my survey in two ways: (i) to reasonably well-known and generally conspicuous asymmetries, and (ii) to external or skeletal asymmetries. Unfortunately, this meant excluding an extensive literature on (i) subtle deviations from bilateral symmetry [fluctuating asymmetry and its relation to developmental stability (8, 16)], (ii) conspicuous asymmetries in internal organs, including the fascinating phenomenon of *situs inversus* (17), and (iii) cerebral asymmetries (18). A focus on animals also eliminated some marvelous work on asymmetry in protozoans (19) and plants (e.g., ref. 20).

I identified from the literature (see *Appendix*) as many taxa as possible exhibiting one of four broadly comparable asymmetry states (symmetrical, antisymmetrical, dextral/right, and sinistral/left). Because "right" and "left" are arbitrary conventions for some traits, they were pooled as DA in most analyses.

For each taxon, one of four methods was used to infer the putative transition: (i) cladistic analysis of morphological characters, (ii) molecular phylogeny, (iii) traditional classification or keys, and (iv) patterns in the fossil record. Each taxon could therefore be assigned to one cell of a matrix of ancestor-descendent combinations. Cases where phylogenetic transitions could not be inferred with confidence are noted by "?"

in the *Appendix*, and separate analyses were conducted in which weakly supported transitions were included or excluded. Where traditional classifications were used, and hence precise phylogenetic information unavailable, I followed others (21) by assuming conspicuously asymmetrical taxa did not exhibit reversals to symmetry, except in the Gastropoda where asymmetry is so pervasive.

From published accounts (citations in next section), I also estimated the stage at which asymmetry appeared ontogenetically, and assigned each taxon to one of the two categories defined in Table 1. The distinction was clear in taxa exhibiting identifiable birth, hatching, or metamorphosis. It was somewhat arbitrary in taxa exhibiting gradual or direct development (22), but I used the midpoint between fertilization and maturity as a rough guide. Uncertain cases are noted by "?" in the *Appendix* and Tables 2 and 3.

Statistical analyses were conducted with STATVIEW II (version 1.03, Abacus Concepts, Berkeley, CA).

Phylogenetic Patterns in Particular Taxa

Evidence for the following patterns is presented fully in the *Appendix*; only notable examples are discussed here (SYM, symmetry; AS, antisymmetry; DA, directional asymmetry).

Vertebrata. Curiously, the evolutionary origin of symmetry in vertebrates remains controversial because of the bizarre asymmetrical development in larval cephalochordates (23), the presumed sister group to the vertebrates (1). Asymmetrical numbers of gill slits also persist in the most primitive living vertebrate [hagfish (24)]. Unfortunately, the true phylogenetic origin of the unusual asymmetrical development in lower chordates is unclear because of uncertainties over the inferred ancestral form of the Chordata (1).

In fishes, the tabulated asymmetries all arise late in development, and at least two clades exhibit the expected phylogenetic sequence SYM → AS → DA. This pattern is particularly striking for the priapium of male phallostethid fishes (Fig. 1). Females are also asymmetrical, and right-sided males mate more easily with left-sided females. Because right-sided males would have a higher fitness in populations where left-sided females predominated (or vice versa), this polymorphism is unstable and should rapidly evolve to fixation. Yet, AS clearly persisted through multiple cladogenic events before fixed right or left forms evolved.

Flatfish also exhibit the phylogenetic pattern SYM → AS → DA. The most primitive living flatfish (*Psettodes*) exhibit AS (24) and, although some uncertainty remains over the exact phylogenetic patterns (27), both right and left clades appear to have evolved from AS. In addition, at least one left-sided clade (Cynoglossidae) has clearly evolved from right-sided ancestors, and species polymorphic for sidedness have also evolved from right ancestors in a few cases.

Scale-eating cichlid fishes (*Perissodus*) exhibit a unique example of the phylogenetic transition SYM → AS. The mouth and jaws in an individual deform either to the right or left to improve feeding efficiency (28). Unlike all other cases of AS, where equal frequency of right and left signals an environmental trigger, frequency-dependent selection appears to maintain different forms at roughly equal frequencies, because individuals of the rarer morph have higher feeding success.

Among birds, although most owls have symmetrical ears, Norberg (29) argues forcefully that ear asymmetries have evolved independently in at least five clades. In each, these presumably early-developing asymmetries exhibit a directional bias, and all appear to be SYM → DA transitions. In contrast, postlarvally developing bills in crossbills and honeycreepers both exhibit a SYM → AS transition.

The asymmetries noted in mammals all appear to develop before birth. The skull asymmetry of many cetaceans and tooth asymmetry in narwhal appear to be SYM → DA transitions (30), whereas the odd tooth asymmetry in the fruit-eating bat *Myonycteris* represents a SYM → AS transition.

Arthropoda: Crustacea. Ontogenetically, lateral plate AS in the peculiar verrucosomorph barnacles arises after metamorphosis (31). It clearly reflects a SYM → AS transition.

Conspicuous claw asymmetry, which is so widespread among the Decapoda, also arises after larval settlement in Nephropidae (13), Xanthidae (32), Belliidae (33), Ocypodidae (34), and Paguroidea (35). As expected, claws in non-brachyuran decapods exhibit a SYM → AS transition in five clades. Significantly, in two of the three apparent SYM → DA transitions (Paguroidea and Coenobitoidea), asymmetry is associated with life in asymmetrical gastropod shells.

Distinctly asymmetrical claws have also evolved many times among brachyuran crabs. Primitively, claws were most likely symmetrical, as in living members of the Raninoidea (36), the sister group to the remaining Brachyura (37). Furthermore, the inferred ancestor of the higher Brachyura (Oxystomata + Cancridea + Brachyrhyncha) was most likely also symmetrical since many extant taxa still exhibit symmetrical claws.

The route by which DA evolved in Brachyuran crabs was only clear in some cases. Right-sidedness evolved at least three times via SYM → DA transitions, and three times via SYM → AS → DA transitions. Curiously, left-sidedness evolved only twice, and both times via SYM → AS → DA. Rathbun (ref. 38, pp. 14–15) made the intriguing observation that “in many species [of Xanthidae + Portunidae + Potamidae + Atelecyclidae] the right chela is always larger than the left” whereas “in no species [of Pinnotheridae + Palicidae + Grapsidae + Cecarcinidae + Ocypode] (Cymopoliidae = Palicidae excepted) is the right chela always larger than the left.” Although two exceptions exist (the Indopacific ocypodid *Thalassuca* and the grapsid *Platycheirograpsus*), her observation suggests claw asymmetry evolves differently in two clades of the Brachyrhyncha.

Arthropoda: Insecta. Abdominal rotation has evolved independently many times in the Diptera (39, 40). Typically, species twist in only one direction, although exceptions are known [e.g., *Clunio* (3)]. Because it develops in the pupae of these holometabolous insects, the widespread SYM → DA transition would be expected. However, abdominal rotation also appears to have evolved via the SYM → DA transition in the hemimetabolous Phasmatodea. More work is required before drawing too strong a conclusion about how abdominal rotation evolved in insects. In addition, except for thrips (Thysanoptera), where the universally left-sided mandibular asymmetry arises early in development (41), I have not attempted to assess the incidence of widespread but often subtle mandibular asymmetry in other insects [e.g., grasshoppers (42) and beetles (43)].

