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Invariance and change in the evolution of living beings

Summary - Bilateral symmetry and a main body axis with precise antero-posterior and dorso-ventral polarity are invariant elements of the body plan of bilaterian animals. However, all these traits have been challenged in some lineages. Same for lesser but not less stable invariants such as the number of cervical vertebrae in mammals, the number of body segments in leeches, the number of trunk segments in centipedes. In many cases, changes from these basically invariant conditions go against a pretended macroevolutionary principle, the so-called Williston's rule, according to which evolution of serially repeated structures should proceed from series of numerous uniform elements towards series comprising a lesser number of more extensively patterned elements. Maximum structural complexity seems to have a low upper limit within each body 'dimension'. This limit, however, can be 'forced' when new structural dimensions appear, as in the case of arthropod and vertebrate appendages. The body architecture of living beings thus appear to be subject to internal and external constraints, which tend to preserve its structural invariance, but can be challenged thus giving rise to new structural solutions. Studying these aspects requires a tight integration of developmental biology with evolutionary biology.

Invarianza e divergenza nel divenire del vivente

Riassunto - Elementi invarianti del piano organizzativo dei Bilateri sono la simmetria bilaterale e la presenza di un asse corporeo con precisa polarità anteroposteriore e dorso-ventrale, ma ciascuno di questi aspetti è stato rimesso in discussione all'interno di singole linee evolutive. Lo stesso si può dire per elementi invarianti di dettaglio, ma di non meno rimarchevole stabilità, quali il numero delle vertebre cervicali nei mammiferi, il numero dei segmenti del corpo nelle sanguisughe, il numero dei segmenti del tronco nei chilopodi. In molti casi, la rimessa in discussione di questi tratti organizzativi invarianti va in direzione opposta a quanto richiederebbe un preteso principio macroevolutivo (la cosiddetta legge di Williston), secondo il quale l'evoluzione porterebbe da strutture ripetitive formate da molte parti uguali a strutture ripetitive in cui queste parti sono in numero ridotto e presentano differenziazioni all'interno della serie. All'interno di ogni 'dimensione' del corpo, sembra che la complessità strutturale raggiungibile non possa superare un valore limite generalizzato e

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piuttosto basso. Questo limite può essere peraltro ‘forzato’ con la comparsa di nuove ‘dimensioni strutturali’, come nel caso delle appendici dei Vertebrati e degli Artropodi. L’organizzazione del vivente appare dunque soggetta a vincoli, sia interni che esterni, che tendono a garantirne l’invarianza strutturale, ma che possono essere rimessi in discussione, dando così origine a nuovi piani organizzativi. Lo studio di questi problemi richiede una stretta integrazione fra biologia dello sviluppo e biologia evoluzionistica.

The comparative method

The comparative method is one of the pillars of modern biology. Scientists cannot content themselves with a naïv appreciation of similarities and differences, for two good reasons. First, the unexperienced eye may fail to appreciate less obvious but interesting similarities actually existing between two animals or plants, or parts of them. Second, similarities (or differences) cannot be simply taken at face value, because they may tell a variety of different stories. Similarities, for example, may document genealogical relatedness, or equivalent adaptations to similar environmental conditions, or both.

Disentangling relatedness from adaptation is obviously important, at least from a modern, evolutionary point of view. But comparative biology is much older than Darwin or, for the sake of argument, Lamarck (see Russell, 1916; Cole, 1949). As nearly always with origins, comparative biology’s birthday is something we cannot strictly identify in a single publication, or in a single author’s work. Nevertheless, we can easily single out an extraordinary sixteen-century book, where an anatomical comparison of unexpected modernity is presented. This is Pierre Belon’s *Histoire de la Nature des Oyseaux* (1555). In this fine ornithology book, the author faces the then new problem of describing the anatomy of birds in some detail. His main difficulty was not so much one of using words and pictures to inform the reader about the shape and size of bones or soft body parts, as was one of choosing a suitable vocabulary to provide names for things that had never been described before. Names, perhaps, were already available, if one was ready, as Belon was, to identify in a bird’s skeleton the same bones the reader presumably knew from human anatomy. Thus, Belon tried to establish a point-to-point correspondence between the hitherto unknown skeleton of the bird and the already known skeleton of the human race. There was little metaphysics behind this comparison. Do not think that Belon was moving from man because our species is the most important one in the living world, one so complete as to offer a reference against which to compare and try to understand the remaining of animal life. He simply acknowledged that human and bird skeleton are similar enough as to allow him to use the same words for what he regarded as the same bones in both of them. That man, rather than bird, was providing the anatomical nomenclature for the other was nothing but an accident of history, human anatomy in the sixteenth century being by far more advanced than bird anatomy was.

