

Asymmetry in the fossil record

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Asymmetry is a fundamental aspect of the biology of all organisms, and has a deep evolutionary history. The fossil record contains evidence of both morphological and behavioural asymmetries. Morphological asymmetry is most commonly expressed as conspicuous, directional asymmetry (either lateral asymmetry or spiral asymmetry) in body fossils. Few examples of fluctuating asymmetry, a form of subtle asymmetry, have been documented from fossils. Body fossil evidence indicates that morphological asymmetry dates to the time of the appearance of the first life on Earth (Archaean Eon). Behavioural asymmetry can be assumed to have been concomitant with conspicuous morphological asymmetry, but more direct evidence is in the form of trace fossils. Trace fossil evidence suggests that behavioural asymmetry, including nervous system lateralization, was in existence by the beginning of the Palaeozoic Era.

Introduction

Asymmetry is an important, and apparently fundamental, aspect of the structure and function of all living organisms. Asymmetry of structure (also known as laterality, chirality, enantiomorphism, or handedness) is expressed in organisms at all scales ranging from basic biochemical levels through organ system and whole-organism levels.¹ Studies of the origin, development, and functional implications of lateralization date from studies on the human brain by Paul Broca and Marc Dax in the 1860s. Since that time, an extensive literature has developed concerning human handedness, language acquisition and learning, and the relationships of these attributes to lateralization of the nervous system.² In 1932 Wilhelm Ludwig surveyed asymmetries in the animal and plant kingdoms,³ and later studies showed that asymmetry is widespread among living organisms.^{4,5} Scattered records of biological asymmetry among ancient organisms have been published.^{6,7} These occurrences in the fossil record reinforce the interpretation that asymmetry is heritable and has a long evolutionary history.

This paper is an overview of biological asymmetry as expressed in the fossil record and is not a comprehensive review of asymmetry in ancient organisms, but draws together salient aspects of the evolutionary record of biological asymmetry. The paper highlights what we now know, and what opportunities lie ahead for future research on the record of biological asymmetry.

Asymmetries in organisms

Most organisms show some deviation from strict lateral symmetry, either in structure or function. Structural asymmetry can be divided into two broad categories: (1) conspicuous asymmetry; and (2) subtle asymmetry. Conspicuous asymmetries are readily apparent to the unaided eye, either as asymmetrical structures on otherwise bilateral organisms (e.g. claws of lobsters, tusks of elephants, or ears of owls) or as whole-body asymmetries (e.g. coiled gastropod shells, flatfish, or spiral leaf arrangements on plant stems). This asymmetry includes: (1) directional asymmetry (or fixed asymmetry), in which there is a strong bias toward dextral or sinistral forms in a species; and (2) random asymmetry, in which dextral and sinistral forms are equally prevalent. Subtle asymmetries are generally not apparent to the unaided eye. Subtle asymmetry includes: (1) directional asymmetry, in which there is consistent but minor bias toward dextral or sinistral forms in a species; and (2) fluctuating asymmetry, in which there occur small random deviations from bilateral symmetry.⁸ Asymmetry in organisms can be expressed behaviourally, and asymmetrical morphology (either conspicuous or subtle) can influence lateralized behaviour.

Asymmetries in ancient organisms

Asymmetry in ancient organisms is expressed primarily in two types of fossils: (1) body fossils, which are remains of ancient organisms (e.g. bones, teeth, shells, cuticle, feathers, skin, and gut tracts); and (2) trace fossils, which are evidence of the activity of ancient organisms (e.g. tracks, trails, burrows, borings, and bite marks).⁷ Body fossils are the primary source of information about morphological asymmetry in ancient organisms although asymmetrical behavioural patterns can be inferred to have accompanied morphological asymmetry. Trace fossils are the primary source of information about behavioural asymmetry in ancient animals, although footprints and burrows left in unconsolidated sediment later lithified can provide information about morphological asymmetries of the tracemakers. In ancient hominids, behavioural asymmetry is also expressed in stone, bone, or other substances worked into tools or other implements.⁵