Gwynne (44) makes a convincing case that DA evolved independently at least twice in the tegmina (wing-covers) of

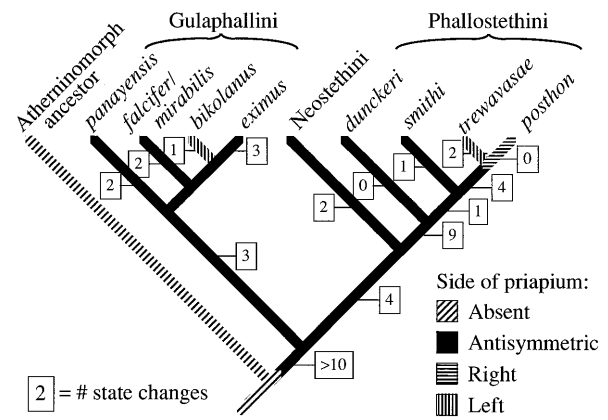


FIG. 1. Phylogenetic variation in the side of the asymmetrical priapium in male phallostethid fishes (from refs. 25 and 26), illustrating the evolutionary changes in asymmetry state expected for a postlarval developing trait. The priapium is a bizarre clasping structure, unknown outside the family Phallostethidae (Atherinomorpha), that evolved from highly modified pelvic bones and is used during mating. Numbers in boxes indicate state changes defining each branch.

ensiferan Orthoptera. In crickets (Gryllidae and relatives), the late-developing tegminal “file” used in stridulation appears to have evolved via a SYM → DA transition. In katydids (Tettigoniidae), on the other hand, it appears to have evolved via a SYM → AS → DA sequence, because a quasi-AS state occurs in the sister group (Haglidae), in which files occur on both wings, but only one may be used for stridulation at a given time.

Annelida and Brachiopoda. Although asymmetries exist in other polychaete families [e.g., side of operculum in some Serpulidae (3)], I only examined the late-developing coiling asymmetry in the calcareous tubes of spirorbid worms in detail. Coiling direction appears to have evolved via the SYM → AS → DA sequence, because the most primitive living spirorbid (*Neomicrobis*) still exhibits AS (45). The widespread sinistral coiling of most genera arose once from a dextral ancestor that itself was derived from AS progenitors. At least three reversals from sinistral to dextral also occurred.

Because the paired valves of brachiopods are dorsal and ventral (1), differences between them are not examples of bilateral asymmetry. However, several Mesozoic rhychonellid clades evolved “obligately” asymmetrical commissures where one side was consistently higher than the other, but the higher side varied at random (46). This kind of shell AS would not develop until well after larval settlement, and hence the SYM → AS transition would be expected.

Mollusca. Conspicuously asymmetrical taxa occur in all three major molluscan classes (Gastropoda, Bivalvia, and Cephalopoda). Although widespread in gastropods, the evolutionary origin of conispiral coiling remains an enigma (47). Gastropods appear to have arisen from a monoplacophoran (Bellerophonacean?) ancestor, but whether the earliest true gastropods exhibited dextral and sinistral shells equally frequently, either within or among species, remains uncertain. In addition, weakly asymmetrically coiled putative monoplacophorans from the early Cambrian are commonly sinistral (e.g., *Archaeospira ornata*), but some are dextral and others exhibit AS (e.g., the nearly mirror-image *Bernella simplex/Hubeispira* pair, and *Latouchella*) (47). Thus, ancestral gastropods might have arisen from a nonplanispiral ancestor. For this reason, conclusions about whether shell coiling exhibited AS or DA in the earliest gastropods must await better fossil data.

Among cemented bivalves, the transition SYM → DA has occurred twice, and the transition SYM → AS → DA at least three times. The fossil record suggests that conispiral coiling in cephalopods evolved via SYM → DA at least five times, but right and left forms arose about the same number of times.

Table 2. Frequencies of asymmetry-state transitions inferred from phylogenetic analyses of asymmetry variation in the higher Metazoa

Inferred ancestral state	No. of independent clades exhibiting derived state																				
	Symmetrical				Antisymmetrical				Right/dextral				Left/sinistral								
	L	L?	P?	P	L	L?	P?	P	L	L?	P?	P	L	L?	P?	P					
	Reliable transitions only*																				
Symmetrical	—	—	—	—	1	—	—	1	25	—	—	—	—	2	6	7	2	4	5	2	
Antisymmetrical	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	8	—	—	—	7	
Right/dextral	4	—	—	—	5	—	—	—	1	—	—	—	—	—	—	—	22	—	—	3	
Left/sinistral	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	
	All transitions†																				
Symmetrical	—	—	—	—	3	—	—	—	1	29	—	—	—	2	2	6	10	3	4	5	3
Antisymmetrical	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	12	—	—	—	14
Right/dextral	4	—	—	—	5	—	—	—	—	5	—	—	—	—	—	—	22	—	—	—	3
Left/sinistral	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—

L, larval; P, postlarval; L?, probably larval or arises well before maturity; P?, probably postlarval or arises near maturity; —, transition not relevant.
 *Includes only inferred state changes without “?” in Appendix.
 †Includes all inferred state changes from Appendix, regardless of strength of inference.

Coiling direction has reversed many times phylogenetically in the gastropods, and probably the cephalopods as well.

Molluscs are also one of the few groups where symmetrical forms can reliably be inferred to have evolved from asymmetrical ancestors. Derived, noncemented chamacean bivalves are more symmetrical than ancestral cemented forms [*Arcinella* (48)], and secondary symmetry has evolved independently from dextral ancestors at least four times among opisthobranch gastropods.

Overall Phylogenetic Patterns

Several broad patterns emerged when all phylogenetically independent transitions were examined as a group (Tables 2 and 3). Most importantly, the SYM → DA transition occurred more frequently than AS → DA among taxa exhibiting early- (8 of 8 cases) versus late- (20 of 36 cases) developing asymmetries (Table 3). This difference was significant regardless of whether all, or only reliable, transitions were used (Table 4, row 1), and it remained significant even if the numerous SYM → AS transitions of crustacean claws were counted only once (Table 4, row 5).

This analysis is somewhat misleading, however, because for each developmental type the number of potential AS → DA transitions depends in part on the number of SYM → AS transitions. For example, if no SYM → AS transitions occurred in clades exhibiting early-developing asymmetry, then no subsequent AS → DA transitions could occur. In fact, SYM → AS transitions were more common than SYM → DA transitions among taxa exhibiting late- (26 of 46 cases) rather than early- (1 of 9 cases) developing asymmetries (Table 3). This result also obtained whether all transitions of crustacean claws were included (Table 4, row 2) or they were counted only once (Table 4, row 6). SYM → AS and AS → DA transitions occurred in similar proportions among taxa exhibiting early- and late-developing asymmetries (Tables 3 and 4, rows 3 and 7), but early-developing cases were too few for this to be a robust test. Regardless of how the tests were done, SYM → DA

transitions were proportionally more common among early-developing asymmetries.

