

# Conserved Versus Innovative Features in Animal Body Organization

ALESSANDRO MINELLI\* AND GIUSEPPE FUSCO

*Department of Biology, University of Padova, I-35131 Padova, Italy*

**ABSTRACT** The origin of evolutionary novelties is a central topic in evolutionary developmental biology (evo–devo) studies. In any new feature, there is a conserved component that is either structural or related to the underlying genetic control, but it is not always obvious what is really new and what is conserved. Nevertheless, disentangling this blending of old and new features is basic to understanding mechanisms of evolutionary change. The origin of arthropod appendages illustrates the complexity in tracing the origin of evolutionary novelties. At the base of the lineage, the main body axis was already segmented and antero-posteriorly patterned, and the genetic tool kit required to form lateral outgrowths was already available. The novelty was possibly the developmental decision to “read” the available axial information and to exploit it for differentiating segmentally patterned and axially segmented appendages. Some important novelties bridge the gap between what have been traditionally distinguished as systemic and local changes. For example, the origin of the body cavities evolved by several animal groups may have been initiated by simple changes in cell-to-cell adhesive properties. Any possible change in an existing ontogenetic pathway has the potential to generate novelties. *J. Exp. Zool. (Mol. Dev. Evol.)* 304B:520–525, 2005. © 2005 Wiley-Liss, Inc.

According to a current mainstream approach to comparative biology, in analysing an organism's structure we can recognize a hierarchy of more or less objectively identifiable homologues (Roth, '91; Striedter and Northcutt, '91; Hall, '94; Wagner, '96; Abouheif, '97). However, we believe that a factorial approach to homology (Minelli, '98, 2003a) would be rooted on firmer ground, and in this paper we go along this way with respect to the issue of evolutionary novelties. Every novelty results from a more or less complex interlacing of conserved features and novel elements. All of these components should be disentangled, as far as possible, and subjected to separate analysis in a suitable historical and adaptational context. A close inspection of a case study will illustrate the meaning and the value of a “factorial analysis” of the origin of novelties.

## EVOLUTIONARY NOVELTIES, INVENTIONS AND INNOVATIONS

Recent advances in developmental genetics, along with the push of the new conceptual framework of evolutionary developmental biology (evo–devo), have drawn attention to a long-neglected part of evolutionary theory, i.e., the origin of variation, to the extent it is not simply accounted for by mutation and sex. Variation is the raw

material available to evolutionary sorting processes (natural selection and random drift; cf. Fusco, 2001), and its origin is a central topic in evo–devo studies. In the evo–devo perspective, it is important to know how phenotypes are constructed during development to understand how variation is produced (cf. also West-Eberhard, 2003).

Searching for a general theory of evolutionary change that overtly incorporates the origin of variation and acknowledges in full its explanatory role in the “flowering” of form, the problem of variation has been addressed from different viewpoints that often suggest different classifications of variation noted in patterns and processes (e.g., Arthur, 2002). In recent debate, distinguishing between the remoulding of existing features and the advent of really new features is possibly the matter that has drawn most interest (e.g., Newman and Müller, 2000).

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\*Correspondence to: Alessandro Minelli Department of Biology Via Ugo Bassi 58 B I 35131 Padova Italy.

E-mail: alessandro.minelli@unipd.it

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As noted by Erwin and Krakauer (2004), in the literature there is a certain degree of fuzziness about terms like evolutionary *novelty*, *invention* and *innovation*. The same word is often given different meanings, and different words are used to express the same concept. However, it is important to note that pairs of specific terms, e.g., *novelty* vs. *innovation*, or adjectival specifications, e.g., *apomorphy* vs. *key apomorphy*, are generally employed to stress the difference between the emergence of a new feature during the evolution of a lineage, and its possible successful spreading through phyletic radiation. Not all novelties produce phyletic radiation, and a novelty can turn out to be a key feature in phyletic radiation long after it first emerges. The success of a novelty generally depends on the environmental context within which it is actually tested.

Let us focus on novelties simply as emergent new features. Several definitions of evolutionary novelty are available. In phylogenetic studies, for example, a novelty is an apomorphy (in the sense of Hennig, '66). For a student of adaptation, a novelty is typically a previously non-existing feature that promotes fitness and was built by natural selection for its current role (adaptation). But, following Gould and Vrba ('82), it can also be a feature evolved for other uses (or none), and later co-opted for its current role (exaptation), or a feature whose origin cannot be ascribed to the direct action of natural selection (non-adaptation). An adaptation is often recognized as a (the) key feature for a clade (Lauder and Liem, '89). For an evolutionary developmental biologist, novelty is a change in the developmental process and in the underlying genetic network (developmental reprogramming sensu Arthur, 2000, 2002).