Most morphological asymmetries described from the fossil record are conspicuous directional asymmetries. Conspicuous asymmetries have been

reported in bacteria, protists, plants, and representatives of most animal phyla having a good fossil record.^{5,7} Some of the most obvious examples in ancient organisms are spiral bacterial strands, coiled tests of foraminiferans, helical stem-and-leaf arrangements in plants, spiral or otherwise curved shells of molluscs and other animals, and asymmetrical paired structures in animals. Most gastropod species are characterized by a strong dextral bias with little intraspecific variation.⁹ Most other organisms seem to show greater degrees of intraspecific variation in directional asymmetry. Some bivalves and brachiopods have asymmetrical valves or have asymmetrical gaps between the valves. Paired food-gathering structures, such as the scolecodonts of annelids and the phosphatic elements of conodonts, show consistent left–right morphological differences. The conical shells of hyolithids (Palaeozoic) show a slight curvature to one side. Preserved gut tracts of hyolithids, however, are strongly asymmetrical, comprising an accordion-like ventral gut segment and a slightly curved, elongate dorsal gut segment that extends much of the length of the shell. The exoskeletons of most solitary corals and conulariids, and the tubes of serpulid worms, show curvature to some degree. Spiral asymmetry is exemplified in the septal arrangement of some Palaeozoic rugose corals and in the zoarial morphology of some marine bryozoans (ectoprocts). Some graptolites show consistent left–right asymmetry. Mesozoic bivalves attached to ammonite shells seem to have had a preference, in some cases, for attaching by the right valve. The zipper-like body plans of some Ediacaran (Proterozoic) animals such as *Dickinsonia* and *Spriggina* involve right and left halves that are not perfect mirror images of each other. Spiral asymmetry is present in some echinoderms, notably early Palaeozoic helicoplacoids, Palaeozoic edrioasteroids, the stalks or anal sacs of some Palaeozoic crinoids, and the Ediacaran echinoderm – like animal *Tribrachidium*. Palaeozoic stylophoran echinoderms (which are alternatively regarded by some as calcichordates) show a strong lateral asymmetry. Spiral asymmetry has been observed in the narrow, elongated skeleton of the Ediacaran cnidarian *Corumbella*. Pronounced lateral asymmetry has been documented in the tusks of Pleistocene elephants. Lateral asymmetry has been noted in the cranial endocasts of Neogene hominids (*Homo erectus*, *Homo sapiens neanderthalensis*, and *Australopithecus*) and in the brain cases of other Cenozoic mammals and Mesozoic dinosaurs.

Random asymmetry, such as the positional switching of the larger (crusher) claw in present-day lobsters and crayfish, has not been well demonstrated from fossils although it can be inferred to have existed based on homology with present-day species.¹⁰ Paired claws of fossil crustaceans commonly show that one claw is larger than the other. However it is not known whether the position of the larger claw switched during life. Oysters and perhaps other shell-secreting animals that often cluster in dense aggregations in which shell crowding occurs could be

expected to show random asymmetry. Examples of some putative fossilized archaeobacteria lack any obvious, consistent pattern to their directional asymmetry and may qualify as cases of random asymmetry. Similarly, fossilized organic strands interpreted to be fungal hyphae that lack any obvious, consistent pattern of symmetry could qualify as a form of random asymmetry.

Subtle asymmetries have rarely been demonstrated, perhaps in part because of the difficulty of differentiating subtle lateral asymmetry from taphonomic effects (including compaction of the remains of organisms in sediment). Perhaps the best examples of subtle asymmetry are in the coiling of foraminiferan tests. Switching of coiling direction in some species (a phenomenon linked to water temperature) is inferred to represent a case of fluctuating asymmetry.⁷

Behavioural asymmetry in many ancient animals can be inferred from lateral morphological asymmetry but more convincing evidence comes from the trace fossil record.⁷ A large number of traces, Neoproterozoic to Cenozoic in age, that were constructed in once-unconsolidated sediment demonstrate asymmetrical behaviour by animals. Even the names applied to some spiral traces (e.g. *Spirophyton*, *Spirorhapse*, *Gyrolites* and *Daimonohelix*) reflect asymmetry of the traces. In *Daimonohelix*, which is a large spiral burrow dug in soil by a Neogene beaver (*Palaeocastor*) using a consistent series of strokes with its teeth, the burrows are nearly equally divided between dextral and sinistral traces. This suggests that the beavers exhibited either random asymmetry (antisymmetry) or fluctuating asymmetry in their digging behaviour over time. Quite possibly, the *Palaeocastor* beavers also exhibited either random asymmetry or fluctuating asymmetry in the laterally disposed biological structures governing digging behaviour (e.g. tooth dimensions, jaw dimensions, musculature, or nervous system apparatus).