For more than two centuries, however, there was very little progress in the development of a comparative method in biology. We must wait for the times of the French school flourished between the last decade of the XVIII and the first three decades of the XIX century, a time of giants such as Georges Cuvier and Étienne Geoffroy Saint-Hilaire; a time at which a number of German scholars like Johann Friedrich Meckel and Johann Wolfgang Goethe also contributed substantially to the development of comparative biology. A synthesis of all these pre-evolutionary efforts is to be found in the works of Richard Owen, to whom we owe the first explicit formulation of the most important concept of comparative biology, that is the concept of homology. To be sure, Owen's (1843) essentialistic definition, according to which homologue is the *the same organ under every variety of form and function*, is largely unsatisfactory to modern standards, as it refers to abstract archetypes, as the one Owen himself depicted for the vertebrate skeleton (cf. Minelli 2003b and references therein).

The way was open, however, for a revisitation of this and related concepts from an evolutionary point of view. It proved not too difficult to identify homology with a proof of genealogical relatedness, while those similarities biologists described as analogies could be interpreted as the result of parallel or convergent histories of adaptation. Thus it became important to clearly distinguish between the two, as analogies might put obstacles in reconstructing phylogenetic relationships. But this was just the beginning of a long story, one still continuing in our very days. As Willi Hennig noted in his ground-breaking book on *Phylogenetic Systematics* (1966), to distinguish between homologies and analogies is not enough. A homology is informative as to phylogenetic relationships only when it represent the uniquely shared novelty (apomorphy) of a group of species. The shared possession of ancestral traits does not help understanding phylogeny, the homology of these traits notwithstanding. On the other hand, there is much more to evolutionary biology than reconstructing the phylogenetic tree of the living. One might even contend that convergence is one of the most convincing arguments in favour of an evolutionary world-view. This explains why homoplasy (i.e. convergence, parallelism and character reversal), long regarded as the phylogeneticist's nightmare, has recently attracted positive interest as a potential source of precious information about evolutionary adaptive histories (see several chapters in Sanderson & Hufford, 1996).

Another critical issue is whether evolutionary change is basically uniform and continuous through time, or happens in major sudden bursts separated by long intervals of evolutionary stasis. The latter view corresponds to the punctuated equilibrium model championed by Nils Eldredge, Stephen Jay Gould and Elizabeth Vrba. This theory has been basically rejected by neontologists, but found some favour among palaeontologists (see Hoffman, 1989 for an illuminating discussion). In recent years the interest for this controversy has continuously decreased, possibly due to the rising hopes of moving from the more conspicuous but superficial level of pattern, as observed by palaeontologists in the fossil record, to the deeper

and more interesting level of the causes and mechanisms by which evolutionary novelty is generated.

Genetic control and generic mechanisms

To a large degree, this fundamental change was due to the extraordinary progress of developmental and molecular genetics. Since the early eighties we have become accustomed to reason in terms of developmental genes, that is, in terms of genes whose precise temporal and spatial expression in the embryo is critically required in order for a specific developmental step to be accomplished. Thus, we speak of segmentation genes, of trunk-patterning genes, and even of eye or heart master genes.

There are problems, however, with the molecular reductionism inspiring this nomenclature (e.g., Nijhout, 1990; Lawrence, 2001; Minelli, 2003a). First, to notice that a point mutation in a given gene causes a specific developmental defect must not be taken as a proof that that gene is *the gene for* the corresponding developmental event. Genes usually have pleiotropic, i.e. multiple effects, at least in so far as we partition the phenotype according to our conventional descriptive criteria rather than according to the actual primary effects of the individual genes. Second, the primary effects of a gene are often quite ‘generic’. There are, for example, genes affecting the production of branched structures such as the tracheal system of a fruitfly, and genes whose effect is the production of anastomoses such as those of the capillaries of our circulatory system. But those genes do not ‘know’ anything of respiration, or of blood, and may exercise their activities on different kinds of pipes. For all the specificity of their effects, these have nothing to do with the specific structure and functioning of individual body organs. Third, major families of so-called developmental genes have turned out to be coding for transcription factors, that is for proteins that regulate the transcription of other genes. But we have also learned that minor changes in their molecular sequence may have the most far-reaching consequences, such as to completely remove these molecules from their original role and to put them ‘to the service of’ completely new developmental events. The latter discovery is a warning towards a naïv evaluation of what is a small change and what is a big change in evolution. Organisms are often very conservative in their organization despite a lot of change at molecular level, and vice versa.