When introducing the discourse into heterochronic change in his book on *Ontogeny and Phylogeny*, Gould set a clear dichotomy between novel and non-novel features: "Evolution occurs when ontogeny is altered in one of two ways: when new characters are introduced at any stage of development [...], or when characters already present undergo changes in developmental timing. Together, these two processes exhaust the formal content of phyletic change." (Gould, '77: p 4). However, "Evolution does not produce novelties from scratch. It works on what already exists" (Jacob, '77: p 1164). This is not only true just for the large-scale transformations that we can trace along the evolutionary history of many higher taxa, e.g., in the transformation of walking legs into the wings, fins or arms of some "tetrapod"

vertebrates. It is certainly also true on a smaller scale, where heritable phenotypic change follows from a more or less extended remoulding of an underlying developmental genetic network.

Clearly, then, no novelty is really brand new, but in all new features there is a conserved component—a structural one, or one related to the underlying genetic control, or still otherwise. What is not always obvious, in this blending of old and new, is *what* is really new and *what* is conserved. In other words, what is the scope of the novelty?

### NOVELTY AND CONSERVATION IN ARTHROPOD APPENDAGES

Let us look at arthropod appendages. There is little doubt that these represent an evolutionary novelty that qualifies also as a key feature of this largest of phyla. If we place the origin of arthropod appendages in the context of the ecdysozoan theory of arthropod affinities, these segmental and segmented appendages distinguish arthropods not only from worm-shaped animals such as nematodes and priapulans, but also from tardigrades and onychophorans, whose unarticulated limbs have not evolved into anything like the fantastic diversity of the arthropod appendages. It would be easy, therefore, to qualify the latter as one of the most obvious key novelties in proto-stome evolution. A closer look will nevertheless show that distinct components, both old and new, are involved in this overall new feature.

Let us start with the appreciation that all extant arthropods possess a patterned series of appendages, i.e., a series of limb pairs that are not all the same along the animal's main body axis. Basically, we identify cephalic sensory appendages such as the antennae, followed by mouthparts and, finally, by appendages involved in locomotion and, often, in gas exchange.

A traditional scenario (Snodgrass, '35; Raff and Kaufman, '83) identifies the differentiation of the different pairs of appendages as a late stage in the evolution of the arthropod lineage. Placing these animals in a superphylum, Articulata, i.e., together with annelids, this reconstruction hypothesized the following main steps. The lineage's ancestor was a homonomously segmented legless worm. In an initial evolutionary stage, this worm acquired unsegmented appendages, one pair per segment. These appendages were all the same, except perhaps for a pair of anterior unsegmented

antennae. The next stage brought about segmentation of the appendages, but these—still with the possible exception of the antennae—were all the same kind. Only from this stage on, increasing degrees of specialization were manifested in the previously homonomous series of appendages, and this was accompanied by growing differences in the size and shape of the corresponding segments along the main body axis.

Unfortunately, the fossil record fails to throw light on the early phase of the evolution of the stem lineage arthropods. These appear in the fossil record, at the base of the Cambrian, at about the same time as stem lineage onychophorans, i.e., stem representatives of what is today the most likely sister group of the arthropods.

Irrespective of our choice between the Articulata hypothesis of arthropod relationships (still advocated by some authors, e.g., Scholtz, 2002, 2003) and the currently favoured Ecdysozoa alternative, Snodgrass' scenario is anyway difficult to reconcile with our current knowledge of protostome development.

What is definitely negated by both comparative morphology and developmental genetics is the hypothesis of a protostome-grade arthropod ancestor that was completely unpatterned along its antero-posterior body axis. Truly unpatterned bilaterians are virtually non-existent (Slack et al., '93). Think, for instance, of the widespread occurrence of tagmosis (body regionalization) or of the presence of mouth, anus or genital pore(s) at some specific location along the main body axis; think of the patterned expression of the *Hox* genes wherever this expression has been studied. Therefore, some regionalization of the main body axis, or simply a number of marked positions of potential or actual differentiation ("hot spots") along that axis (Minelli and Schram, '94), was probably already present before the origination of the first arthropod appendage.

As a consequence, we might expect that the first arthropod appendages could have already formed a heteronomous series at the very time they originated. This is probably true to the extent that the most anterior appendages, the pair to which Boxshall (2004) conventionally gives the crustacean name of antennules, were probably different from all post-antennular ones even in the oldest arthropods. This point is supported by the little we know about trilobite appendages (Bruton and Haas, '99), stem crustaceans (as summarized in Boxshall, 2004), and also the Cambrian "great appendage" arthropods.

Let us try to reconstruct what may have happened during the evolution of the arthropod stem group. The main body axis was already segmented (more or less overtly, cf. Minelli and Fusco, 2004) and antero-posteriorly patterned. On the other hand, the genetic tool kit that was required to form lateral outgrowths was also already available (Panganiban et al., '97). However, availability of positional information, the developmental decision of "reading" this information, and the exploitation of the information for appendage differentiation are independent elements of the story. For example, in cephalocarid crustaceans, no difference in limb type is associated with the head to thorax boundary. "It does not seem implausible that the anterior segments of the common arthropod ancestor already possessed unique molecular identities, defined by *Hox* genes, and that these may have become fixed, even if they were not reflected in the overt specialization of appendages. They may have controlled patterns of cell specialization into mesoderm or nervous system, and only subsequently acquired more extensive roles in the control of external segment morphology" (Akam, 2000: p 4440).