Bilateral burrows referred to as *Rusophycus*, which were made in marine sediments mostly by Palaeozoic trilobites, often show that the trilobites' legs dug deeper into the sediment along one side than they did along the other side. Although a systematic study of these and similar burrows has not been published, some examined specimens and published illustrations indicate that there may have been slight lateral bias in digging behaviour.

Perhaps the strongest case for directional asymmetry in behaviour from the fossil record comes from sub-lethal predation scars (bite marks) on Palaeozoic trilobites.⁷ A strong tendency for sub-lethal bite marks on trilobites to occur on the right side suggests that lateralized behaviour (and by inference, a lateralized nervous system) was in place in predatory animals and probably also their prey by about the beginning of the Palaeozoic. Some predators of trilobites evidently preferred to attack the right sides of trilobites, and the trilobites also likely exhibited stereotyped, lateralized escape movement.

Coprolites (fossilized excrement) commonly show a spiral or accordion-like shape that is unrelated to compaction in sediment. Presumably, deviations from perfect symmetry in these fossils reflect structural or functional asymmetry within the gut tracts of the animals that produced them.

Origins and adaptive value of asymmetry

Directional asymmetries of structure or function are evidently heritable, and can be inferred to have some adaptive value in many species. In many cases, and as best documented among present-day organisms, species show a rather consistent proportion of individuals showing the same style of directional bias (e.g. gastropod species characterized by a dextrally coiled shell). Along with indications that asymmetries date to the earliest records of prokaryotic life on Earth (Archaean Eon), of multicellular eukaryotic life (Proterozoic Eon), and of multicellular animals (late Proterozoic Eon to earliest Phanerozoic Eon), this information suggests that asymmetry is heritable. Studies on modern organisms suggest that inheritance of handedness is possible both by normal means of mendelian (genetic) inheritance and by non-genic inheritance through cellular cytoplasm.^{11,12}

The origin of lateralization involves both ontogenetic and phylogenetic factors.⁷ In humans, some anatomical or behavioural asymmetries are observable at birth or even in foetal stages. Speech and language functions, however, seem to become increasingly lateralized through early ontogeny, reaching full lateralization about the time of puberty. In some animals, morphological or behavioural asymmetries result from innate developmental programmes that are modified through early experience. Asymmetry in the claws of lobsters, for example, develops early in ontogeny only if objects that can be manipulated are present in the environment in which the animals grow.¹⁰ So far, studies on the ontogenetic origins of biological asymmetry from fossils have not been published.

Available evidence suggests that asymmetry in structure or function has adaptive value, but it is unlikely that all asymmetries expressed in ancient and present-day organisms are homologous. Some patterns of lateralization, such as the tendency toward right-handedness in *Australopithecus* and *Homo*, may be homologous, but many other vertebrates have a tendency toward left-handedness in the limbs. Even within vertebrates homologous patterns of asymmetry cannot always be assured and extension to the rest of the animal kingdom does not seem reasonable in view of current information.

It is commonly assumed that asymmetry is adaptive because of its widespread, persistent pattern in biological organisms. Evidence that lateral asymmetries were present in organisms as far back in time as the Archaean tends to support the view that asymmetry or structural characters concomitant with it are adaptive. Under

what circumstances might asymmetry have been adaptive? Asymmetry has been studied most in humans, where a correlation often has been drawn between an asymmetrical structure and function of the brain, and hand or language dominance.^{2,5} In humans and other primates, the tendency toward a consistent way of manipulating objects could result in greater skill and efficiency in their use. Asymmetry in the strength of one limb of a bilateral pair could confer a postural or other advantage, and could result in quicker response time to stimuli. It has also been observed that aim-directed movement in bilateral animals is not possible if an organism shows absolute symmetry of structure and function. Instead, one side must always lead. It is apparent that not all animals have resorted to the same solution to the problem of achieving a lead side. Also, there appears to be no particular interspecies advantage conferred by right- or left-dominance. Any advantage is likely to be effective mostly within a species.⁷

In some species, such as *Homo sapiens*, a small minority of individuals show handedness that is opposite to that of the majority of individuals, and that minority population remains proportionately the same across many generations. Patterns of tool use among ancient hominids indicate that a certain small percentage of left-handedness has been a persistent characteristic of *H. sapiens* and close relatives. Similarly, the pattern of sub-lethal bite marks on Palaeozoic trilobites indicates that bites are concentrated on the right side, but there is a persistent (and much smaller) tendency for bite marks to occur on the left side. Palaeozoic trilobites may have more easily eluded predators if their escape behaviour involved lateralized movement in the direction opposite that of most members of the same species (which would be the direction of motion anticipated by most predators). By implication, Palaeozoic predators of trilobites must have been differentially efficient at successfully subduing and devouring prey if they exhibited within-species lateral biases. Both of these ancient examples suggest that there is some adaptive value in being somewhat different (behaviourally or otherwise) from the majority population in terms of lateral bias.