Nevertheless, the major focus in the research efforts aiming at understanding the basis of morphological evolution is still at the genetic level. This is very well expressed in a number of recent volumes, such as Raff (1996), Gerhart & Kirschner (1997), Gehring (1998), Coen (1999), Carroll *et al.* (2001), Davidson (2001), and Wilkins (2002). Some authors, however, have taken a different view; see, for example, Keller (2000), Oyama (2000a, b), Minelli (2003a), Müller & Newman (2003) for a sample of less gene-centric views.

Invariance and change

Bilaterians, or triploblastic animals, are a major branch of the phylogenetic tree. Among the structural traits shared by the large majority of its representatives are some conspicuous features of symmetry and polarity. These animals have a well-distinct antero-posterior and dorso-ventral polarity, and a conspicuous plane of mirror symmetry divides their body into left and right halves. These traits seem to be so important and fundamentally entrenched that any challenge to them should be exceedingly difficult, or so fundamental as to characterize a major subgroup within bilaterians. Evolution, however, has proceeded otherwise.

Crustaceans, for example, are basically symmetrical, but for the more or less conspicuous differences in size and shape of the large claws of many decapod species. There are, however, crustaceans lineages that obviously depart from this original condition. The best-known among these groups is the hermit crabs, but a distinct body asymmetry has also evolved in parasitic isopods and copepods. What is still more interesting, however, is the fact that a conspicuous departure from bilateral symmetry can be occasionally reversed, as in the king crabs (Lithodidae), which, despite their perfect crab-like features, are nothing but a re-symmetrized and fairly recent offshoot of the hermit crab radiation (Cunningham *et al.*, 1992).

Profound and repeated changes in body symmetry have equally affected the echinoderms. It is well-known that these animals pass through a bilaterally symmetrical larval stage that gives rise to a mostly pentaradial adult, but let us not overlook the independent evolutionary trends towards a secondary bilateral symmetry exhibited by several families in this phylum. Same for the top one in the hit parade of asymmetrical bilaterians, i.e. the gastropods, where the widespread trend towards resymmetrization is quite conspicuous in the external shape of terrestrial slugs, nudibranchs and sea hares.

There is hardly a feature, indeed, that we can regard as fixed, invariant forever. Not even the antero-posterior, or the dorso-ventral polarity.

The antero-posterior body axis

There are indeed very few features which seem to be so universal and clearly defined as the antero-posterior body axis, but this is not necessarily so.

Take, for instance, an insect, or an earthworm. There is no doubt as to which end of the body is the fore, and which the rear one. In case of doubt, let us wait for the animal to move, it will tell us immediately. In the case of both insects and earthworms, the digestive tract would tell us the same, as it opens with the mouth anteriorly, with the anus posteriorly.

With other animals, however, things are not so simple. Take, for instance, a snake. Inexperienced people might expect it to have the anal opening at the very end of the body. The anus, however, lies at the end of the trunk, rather than at the

end of the body, and snakes, like the majority of vertebrates, possess a tail that is posterior to the trunk, i.e., posterior to the anus.

Take, otherwise, a shark. A feature that adds to this animal's sinister aspect is its mouth's unexpected position. We would expect it to be terminal, but it is ventral instead. In this case, where is the 'true' fore end of the body? On the tip of the snout, or at the level of the teeth?

And what about the rear end of the body? In a dog or a cat, one will probably say that the body ends where the tail begins. In these animals, indeed, the tail has all the appearance of an appendix. But where does a snake's body end? In this case, to recognize a boundary between trunk and tail may seem little more than anatomist's sophistry.

If these questions of vertebrate anatomy are not weird enough, invertebrates could provide a lot of still more complicated issues. Extreme cases would be provided by sedentary polypoid animals, where the most obvious body axis is clearly not an anterior-posterior one, but one going from the point of attachment to the substrate to the diametrically opposite point, which is usually in the middle of mouth. Things are little controversial in the case of cnidarians, such as hydras and coral polyps, because these animals (which are not bilaterians) have a simple digestive cavity with one opening only, but things are different in bilaterian polyps, such those of the bryozoans.