When all data were included, and SYM → DA and AS → DA transitions were pooled, phylogenetic transitions between forms of DA (right ↔ left) were more common among taxa exhibiting early- (22 of 30 cases) versus late- (8 of 44 cases) developing asymmetries (Tables 3 and 4, row 4). This pattern, however, was due to the widespread asymmetry reversal observed in gastropods, because when they were counted only once the pattern disappeared (Table 4, row 8).

DA → AS transitions were too infrequent to be analysed statistically (Tables 2 and 3). However, they are noteworthy because in all cases—coiling direction in gastropods and sidedness in flatfish (see Appendix)—the traits did not exhibit ideal AS (roughly equal frequencies of dextral and sinistral forms) as expected for an asymmetry triggered by random external environmental stimuli. In gastropods, the frequency of coiling morphs depends on the allele frequencies at one (or two) loci (12). Significantly, sidedness in the AS flatfish species derived from directionally asymmetrical ancestors has at least a partial genetic basis, and the frequencies of eye-side morphs often departs from 50:50 (49). In contrast, right/left frequencies do not depart from random in the most primitive living flatfish [*Psettodes* (24)]. Phylogenetic reversion to ideal AS thus appears rare indeed, if it occurs at all, regardless of whether the asymmetry is early or late developing.

Finally, reversions to symmetry from any form of asymmetrical ancestor were also rare (Tables 2 and 3). However, this is in part an artifact of the way in which asymmetry transitions were counted (see *Methods*). Too few fully resolved phylogenies were available to determine with confidence how often reversions to symmetry actually occurred. Conclusions about reversions to symmetry are thus premature.

Interplay Between Ontogeny and Phylogeny

As Raff notes so pointedly “the mechanisms by which animals change form in evolution [reflect a] tension between the demands

Table 3. Frequencies of asymmetry-state transitions pooled from Table 2

Ancestral state	No. of independent clades exhibiting derived state*							
	Symmetrical		Antisymmetrical		Directional (D+S)		Totals	
	L+L?	P+P?	L+L?	P+P?	L+L?	P+P?	L+L?	P+P?
Symmetrical	—	—	1 (3)	26 (30)	8 (11)	20 (24)	9 (14)	46 (54)
Antisymmetrical	0 (0)	0 (0)	—	—	0 (1)	16 (27)	0 (1)	16 (27)
Directional (D+S)	4 (4)	0 (0)	5 (5)	1 (5)	22 (22)	8 (8)	31 (31)	9 (13)

Abbreviations are as in Table 2.
 *Right/dextral (D) pooled with Left/sinistral (S) as Directional; L pooled with L? and P pooled with P?. Numbers outside parentheses are from the “Reliable transitions” section of Table 2; numbers inside parentheses are from the “All transitions” section of Table 2. Entries under Directional → Directional indicate Right → Left pooled with Left → Right transitions.

Table 4. Results from statistical tests of independence between ontogenetic origin of asymmetry (larval versus postlarval) and various phylogenetic transitions between asymmetry states

Comparison	Reliable transitions only			All transitions		
	N	χ^2	P	N	χ^2	P
All taxa included						
AS \rightarrow DA vs. SYM \rightarrow DA	44	3.83	0.050	63	6.13	0.013
SYM \rightarrow AS vs. SYM \rightarrow DA	55	4.53	0.033	68	3.91	0.048
SYM \rightarrow AS vs. AS \rightarrow DA	43	0.07	0.79	61	0.12	0.73
SYM or AS \rightarrow DA vs. right \leftrightarrow left	74	20.3	<0.001	92	24.8	<0.001
Selected taxa compressed						
AS \rightarrow DA vs. SYM \rightarrow DA*	36	3.98	0.046	48	7.16	0.007
SYM \rightarrow AS vs. SYM \rightarrow DA*	43	4.08	0.044	49	3.79	0.052
SYM \rightarrow AS vs. AS \rightarrow DA*	33	0.05	0.83	45	0.23	0.63
SYM or AS \rightarrow DA vs. right \leftrightarrow left†	53	<0.01	0.98	70	<0.01	0.98

N, total transitions; χ^2 , chi-square values from a contingency table analysis (corrected for continuity) of data in Table 3 (degrees of freedom = 1 for all tests); P, probability; SYM, symmetry; AS, antisymmetry; DA, directional asymmetry; SYM \rightarrow AS etc. (SYM ancestor yields AS descendent).

*Crustacean claws counted only once in each category.

†Gastropoda counted only once in each category.

of natural selection and the internal rules that govern the expression of genes and the development of embryos" (ref. 50, p. 294). To this one might also add the external milieu, since even internal "rules" may vary depending on external environmental conditions. Bilateral asymmetry offers an unusually powerful tool for exploring the effects of genes and environment on the interplay between ontogeny and evolution because (i) both genetically and environmentally triggered asymmetries may be enumerated, and (ii) asymmetries may be readily identified across the diverse landscape of higher Metazoa.

Three examples, each from different phyla, illustrate nicely how early-developing and late-developing asymmetries evolve differently. First, flatfish, in addition to being externally asymmetrical, also exhibit visceral asymmetries like all other vertebrates. Unlike differentiation of the eyed side, which begins at metamorphosis, visceral asymmetries arise early in development. Significantly, with rare exceptions, visceral asymmetries retain the same orientation regardless of whether fish are right- or left-sided, even in species that are polymorphic for sidedness (24). Thus the lateral bias of early-developing visceral asymmetries persist, whereas late-developing sidedness, as outlined above, is rather labile evolutionarily.

Second, the contrast between the causes of early- and late-developing asymmetries may help explain a great mystery of animal asymmetry, or what Galloway called "a secret treason in the Universe" (ref. 51, p. 204). Why are gastropod molluscs so overwhelmingly dextral? This is puzzling for three reasons. First, functional advantages to dextrality are hard to imagine. Second, dextral and sinistral shell asymmetries have evolved roughly equally frequently in fossil cephalopods and in living and fossil bivalves (refs. 52–54 and above). Third, sinistral shells were not only more common among early monoplacophorans and gastropods (47), but among living taxa they have also evolved repeatedly from dextral ancestors (ref. 54 and Appendix). So phylogenetic bias or inertia cannot be the entire answer.

Differences in the ontogenetic timing of molluscan asymmetry offer a clue. As noted first by Crampton (55), and confirmed by others (12, 56), spindle bundles orient differently relative to the plane of first cleavage in embryos of sinistral and dextral gastropods. This orientation determines the sense of spiral cleavage, which in turn influences the coiling direction of the shell. In contrast, meroblastic cleavage in the large yolky eggs of living cephalopods (57) bears no resemblance to the spiral cleavage so widespread in the Mollusca (11), and shell asymmetries appear late in development (52). Unfortunately, because conispirally coiled cephalopods went extinct, the association between adult coiling direction and early cleavage asymmetry can no longer be tested. Finally, although bivalves undergo typical spiral cleavage (11), their pediveliger larvae

are symmetrical (1), and they do not attach to the substratum until the postlarval dissoconch stage or later (58).