What is the adaptive value of spiral asymmetry? There are few satisfactory hypotheses. A spiral or helical structure has evolved, undoubtedly independently, a number of times in geological history, and more than one explanation may be required for the evolution of spiral structures. A helical shape occurs, for example, in some eubacteria, in the flagella of some protists, in the stem or stem-and-leaf arrangement (phyllotaxis) of many plants, in the shells of molluscs and brachiopods, in the overall shape of some echinoderms (helicoplacoids and edrioasteroids) or in the columns of some stalked crinoids, and in the axes of some bryozoans (notably the ectoproct *Archimedes*). It has been suggested that in protists and eubacteria, spiral structures, especially flagella, confer an advantage in motility by allowing organisms to propel themselves through water by means of viscous shear rather than by accelerating fluid.¹³ A spiral morphology in an

echinoderm or bryozoan may assist with directing food-bearing currents toward the animal and may result in more efficient removal of waste products. A spiral stem in a climbing vine may provide a firmer footing for the vine against the host structure. The adaptive value of a spiral design in the shell of a gastropod, however, remains unexplained.¹⁴

Spiral or helical asymmetry may be partly related to proteins underlying the structure of organisms. For some organisms, it is conceivable that a helical design is the simplest method of scaling-up from the level of amino acids (left-handed enantiomers), to the whole-organism level. Against this hypothesis is evidence that the hierarchical nature of asymmetry in organisms is not necessarily related to direct connections between separate levels. Asymmetrical proteins, for example, apparently exert little or no influence on the assembly of protein molecules.¹⁵ Additional work is needed to understand why, as J. W. Galloway has observed, the helix is 'biology's favourite shape'.¹⁶

Conclusions

The fossil record is replete with evidence of morphological and behavioural asymmetry. Morphological asymmetries have been identified in archaeobacteria, eubacteria, protists, fungi, plants and animals. Behavioural asymmetry can be inferred from certain morphological asymmetries and from the trace fossil record. Asymmetry in prokaryotes evidently dates from the time of the first appearance of life on Earth (Archaean Eon). Asymmetry in eukaryotes probably also dates to the time of the first eukaryotes, but was certainly in place by the time of the appearance of the earliest multicellular eukaryotes (early Proterozoic Eon).

Much remains to be learned from the fossil record of biological asymmetry. Most accounts of asymmetry from the fossil record are anecdotal, and statistics highlighting patterns of conspicuous, directional asymmetry are available in only a few instances. In many cases, perceived left–right differences in bilateral organisms are the result of observations made in connection with other studies, or based on conspicuous lateral differences evident from published illustrations. Often, cases for lateral asymmetry have been made principally by reference to assumed homologues among modern organisms. Spiral or helical structures in ancient organisms, and the factors that have led to their long evolutionary history, have been addressed in only a small number of studies.

One potentially fruitful endeavour would be to explore whether lateral asymmetry in developmental timing of organisms is expressed in the fossil record. Teratologies in animals (e.g. in trilobites) are moderately common in certain stratigraphic formations, and would seem to offer an opportunity for assessing lateral developmental differences within some species.

Studies of the origin of lateralization that rely upon fossils have dealt exclusively with phylogenetic origins. With the availability of good ontogenetic material for many ancient species (e.g. arthropods that moulted their exoskeletons, or aqueous animals that secreted calcified skeletal material incrementally), it should be possible to address questions of the ontogenetic origin of lateralization in some species.

Finally, trace fossils offer a virtually untapped opportunity for assessing lateral behavioural differences in ancient animals. Traces produced in originally unconsolidated sediments would, for example, allow the assessment of whether the left or right limbs of a bilateral animal were dominant for digging, whether the left or right foot of an animal was dominant, or whether an animal preferred to turn left or right. Healed wounds on vertebrate skeletons (e.g. herbivorous dinosaurs) could be tallied to determine whether predatory dinosaurs had a lateral bias in attack direction. Scratches on teeth, whether of herbivorous or carnivorous animals, could be used to assess lateral preferences in chewing behaviour. These examples are just a few of the many interesting possibilities that exist for closing the gaps in our understanding of the evolutionary history of behavioural lateralization.

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