These animals have indeed a true digestive tube with two openings, both of them lying opposite to the point of attachment to the substrate. In this case, with the general shape of the animal being dominated by a body axis perpendicular to the point of attachment of the polyp to the substrate, what does the mouth-to-anus axis represents? Clearly, this axis does not overlap the external antero-posterior axis, as in the insect and the earthworm. There is, perhaps, a way out of this paradox.

We might suggest (Minelli, 2003a) that in the animal's body there are two main components, whose ontogenetic development and evolutionary history are to a certain degree independent. Borrowing from Romer's (1972) inspiring terminology, we may call these components the external and the internal animal respectively. The external animal (in terms of classical embryology, a derivative of the ectoderm and the mesoderm) and the internal animal (a derivative of the endoderm) must necessarily fit together, but are not completely interdependent. To a certain extent, each one of them evolves to deploy its own polarity and patterning. Thus, what we usually describe as the animal's antero-posterior body axis is, indeed, the main body axis of the external animal. That the internal animal may develop and pattern its longitudinal axis on its own is variously shown by all those animals where mouth, anus, or both, do not occupy the extreme fore and rear position of the trunk, as described in terms of the external animal. Hence the ventral position of the mouth in a shark or, still more conspicuously, in a planarian. Or the coiled form of many intestinal tracts, which does not simply mirrors the functional requirements for an adequately long tube, but also the fact that the morphogenesis of this tube is largely

independent from the external body's architecture. To find beautiful examples of this state of affairs we do not even need to look for sedentary polypoid forms. Sipunculans, a little group of marine worms which mainly live loose in sandy or gravely grounds have an elongated sac-like shape, with obvious external antero-posterior polarity, and the mouth at one end. The anus, however, is not located at the opposite end. The quite long intestine runs along most of the sac's length, then it coils onto itself, to finally open a close distance from the mouth.

Understanding these features, and their origin, is clearly a question of developmental biology as it is one of evolutionary biology. Indeed, these questions are a characteristic example of the subject matter of *evolutionary developmental biology*.

Evolutionary developmental biology and the theories of Étienne Geoffroy Saint-Hilaire

This discipline may be regarded as one of the newest branches of biology. Indeed, a deliberate integration of two traditions so different as are developmental biology and evolutionary biology, is a research project that only in the last few years is taking form and substance (Hall, 1998; Arthur, 2002). Many interesting questions currently debated in evolutionary developmental biology, however, are all but new. Some of these questions were already addressed by the founding fathers of comparative anatomy, or comparative embryology, but could not be resolved because of the inadequate knowledge of the time. Geoffroy Saint-Hilaire does often emerge as a kind of hero, whose profound insights had been often vilified because they did not fit into the dominant paradigm of his age (Appel, 1987) but are finding a place at last in today's evolutionary developmental biology. Let me mention three interrelated issues: unity of plan, dorso-ventral patterning, and vertebrate-to-squid equivalence.

Central to Geoffroy's research agenda was his idea that all animals share a common structural plan, all differences between then being mainly a matter of degree and proportions. A corresponding proposition has been formulated just 10 years ago based on the growing knowledge of a class of developmental genes, which are basically shared by all animals (all bilaterians, at least), their expression early in ontogeny providing a universal reference system of positional information along the anterior-posterior body axis. This means that the main body axis is 'the same' in all animals or, at least, in all bilaterians. In terms of the previous discussion on the sometimes contradictory evidence of body polarity, this axis is the one realized by the external animal. The universally shared genes under whose control it develops are those of the so-called *zootype* (Slack *et al.*, 1993). In a sense, this is a physical (molecular) equivalent of Geoffroy's abstract animal body plan.

Second, dorso-ventral polarity. Zoologists have always been puzzled by the fact that in animals such as arthropods and annelids the main nervous cords are ventral, whereas in others, such as vertebrates, the main nervous axis is dorsal. Geoffroy suggested that an arthropod's back is in fact the same as a vertebrate's belly, but this concept was systematically disregarded as wholly speculative. In this

case too, however, there seems to be good reasons to acknowledge that Geoffroy was right. Molecular developmental genetics has demonstrated indeed that genes specifying the dorsal side of a vertebrate embryo are homologous to genes that specify the ventral side in arthropods, and vice versa (Arendt and Nübler-Jung, 1994; Nübler-Jung and Arendt, 1994; De Robertis and Sasai, 1996).