Shell asymmetry is therefore intimately tied to early cleavage phenomena in conispirally coiled gastropods, whereas it arises much later in cephalopod and bivalve development. As a consequence, invariant cytoplasmic asymmetries arising from many possible sources (14) may create a persistent bias to molecular interactions affecting cleavage orientation (12).

Finally, two examples from crustacea illustrate how a non-random environmental trigger may bias late-developing asymmetries. The postlarval prediction of Table 1 presumes that the environmental induction of asymmetry is random with respect to side. Where it is not random, the phylogenetic pattern of asymmetry variation should mimic that of the larval prediction. Two clades of gastropod-shell-inhabiting hermit crabs exhibit different claw asymmetries. Left is usually larger in the Coenobitoidea, whereas right is larger in paguroid crabs (21). In addition, most calappid crabs (Oxystomata) have a large, distinctive tooth on their right claw that they use to peel the shells of gastropod prey (59). None of these clades appears to have passed through an AS stage, as expected for a late-developing asymmetry. The "secret treason" of gastropod shell dextrality seems to have affected other phyla.

The above patterns allow a central question in evolutionary biology to be addressed: how important is environment-driven versus mutation-driven variation in the evolution of novel forms, in this case, DA? As argued elsewhere (unpublished work), phylogenetic transitions from ideal AS \rightarrow DA imply replacement of an external environmental trigger by a genetic one (genetic assimilation), whereas SYM \rightarrow DA transitions depend only upon the origin and fixation of new mutations (conventional evolution). The disproportionate occurrence of the SYM \rightarrow AS \rightarrow DA sequence among late-developing asymmetries (Tables 2 and 3) suggests that genetic assimilation may have contributed significantly to the evolution of DA. If anything, these counts underestimate the prevalence of genetic assimilation, because AS is a transitional state that may not persist among living descendants.

Unfortunately, nagging questions still remain about how any asymmetries ultimately become fixed towards one side. Although the cascade of differential gene expression influencing early-developing asymmetries has been partially unravelled in both vertebrates (e.g., see ref. 60) and invertebrates [*Coenorhabditis* (61)], the positional cues by which genes "recognize" which side of the midline they are on remains elusive. As others have before (6, 14), I find it difficult to escape the conclusion that inhomogeneities in either the external or the cytoplasmic environment provide initial symmetry-breaking information during development.

Appendix

Number of phylogenetic transitions between asymmetry states in animals exhibiting conspicuous external or skeletal asymmetry

Inferred ancestral state, taxon (trait)	No. of independent clades exhibiting derived state				
	Symmetrical	Antisymmetric	Right/dextral	Left/sinistral	Phylo. Onto.
Symmetrical					
Chordata					
Vertebrata, Pisces					
Pleuronectiformes (eyed side) ¹	—	1			I P
Phallostethidae (priapium side) ²	—	1			I P
Anablepinae (side of gonopodium bend) ³	—	1			III P
Cichlidae (side of mouth deflection) ⁴	—	1			III P
Vertebrata, Aves					
Carduelinae, Drepanidae (side of tip of upper mandible) ⁵	—	2			III P
Strigiformes [larger (skin) or higher ear opening] ⁶	—		2	3	III L?
Haematopodidae (more robust side of skull) ⁷	—		1		III P?
Charadriidae (direction of bill twist) ⁸	—		1		III P?
Vertebrata, Mammalia					
Cetacea (deviation of dorsal skull midline)	—			1–2 ⁹	II L
Monodontidae (side of tusk in male)	—			1 ¹⁰	III L?
Chiroptera (side of missing lower internal incisor) ¹¹	—	1			III L
Arthropoda					
Crustacea, Cirripedia, Verrucomorpha (side of lost lateral plates) ¹²	—	1			I P
Crustacea, Decapoda (side of larger first claw in all groups)					
Astacidea ¹³ , Caridea (Alpheoidea) ¹⁴	—	2			III P
Thalassinidea					
Axioidae ¹⁵ , Callianassoidea ¹⁶	—	2			I P
Anomura: Aeglidae, Porcellanidae, Paguroidea, Coenobitoidea ¹⁷	—	1	1	2	I P
Brachyura					
Oxystomata, Dorippidae, Calappidae ¹⁸	—		2		III P
Cancridea ¹⁹	—	1 + 1?	1?		III P
Brachyrhyncha					
Xanthoidea ²⁰	—	>1?	>1?		III P
Grapsidae ²¹	—	1?	1?	1?	III P
Gecarcinidae ²²	—	1			III P
Ocypodoidea	—	1 ²³	1 ²⁴		II, III P
Insecta					
Orthoptera (side of tegmen with file) ²⁵	—	1	1		I P?
Phasmatodea (abdomen twisting direction, male) ²⁶	—		1		IV P?
Thysanoptera (side of mandibular stylet) ²⁷	—			1	III L
Diptera (abdomen twisting direction, male) ²⁸	—	>1?	>>1?	>>1?	III L
Annelida, Polychaeta, Spirorbidae (coiling direction of tube) ²⁹	—	1			I P
Mollusca					
Gastropoda (coiling direction of conspiral shell) ³⁰	—	1?	1?		III L
Bivalvia (shells of cemented clades only)					
Anomiacea, Pectinacea (attached/smaller side) ³¹	—		2		III P
Pandoracea (bottom/larger side) ³²	—		1		III P
Ostreacea, Chamacea, Hippuritacea (attached/larger side) ³³	—	3†			IV P
Unionacea (attached/larger side) ³⁴	—	1			III P
Cephalopoda (side of hectocotylus or spadix in male) ³⁵	—	≥2			III P
Ammonoidea ³⁶ , Nautiloidea ³⁷ (shell coiling direction)	—		2†	≥5†	IV P?
Brachiopoda					
Orthida†, Rhynchonelloida† (more dorsal side of commissure) ³⁸	—	≥4			IV P
Antisymmetrical (AS)					
Chordata, Vertebrata, Pisces					
Pleuronectiformes (eyed side)	—		1 + 2 ^{7,39}	1 + 4 ^{2,40}	I P
Phallostethidae (priapium side)	—		2 ⁴¹	1 ⁴²	I P
Arthropoda					
Crustacea, Decapoda					
Thalassinidea (side of larger first claw)	—		1 ⁴³	1 ⁴⁴	I P
Brachyura, Cancridea ⁴⁵	—		1?		III P
Brachyura, Brachyrhyncha					
Xanthoidea (side of larger claw) ⁴⁶	—		>1?		III P
Grapsidae (side of larger claw) ⁴⁷	—		1?	1?	III P
Ocypodidae (side of larger claw)	—		1 ⁴⁸	1 ⁴⁹	II, III P
Insecta, Orthoptera (side of tegmen with file) ⁵⁰					
Annelida, Polychaeta, Spirorbidae (coiling direction of tube) ⁵¹	—		1		I P
Mollusca					
Gastropoda (coiling direction of conspiral shell) ⁵²	—		1?		III L
Bivalvia					
Ostreacea, Chamacea, Hippuritacea (attached/larger side) ⁵³	—		≥2	≥3	III P
Cephalopoda (side of hectocotylus) ⁵⁴	—			1	III P
Right/dextral					
Chordata, Vertebrata					
Pisces, Pleuronectiformes (eyed side)	1 + 4 ^{7,55}	—		1 ⁵⁶	I P
Aves, Strigiformes (larger ear opening, skin only) ⁵⁷	—			1	III P
Annelida, Polychaeta, Spirorbidae (coiling direction of tube) ⁵⁸	—			1	I P
Mollusca, Gastropoda					
Prosobranchia (coiling direction of conspiral shell)	≥1 ^{*59}	—		≥7 ⁶⁰	III L
Pulmonata (coiling direction of conspiral shell)	≥4 ^{*61}	—		≥14 ⁶²	III L
Opisthobranchia (coiling direction of body) ⁶³	≥4	—			III L
Left/sinistral					
Arthropoda, Crustacea, Anomura, Diogenidae (side of larger claw) ⁶⁴	1	—		III	P
Annelida, Polychaeta, Spirorbidae (coiling direction of tube) ⁶⁵	—	3		—	III P
Mollusca, Cephalopoda, Ammonoidea† (shell coiling direction) ⁶⁶	—	1		—	IV P?

Tabulated values are the number of independent evolutionary changes either within the clade or inferred to have taken place along the lineage leading to the base of the clade (i.e., the end state is found in all members of the group, but not in the sister group; ? inferred state changes somewhat ambiguous because of an unresolved phylogeny or classification). Phylo., method for inferring phylogenetic transition (I, cladistic analysis of morphological traits; II, molecular phylogeny; III, classification/keys; IV, pattern in the fossil record); Onto., presumed ontogenetic stage at which asymmetry is first expressed (L, larval; P, postlarval; L?, probably larval or arises well before maturity; P?, probably postlarval or arises near maturity; see *Methods* for more details); *, not ideal AS since, although left and right forms are discrete phenotypes, their frequencies depart significantly from equal; †, extinct; —, not relevant. In the footnotes, literature sources are identified as: D, asymmetry data; T, phylogenetic tree; or C, classification, and the entry for each taxon should be preceded by “inferred ancestor of” to indicate the point at which the putative transition occurred.

- ¹Entire Pleuronectiformes; D (24), T (27); as in *Psettodes*, sister group to all remaining taxa.
- ²Entire Phallostethidae; D and T (26).
- ³Entire Anablepinae; D (3, 62), C (62).
- ⁴*Perissodus*; D and C (63).
- ⁵(i) *Loxia* (crossbill) [D (3, 64); T (65)], (ii) *Loxops coccineus* (honey creeper) [D and C (66)].
- ⁶Five owl clades: (i) *Tyto* (L skin aperture higher), (ii) *Phodilus* (L skin aperture higher), (iii) *Bubo + Ciccaba + Strix* (R skin aperture larger), (iv) *Rhinoptyx + Asio + Pseudoscops* (L skull aperture higher), and (v) *Aegolius* (R skull aperture higher); D and C (29).
- ⁷*Haematopus* (oystercatcher, Haematopodidae); D (67), C (64).
- ⁸*Anarhynchus frontalis* (Charadriiformes); D (3, 68), C (68).
- ⁹Two clades: (i) Delphinoidea + Iniidae + Ziphiioidea, (ii) Physteroidea; D and T (30, 69); may only be one event since facial precedes skull asymmetry.
- ¹⁰*Monodon*; D (70), T (30).
- ¹¹*Myonycteris brachycephala* (fruit bat); D and C (71); all other bats have symmetrical dental formulae.
- ¹²Entire Verrucomorpha; D (31, 72), T (figure 10 of ref. 73).
- ¹³Entire Nephropidae; D (74, 75), C (76).
- ¹⁴Asymmetrical alpheids: *Alpheus*, *Synalpheus*, some *Beteus*; D (77), C (76); assumes ancestor was symmetrical like sister family (Hyppolytidae) and symmetrical species of *Beteus* (Alpheidae).
- ¹⁵Conspicuously asymmetrical clades; D (78), T and C (79).
- ¹⁶Antisymmetrical subclade (Callianieidae + Thomassiniidae + Ctenochelidae + Callianassidae); D (80, 81), T and C (79).
- ¹⁷Four clades: (i) Aegliidae (L-sided), (ii) Porcellanidae (AS), (iii) Paguroidea (R-sided), (iv) Coenobitoidea (L-sided except for a few R-sided Diogenidae); D (21), T (cladistic re-analysis of information in refs. 21, 76, and 82 by A.R.P.).
- ¹⁸Two clades: (i) *Ethusa microphthalma* + *E. lam* clade (Dorippidae), (ii) peeling-toothed Calappidae; D (36), C (76); assumes ancestral Dorripoidea and Leucosioidea were symmetrical [for (i), other *Ethusa* and remaining Dorippidae are symmetrical; for (ii) sister family (Leucosioidea) and two calappid genera (*Hepatus*, *Hepatella*) are symmetrical and lack peeling teeth].
- ¹⁹Three clades: (i and ii) AS (*Acanthocyclus*, one spp. of *Trachycarcinus*), (iii) R-sided (*Peltarion* + *Trichopeltarion*); D (83), C (76); assumes ancestral Cancroid was symmetrical [claw asymmetry is weak in sister family (Cancridae), some atelecyclid genera are nearly symmetrical (*Erimacrus*, *Thelmessus*, *Trachycarcinus* one spp.)].
- ²⁰Two asymmetrical groups: (i) AS (*Chlorodopsis*, one spp. of *Eriphaea*, *Xantho*), (ii) R-sided (most genera); D (refs. 59 and 84; G. J. Vermeij, unpublished data), C (76); pronounced R-sidedness occurs in most xanthid genera (e.g., *Baptozius*, *Carpilius*, *Eriphaea* four spp., *Epixanthus*, *Glabropilumnus*, *Heteropanope*, *Lophopanopeus*, *Lydia*, *Menippe*, *Mymenippe*, *Neopanope*, *Ozius*, *Pilumnus*, *Sphaerozius*), ancestral state of Xanthoidea (known from lower Cretaceous) unclear.
- ²¹Three asymmetrical groups: (i) AS (*Glyptograpsus*, *Goniopsis*), (ii) R-sided (*Platychirograpsus*), (iii) L-sided (*Geograpsus*, *Leptograpsus*, *Sarmatium*); D (38), C (76); assumes ancestral Grapsid was like symmetrical genera (*Cyrtograpsus*, *Metopaulias*, *Percnon*, *Planes*), phylogenetic relations among asymmetrical genera unclear.
- ²²AS groups; D (38), C (76); assumes ancestral gecarcinid was like symmetrical *G. lagostoma*, most taxa exhibit AS (American *Cardisoma*, other species of *Gecarcinus*).
- ²³*Ocyrode* + *Uca* clade; D (85, 86), T (87); assumes ancestral ocyropodid was like symmetrical palcidid, an old family from lower Cretaceous (see footnote 24).
- ²⁴Asymmetrical *Cymopolia*; D and C (38); assumes ancestral palcidid was like symmetrical *Cymopolia* spp. (8 = symmetrical, 2 = subsymmetrical, 7 = strongly R-sided).
- ²⁵Two clades: (i) Haglidae + Tettigoniidae (katydid), (ii) Gryllidae (crickets) + Gryllotalpidae; D (44, 88), T (44); haglids, files on both wings and can “switch sing” (a behavioral AS); tettigoniids, L file only; most gryllids, R file only.
- ²⁶Lower Permian Embiidae (twisting sense viewed from head); D (89), T (90).
- ²⁷Entire Thysanoptera (thrips); D (41), T (90).