Third, the vertebrate-squid story. Following their master's path, two of Geoffroy's students, of which we only know the family names, Meyranx and Laurencet, suggested an equivalence between a vertebrate's and a squid's organization. In particular, in order to account for the different relative position of mouth and anus in the two kinds of animals, they suggested that you can equate a vertebrate's main body axis to a squid's one if you just imagine the former to be bent onto itself to get a U-shaped gut. The argument, indeed, is somewhat similar to the explanation I have suggested for the sipunculan's body.

Segments

Segmentation is a conspicuous feature of the body organization of three major animal lineages, i.e. the annelids, the arthropods, and the vertebrates. Previous opinion notwithstanding, segmentation was acquired by these three groups independently. Within each of them, the segmental architecture has extensively evolved, giving rise to a variety of morphological solutions that are mainly related to locomotion, but may affect virtually all remaining systems, from the nervous to the excretory one. To give an example of how different architectures may be based on a common segmental basis, let us just think of the difference between a centipede and a spider.

Despite the enormous evolutionary potential of a segmented body, however, this modular architecture is often characterized by an unexpected degree of invariance. Let's get one example from each of the three main groups of segmented animals. In annelids, to begin with, there are often big differences in the number of body segments between closely related species, sometimes even within one species, but in a major annelid subgroup, the leeches, the number of body segments is rigorously fixed, 32 in all leech species known to date. To move on to arthropods, in adult centipedes the number of leg-bearing segments is always 15 in two major subgroups, the scutigermorphs and the lithobiomorphs, and either 21 or 23 in the scolopendromorphs. As for vertebrates, the best known example of constancy in segment number is the presence of 7 cervical vertebrae in virtually all mammals, the various length of their neck notwithstanding. (The exceptions are the manatee and the 2-toed sloth with 6, and the 3-toed sloth with 8 cervical vertebrae.)

It is hard to imagine that these fixed numbers can have a precise adaptive significance. In other terms, is it quite unlikely that these values are so constant because of strong selection against any leech with other than 32 body segments, any scolopender with 22 pairs of legs, or a mammal with a dozen cervical vertebrae

(Dover, 2000; Arthur, 2000). A much more plausible alternative is that natural selection does not find individual variation on which to work. In other terms, we must expect that leeches with 31 or 33 segments are simply not formed, because of the developmental rules by which a leech's body is built. Same for the centipedes, or the mammals. If so, it is into development, rather than evolution, that we must look for explanations of this invariant morphological behaviour (Minelli, 2003c).

But this is just the first half of the story.

If you count the external rings, or annuli, into which the body surface of a leech is subdivided, you will always find many more units than the 32 segments all leech are decreed to have. Ring number varies according to species, from about sixty to about one hundred, or more. According to traditional textbook descriptions, each leech segment – a few of those at the two ends being excluded from this opportunity – may be subdivided into a variable number of rings, more often 3 or 5. Rings are quite superficial, that is, this subdivision does not affect the internal anatomy, e.g. the arrangement of nephridia or nervous ganglia, where the basic segmentation still remains visible.

But let's imagine a certain degree of heterochrony, with this subdivision of segments into rings occurring at an earlier ontogenetic stage than they do in leeches. Would it not be possible for these secondary body units to be 'promoted' to the level of full segments, each of them being now endowed with a complete set of segmentally repeated organs?

I think that something of the sort happens in most arthropods, to a lesser or greater degree according to the group. Comparative morphology and developmental biology, including developmental genetics, suggest that arthropod body segments are probably built in two stages, i.e. by first laying down a fixed number of primary segments, then – but without long delay – allowing them (the three most anterior ones excluded) to subdivide into two or more secondary units each; these latter, rather than the primary units, would be the morphological segments we actually observe (Maynard Smith, 1960; Minelli and Bortoletto, 1988; Minelli, 2000a, 2001). In an insect or a shrimp, for example, there would be two secondary segments per primary one; larger degrees of multiplication would characterize more elongate arthropods such as centipedes and millipedes.

In this respect, it is also interesting to note that modern phylogenetic research does not put the more elongate, worm-like forms of millipedes and centipedes at the root of the respective trees but, to the contrary, regards them as recently derived branches (Enghoff, 1990; Foddai and Minelli, 2000; Regier and Shultz, 2001). This is in overt contrast to the macroevolutionary principle known as Williston's rule (e.g., Sanders and Ho, 1983). According to this principle, serial structures such as trunk segments in annelids or arthropods should show an evolutionary trend from higher to lower numbers of parts and from uniform to patterned series, with a resulting increase in structural complexity. In both centipedes and millipedes, however, the main evolutionary trend is towards an increase in segment number and a decrease in the structural complexity of the trunk (Minelli, 2003d).

Axis paramorphism

A macroevolutionary principle, however, seem to hover over morphological complexity. I have no trouble acknowledging that one might offer many alternative definitions of complexity or, better, alternative ways to measure it. Nevertheless, one of the aspects any possible measure of complexity would probably take into account, either directly or indirectly, is *the number of kinds* of structural elements that form a given feature. That any one of those kinds occurs in a lesser or greater number of copies is basically uninteresting: a millipede with two hundred pairs of legs is hardly more complex than a millipede whose pairs of legs are ‘only’ one hundred. On the other hand, the spatial arrangement of the parts is another aspect that may contribute to complexity, but here – for the sake of simplicity and also in view of the fact that we are basically dealing with linear arrangements of parts, such as body regions along the main body axis – I will disregard it. Thus, let us only consider the number of kinds of elements in a given arrangement.

From this limited point of view, a striking fact seems to emerge from a consideration of the whole animal world (but also, indeed, from plants.) This fact is, that in any series of structural elements distributed along a given body axis the number of kinds of elements is always small, often three or four, five at the highest. Examples are an animal’s body regions (for instance, head and trunk; or head, thorax and abdomen), the number of kinds of digits in a tetrapod hand or foot, the number of kinds of teeth in the mouth of a mammal, or the number of kinds of elements in a flower (sepals, petals, stamens, carpels).

To a certain extent, this is possibly an artefact of our perception schemes, or of the ways we articulate taxonomies. Nevertheless, even if we allow for a certain degree of arbitrariness in the above descriptions, we can hardly dismiss the fact that structural complexity along any body axis is strictly limited.

If we follow Stuart Kauffman’s (1993) arguments on the intrinsic limits of adaptive systems, we can probably find an explanation for this observation. In any system composed by many ‘comparable’ parts (for example, body regions, or kinds of teeth), as the number of those parts and the richness of interactions between them increase, chances will also rapidly increase that these parts will present conflicting constraints of design. As a consequence, an optimization of design will become increasingly difficult, any adaptive selective regime notwithstanding. This is clearly not a problem of biology, but a more general question of optimization of complex systems, from which biological systems cannot escape.

However, along the evolutionary time scale and thanks to the plasticity of their developmental systems the living organisms have repeatedly found a way out of the strictures of this constraint. If the potential for complexification of a given body axis is readily exploited, new avenues open if additional axes are created. This happened, for instance, with the evolution of body appendages (Minelli, 2000b, 2003e).

The problem is, however, how can organisms evolve new axes in the first

instance. It might be not that difficult to modify something that already exists, but from where does a completely new element originate?

There is a sense, however, in which the first appendages of, say, vertebrates or arthropods should perhaps *not* be regarded as completely novel features. Between the main body axis and the appendages of the same animal there is some degree of homology that may justify an hypothesis of *axis paramorphism*: that is, the hypothesis that secondary axes (appendages) are nothing but evolutionarily divergent duplicates of the primary body axis (Minelli, 2000b, 2003a). In a very simplified formulation, one might regard a burgeoning appendage as a kind of lateral bud. Not one, however, destined to acquire complete independence as a separate individual. Rather, as a kind of bud that will remain co-ordinated with the main body axis, but progressively acquiring its own patterning and complexity. One might speculate that one of the reasons behind the astonishing evolutionary success of both arthropods and vertebrates may have been this very capacity to rejuvenate their body structure by evolving additional lateral axes (Minelli, 1996).

Evolutionary developmental biology

Studying unity and diversity of living beings goes thus far beyond the traditional limits of comparative anatomy and embryology, to become a central issue of today's biology. Here is where evolutionary biology meets developmental biology, because change and invariance are not fully explained in terms of natural selection but also require an adequate understanding of what is developmentally feasible and thus available to be tested for adaptation, and what is not. Selection will remove monsters from the world scene, but it is to development to decide whether these monsters may, or may not, be generated. A four-winged drosophila is not the same as the chimaera of old tales.

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