- ²⁸Three asymmetrical groups (twisting sense viewed from head): (i) AS [e.g., *Chunio marinus* (Chironomidae) and possibly *Culex* + *Aedes* (Culicidae)], (ii) dextral [e.g., *Bomblyus discolor* (Bombyliidae), *Chrysotaxum cautum* (hover fly)], (iii) sinistral [e.g., *Volucella pellucens*, *Calliphora* (Calliphoridae), some Dolichopididae and many other Cyclorhapha]; D (3, 91), C (91).
- ²⁹*Neomicrorbis*; D (45), T (unpublished cladistic analysis by A.R.P.); most primitive genus in family (seven thoracic setigers and broods in tube, similar to Serpulidae); assumes serpulid sister group to ancestral spirorbid was not regularly coiled.
- ³⁰Entire Gastropoda; D and C (47); see text for discussion of this problematical issue.
- ³¹(i) jingle shells, (ii) scallops; D (living species only; ref. 92), C (93).
- ³²Epibenthic pandorid; D (92), C (93).
- ³³Early fossils in three clades: (i) oysters, (ii) jewel box shells (Eocene *C. calcarata* exhibits AS), (iii) rudists; D (fossil observations, ref. 48), C (93).
- ³⁴Cemented aetheriid; D (92), C (93).
- ³⁵(i) Spadix-bearing Nautiloidea, (ii) hectocotylus bearing Octopoda; D and C (57, 94); assumes ancestral Nautiloidea lacked a spadix, and ancestral Octopoda were like primitive vampyromorphs and cirroteuthids, which lack a hectocotylus.
- ³⁶Two sinistrally coiled clades: (i) some Heteroceratidae, (ii) nearly all Turritellidae; D and T (52).
- ³⁷Five clades: (i and ii) dextral (Brevicoceratidae, Lechritrochoceratidae), (iii–v) sinistral (*Trochoceras*, *Larieroceras*, *Sphyradoceras*); D and T (53).
- ³⁸Clades exhibiting “obligate” commissural AS: (i) *Streptis* [Orthida (one of five spp.)], (ii–v) Rhynchonelloidea: *Stolomorhynchia* (one of three spp.), “*Rhynchonella*” (two of five spp.), *Torquirhynchia* (five of five species); D and C (46); assumes ancestral forms were like symmetrical species in each genus.
- ³⁹Three dextral clades: (i) *Lepidoblepharon*, and possibly (ii) *Brachypleura* and (iii) Pleuronectidae + Samaridae + Achiridae + Soleidae + Cynoglossidae; D (62), T (27); total number of transitions requires better resolution of polytomies.
- ⁴⁰Five sinistral clades: (i) *Citharoides*, and possibly (ii) *Eucitharus*, (iii) Scopthalmidae, (iv) Paralichthyidae, (v) (Achiropsettidae + Bothidae); D (62), T (27); total number of transitions requires better resolution of polytomies.
- ⁴¹Two clades: (i) *Phenacostethus posthon*, (ii) *Mirophallus bikolanus*; D (25), T (25, 26).
- ⁴²*Phenacostethus trevavasae*; D and T (25).
- ⁴³R-sided *Ctenocheles*; D, *C. balssi* (95) and other Calliannasoidea (80, 81), T (79).
- ⁴⁴L-sided *Axiopsis*; D [other *Axiidae* (78), *A. princeps* (95)], T (79).
- ⁴⁵*Peltarion* + *Trichopeltarion* clade in Atelecyclidae (see footnote 19).
- ⁴⁶R-sided genera (see footnote 20).
- ⁴⁷Two asymmetrical groups: (i) R-sided (*Platychirograpsus*), (ii) L-sided (*Geograpsus*, *Leptograpsus*, *Sarmatium*) genera (see footnote 21).
- ⁴⁸*Thalassuca* clade; D (86), T (87).
- ⁴⁹L-sided *Ocyrode*; D (96, 97), C (76); *O. gaudichaudii* are predominantly L-sided, whereas other *Ocyrode* are AS.
- ⁵⁰Entire Tettigoniidae; D (44, 88), T (42) (see footnote 25).
- ⁵¹*Anomalorbis*; D (45), T (unpublished cladistic analysis by A.R.P.); second most primitive genus (4 complete thoracic setigers; broods in tube).
- ⁵²Dextral gastropods (see footnote 30).
- ⁵³Five clades: (i) R-attached and (ii) L-attached Chamidae [fixed-sidedness has evolved multiple times, unclear if all evolved from AS ancestors; D and C (48)], (iii) living Ostreidae [assumes ancestral oyster AS (see footnote 33); D (92), C (93)], (iv) R-attached and (v) L-attached fossil rudistids [D and C (ref. 48, p. 407)].
- ⁵⁴L-sided *Loligo* (e.g., *L. pealei*; Decapoda); D (98), ancestral AS implied by sister taxa (Nautiloidea and Octopoda; see footnote 35).
- ⁵⁵AS species in five taxa: (i) *Platichthyes*, [and possibly (ii) *Hippoglossina*, (iii) *Paralichthyes*, (iv) *Tephrinectes*, (v) *Xystreurus*]; D (24), T (27); total number of transitions requires better resolution of polytomies.
- ⁵⁶Cynoglossidae; D (62), T (27).
- ⁵⁷*Strix rufipes*; D and C (29); only species with larger L ear among owls.
- ⁵⁸Clade containing all genera except *Neomicrorbis*, *Anomalorbis*, *Paradexiospira*, *Prodexiospira* + *Circeis*; D (45), T (unpublished cladistic analysis by A.R.P.).
- ⁵⁹Species exhibiting coil polymorphism: *Campeloma rufum* and *C. crassula* (Viviparidae); D (99, 100), C (54); assumes dextrality ancestral.
- ⁶⁰Sinistral species/subclades in: Trochidae (*Calliostoma incerta*), Triphoridae, Cyclophoridae (*Diplomatina*), Buccinidae (in each of *Volutopsis* and *Neptunea*), Melongenidae (*Busyon*), Turridae (*Antiplanis*); D and C from ref. 54; assumes dextrality ancestral in all families.
- ⁶¹Species exhibiting coil polymorphism: (i) *Lymnaea peregra* (Lymnaeidae) (12, 101), (ii) *Partula* (Partulidae) (102), (iii) *Liguus poeyanai* (Bulimulidae) (3), (iv) *Lacinaria biplicata* (103); C (54); assumes dextrality ancestral in all genera.
- ⁶²Sinistral species/subclades in: Ancylidae (*Ancylus rivularis*), Physidae, Planorbidae, Achatinellidae, Partulidae (*Partula*), Vertiginidae (*Vertigo*), Chondrinidae (*Gastrocopia*), Pupillidae (*Pupilla*), Enidae (*Jamnia*), Clausiliidae, Camaenidae (each of *Camaena*, *Syndromus*, *Eulota*, *Amphidromus*); D and C (3, 54); assumes dextrality was ancestral in each family.
- ⁶³Subclades in each of four orders: (i and ii) symmetrically shelled (Cephalispeida, Sacoglossa), (iii and iv) secondarily symmetrical unshelled (Nudibranchia,

Gymnosomata); D and C (10); assumes ancestral forms resembled the living dextrally coiled taxa within each order.

⁶⁴R-sided Diogenidae (see footnote 17).

⁶⁵Dextral subclade in three genera: (i) *Protolaeospira* (*Dextralia*), (ii) *Spirorbis* (*Spirorbella*), and (iii) *Janua* (*Janua*, *Dexiospira*, and *Pillaiospira*); D and C (45); assumes ancestors of each genus exhibited sinistral pattern of most spirorbids.

⁶⁶Nostoceratidae; D and T (52); arose from the largely sinistral Turritulidae.

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- Ruppert, E. E. & Barnes, R. D. (1994) *Invertebrate Zoology* (Saunders, Orlando, FL).
- Ludwig, W. (1932) *Das Rechts-Links Problem im Tierreich und beim Menschen* (Springer, Berlin).
- Neville, A. C. (1976) *Animal Asymmetry* (Arnold, London).
- Lauder, G. V., Huey, R. B., Monson, R. K. & Jensen, R. J. (1995) *Bioscience* **45**, 696–704.
- VanValen, L. (1962) *Evolution* **16**, 125–142.
- Wolpert, L. (1978) *Behav. Brain Sci.* **2**, 324–325.
- Palmer, A. R., Strobeck, C. & Chippindale, A. K. (1993) *Genetica* **89**, 201–218.
- Palmer, A. R. (1996) *Bioscience* **46**, 518–532.
- Boklage, C. E. (1978) *Behav. Brain Sci.* **2**, 282–286.
- Schmekel, L. (1985) in *The Mollusca: Evolution*, eds. Trueman, E. R. & Clarke, M. R. (Academic, New York), Vol. 10, pp. 221–267.
- Verdonk, N. H., van den Biggelaar, J. A. M. & Tompa, A. S., eds. (1983) *The Mollusca: Development* (Academic, New York), Vol. 3.
- Freeman, G. & Lundelius, J. W. (1982) *Roux Arch. Dev. Biol.* **191**, 69–83.
- Govind, C. K. & Pearce, J. (1989) *J. Exp. Zool.* **249**, 31–35.
- Brown, N. A., McCarthy, A. & Wolpert, L. (1991) in *Biological Asymmetry and Handedness*, ed. Wolpert, L. (Wiley, New York), pp. 182–212.
- Kinsbourne, M. (1978) *Behav. Brain Sci.* **2**, 302.
- Markow, T. A., ed. (1994) *Developmental Instability: Its Origins and Evolutionary Implications* (Kluwer, Dordrecht, The Netherlands).
- Wolpert, L., ed. (1991) *Biological Asymmetry and Handedness* (Wiley, New York).
- Bradshaw, J. L. & Rogers, L. J. (1993) *The Evolution of Lateral Asymmetries, Language, Tool Use, and Intellect* (Academic, San Diego).
- Frankel, J. (1989) *Pattern Formation: Ciliate Studies and Models*, (Oxford Univ. Press, New York).
- Jürgens, G. (1995) *Cell* **81**, 467–470.
- Martin, J. W. & Abele, L. G. (1986) *J. Crustacean Biol.* **6**, 576–616.
- McEdward, L. R. & Janies, D. A. (1993) *Biol. Bull. (Woods Hole, Mass)* **184**, 255–268.
- Jeffries, R. P. S., Brown, N. A. & Daley, P. E. J. (1996) *Acta Zool. (Stockholm)* **77**, 101–122.
- Hubbs, C. L. & Hubbs, L. C. (1945) *Pap. Mich. Acad. Sci. Arts Lett.* **30**, 229–311.
- Parenti, L. R. (1986) *Proc. Calif. Acad. Sci.* **44**, 225–236.
- Parenti, L. R. (1989) *Proc. Calif. Acad. Sci.* **46**, 243–277.
- Chapleau, F. (1993) *Bull. Mar. Sci.* **52**, 516–540.
- Hori, M. (1993) *Science* **260**, 216–219.
- Norberg, R. Å. (1977) *Philos. Trans. R. Soc. London Ser. B* **280**, 375–408.
- Milinkovitch, M. C. (1995) *Trends Ecol. Evol.* **10**, 328–334.
- Newman, W. A. & Hessler, R. R. (1989) *Trans. San Diego Soc. Nat. Hist.* **21**, 259–273.
- Hart, J. F. L. (1935) *Can. J. Res.* **12**, 411–432.
- Jones, M. B. (1978) *N. Z. J. Zool.* **5**, 783–794.
- Naidu, K. G. R. B. (1951) *Proc. Indian Acad. Sci. Sect. B* **B33**, 32–41.
- Reese, E. S. & Kinzie, R. A. I. (1968) *Crustaceana* **2**, Suppl., 117–144.
- Rathbun, M. J. (1937) *Bull. U.S. Natl. Mus.* **166**, 1–278.
- Spears, T., Abele, L. G. & Kim, W. (1992) *Syst. Biol.* **41**, 446–461.
- Rathbun, M. J. (1918) *Bull. U.S. Natl. Mus.* **97**, 1–461.
- Griffiths, G. C. D. (1972) *The Phylogenetic Classification of Diptera Cyclorhapha, with Special Reference to Structures on the Male Postabdomen* (Junk, Dordrecht, The Netherlands).
- Wood, D. M. (1991) in *Proceedings of the Second International Congress of Dipterology*, eds. Weismann, L., Orszagh, I. & Pont, A. C. (SPB Academic, The Hague), pp. 255–272.
- Heming, B. S. (1993) in *Functional Morphology of Insect Feeding*, eds. Schaefer, C. W. & Leschen, R. A. B. (Ent. Soc. Am., Lanham, MD), pp. 3–41.
- Chapman, R. F. (1964) *Proc. Zool. Soc. London* **142**, 107–121.
- Ball, G. E. (1992) *J. N.Y. Entomol. Soc.* **100**, 325–380.
- Gwynne, D. T. (1995) *J. Orthopteran Res.* **4**, 203–218.
- Fauchald, C. (1977) *Nat. Hist. Mus. Los Angeles Co. Sci. Ser.* **28**, 1–190.
- Fürsch, F. T. & Palmer, T. (1984) *Lethaia* **17**, 251–265.
- Morris, N. J. (1990) in *Major Evolutionary Radiations*, eds. Taylor, P. D. & Larwood, G. P. (Clarendon, Oxford), pp. 73–90.
- Kennedy, W. J., Morris, N. J. & Taylor, J. D. (1970) *Paleontology* **13**, 379–413.
- Policansky, D. (1982) *Sci. Am.* **246**, 116–122.
- Raff, R. A. (1996) *The Shape of Life: Genes, Development, and the Evolution of Animal Form* (Univ. Chicago Press, Chicago).
- Galloway, J. (1987) *Nature (London)* **330**, 204–205.
- Arkell, W. J., Kummel, L. & Bright, C. W. (1957) in *Treatise on Invertebrate Paleontology, Part L*, ed. Moore, R. C. (Univ. Kansas Press, Lawrence), pp. L80–L475.
- Flower, R. H. (1955) *Evolution* **9**, 244–260.
- Vermeij, G. J. (1975) *Nature (London)* **254**, 419–420.
- Crampton, N. E. (1894) *Ann. N.Y. Acad. Sci.* **8**, 167–170.
- Meshcheryakov, V. N. & Belousov, L. V. (1975) *Roux Arch. Dev. Biol.* **177**, 193–203.
- Wells, M. J. & Wells, J. (1977) in *Reproduction of Marine Invertebrates. IV. Molluscs: Gastropods and Cephalopods*, eds. Giese, A. C. & Pearse, J. S. (Academic, New York), pp. 291–336.
- Yonge, C. M. (1967) *Philos. Trans. R. Soc. London Ser. B* **252**, 49–105.
- Ng, P. K. L. & Tan, L. W. H. (1985) *Crustaceana* **49**, 98–100.
- Beddington, R. (1996) *Nature (London)* **381**, 116–117.
- Wood, W. B. & Kershaw, D. (1991) in *Biological Asymmetry and Handedness*, ed. Wolpert, L. (Wiley, New York), pp. 143–164.
- Nelson, J. S. (1994) *Fishes of the World* (Wiley, New York).
- Hori, M. (1991) *Ecol. Int. Bull.* **19**, 89–96.
- Tordoff, H. B. (1954) *Condor* **56**, 346–358.
- Marten & Johnson (1986) *Condor* **88**, 409–420.
- Hatch, J. J. (1985) *Condor* **87**, 546–547.
- Webster, J. D. (1941) *Condor* **43**, 175–180.
- Johnsgard, P. (1981) *The Plovers, Sandpipers and Snipes of the World* (Univ. Nebraska Press, Lincoln).
- Ness, A. R. (1967) *J. Zool. (London)* **153**, 209–221.
- Arvy, L. (1977) in *Investigations on Cetaceans*, ed. Pilleri, G. (Brain Anat. Inst., Bern, Switzerland), Vol. 8, pp. 161–212.
- Juste, J. & Ibanez, C. (1993) *Can. J. Zool.* **71**, 221–224.
- Newman, W. A. (1989) *Bull. Mar. Sci.* **45**, 467–477.
- Glenner, H., Grygier, M. J., Höeg, J. T., Jensen, P. G. & Schram, F. R. (1995) *Zool. J. Linn. Soc.* **114**, 365–404.
- Przibram, H. (1907) *Arch. Entwicklunsmech. Org.* **25**, 1–343.
- Herrick, F. J. (1895) *Fish. Bull.* **15**, 1–252.
- Bowman, T. E. & Abele, L. G. (1982) in *The Biology of Crustacea: Systematics, the Fossil Record, and Biogeography*, ed. Abele, L. G. (Academic, New York), Vol. 1, pp. 1–27.
- Darby, H. (1934) *Carnegie Inst. Wash. Pap. Tortugas Lab.* **28**, 349–361.
- Sakai, K. & Saint Laurent, M. d. (1989) *Naturalists (Tokush. Biol. Lab., Shikoku Univ.)* **3**, 1–104.
- Poore, G. C. B. (1994) *Mem. Mus. Victoria* **54**, 79–120.
- Sakai, K. (1969) *Publ. Seto Mar. Biol. Lab.* **17**, 209–252.
- Sakai, K. (1992) *Naturalists (Tokush. Biol. Lab., Shikoku Univ.)* **4**, 1–33.
- McLaughlin, P. A. (1983) *J. Crust. Biol.* **3**, 608–621.
- Rathbun, M. J. (1930) *Bull. U.S. Natl. Mus.* **152**, 609 pp.
- Abby-Kalio, N. J. & Warner, G. F. (1989) *Zool. J. Linn. Soc.* **96**, 19–26.
- Crane, J. (1975) *Fiddler Crabs of the World* (Princeton Univ. Press, Princeton).
- Jones, D. S. & George, R. W. (1982) *Crustaceana* **43**, 100–102.
- Sturmbauer, C., Levinton, J. S. & Christy, J. (1996) *Proc. Natl. Acad. Sci. USA* **93**, 10855–10857.
- Masaki, S., Kataoka, M., Shirato, K. & Nakagahara, M. (1987) in *Evolutionary Biology of Orthopteroid Insects*, ed. Baccetti, B. (Horwood, Chichester), pp. 347–357.
- Kukalová-Peck, J. (1991) in *The Insects of Australia*, ed. Naumann, I. D. (Melbourne Univ., Carlton, Australia), pp. 141–179.
- Kristensen, N. P. (1991) in *The Insects of Australia*, ed. Naumann, I. D. (Melbourne Univ., Carlton, Australia), pp. 125–140.
- Colless, D. H. & McAlpine, D. K. (1991) in *The Insects of Australia*, ed. Naumann, I. D. (Melbourne Univ., Carlton, Australia), pp. 717–803.
- Nicol, D. (1958) *J. Wash. Acad. Sci.* **48**, 56–62.
- Purchon, R. D. (1987) *Phil. Trans. Roy. Soc. London Ser. B* **316**, 277–302.
- Haven, N. (1977) in *Reproduction of Marine Invertebrates, IV. Molluscs: Gastropods and Cephalopods*, eds. Giese, A. C. & Pearse, J. S. (Academic, New York), pp. 227–241.
- Makarov, V. V. (1962) *Fauna of USSR, Crustacea, Vol. X. No. 3. Anomura* (Isreal Program for Scientific Translations, Washington, DC).
- Trott, T. J. (1987) *Crustaceana* **52**, 213–215.
- Haley, S. R. (1969) *Crustaceana* **17**, 285–297.
- Arnold, J. M. & Williams-Arnold, L. D. (1977) in *Reproduction of Marine Invertebrates, IV. Molluscs: Gastropods and Cephalopods*, eds. Giese, A. C. & Pearse, J. S. (Academic, New York), pp. 243–290.
- VanCleave, H. J. (1936) *Am. Nat.* **70**, 567–583.
- Bickel, D. (1966) *Nautilus* **79**, 107–108.
- Boycott, A. E., Diver, C., Garstang, S. L. & Turner, F. M. (1930) *Philos. Trans. Roy. Soc. London Ser. B* **219**, 51–131.
- Gould, S. J., Young, N. D. & Kasson, W. (1985) *Evolution* **39**, 1364–1379.
- Degner, E. (1952) *Mitt. Hamburger Zool. Mus. Inst.* **51**, 3–61.