There is no need to assume an antero-posterior trend towards the specialization of an ever-increasing number of appendages along the lineage leading to crown arthropods. The taxonomically scattered occurrence in Cambrian arthropods of species with a variable number of specialized appendages does not support such a claim (Boxshall, 2004).

The next point to be disputed is whether the "real" arthropod appendage, i.e., one articulated into segments, derives from an unarticulated limb, such as the lobopods of the onychophorans. To put it in more explicit terms, the question is whether in the arthropod stem lineage there existed animals with an arthropodan (segmented and strongly cuticularized) trunk, but with pre-arthropodan (unsegmented and basically soft) appendages.

As has been repeatedly remarked (Minelli, '96, 2000, 2003a), across all the metazoans there seems to be a widespread correspondence between the organization of the appendages and the organization of the main body axis of the same animal. This led Minelli (2000) to interpret metazoan appendages (secondary axes) as axial paramorphs of the main body axis, i.e., as the product of a duplicate expression of genes already involved in growth and patterning of the main axis. In the light of the paramorphism hypothesis, the ability to produce

periodically arranged structures along the main axis was exploited to produce segmentation in the appendages.

In this perspective of paramorphic relationships between a main body axis already segmented and patterned in antero-posterior sequence and its serial appendages, which to some extent are therefore already diverse and themselves segmented since their very first expression, it becomes sensible to rephrase the old and still hotly debated question about the mutual relationship between the antenna and the conventional (locomotory) leg of the arthropod. The question is whether the antenna must be regarded as a specialized leg, or vice versa. In other words, whether the antenna, or the leg, is closer to the ancestral condition of the first arthropod appendages; that is, as it is now more fashionable to say, the question turns around the identity of the default state of the arthropod appendage. The balance between the two basic alternatives (antenna first, or leg first) has repeatedly shifted during the last few years, in the light of newer developmental genetic evidence. For example, Dong et al. (2001) favoured the “antenna first” hypothesis, whereas Casares and Mann ('98) supported the “leg first” hypothesis. In a later paper, however, the same authors have adopted a less clear-cut option, according to which the default appendage of arthropods would be somehow intermediate between a leg and an antenna, and would be articulated into a proximal segment and a distal tarsus (Casares and Mann, 2001). Relevant gene expression data in tardigrades and onychophorans would be critically important. However, the point is that, once we assume the paramorphic development of arthropod appendages from an ancestor with extensive patterning along the main body axis, the whole question of the primacy of the leg vs. the antenna would become meaningless. In other terms, a “default appendage” would have never existed (Minelli, 2003b and references therein).

### HIERARCHY OF EVOLUTIONARY NOVELTIES?

Having determined that in the study of evolutionary novelties it is necessary to disentangle the more or less complex network of conserved and truly novel features, let us now look for the level, or levels, at which we may find the causal changes from which the novelties actually derive.

A traditional view asks one to distinguish between the novelties derived from the evolution

of new cell properties, and those derived from new body patterning: “Evolutionary novelties on the cellular level tend to differ quite drastically, in several respects, from structural novelties. First of all, the genetic basis is usually simpler—indeed, a single gene mutation may be the primary basis of the novelty. Second, the new function may not require any reconstruction of the ‘type’” (Mayr, '60: p 353). This distinction would map well onto Müller's ('90) distinction of two categories of evolutionary novelties: the generation of entire new body plans, apparently requiring new ways to control the overall body pattern, and the evolution of lesser novelties from restructuring and transformation of existing body plans, which might be generated from simple “local” changes in cell properties. However, the question is: is there a really firm divide between the two categories?

Developmental genetics seems to deny any significant divide, to the point that Davidson, in his authoritative and well-argued book on *Genomic Regulatory Systems* felt confident to write: “For anyone interested in mechanism, there is [...] no other way to conceive the basis of evolutionary change in bilaterian form than by change in the underlying developmental gene regulatory networks” (Davidson, 2001: p 201). An even more extreme reductionist view would argue that a novelty is simply a new allele, or a new allele combination in a new genotype, which, through a cascade of causal processes, first at the genetic and later at the developmental level, causes a change in an ontogenetic trajectory or, more precisely, in a given genotype's reaction norm. Therefore, from a reductionist's perspective, all novelties emerge at the same level: the level of the gene. The only possible qualifications, if any, would refer to the genetic novelty's specific influence either in shaping the phenotype, or in modifying physiology or behaviour.

However, the apparent truism of this simplistic view should be reshuffled in the light of the observation: “There are no known genes that individually encode a large amount of information specifying the structure or patterns of an organism” (Britten, 2003: p 75). This means that even when developmental or morphological novelties can be correlated with specific mutations, the only major effects for which we can strictly credit a mutation are those of a negative, e.g., loss of organs, rather than a positive nature.

The problem is that there is no correlation between the level of biological organization at which the novelty is most conspicuous (cellular/



local vs. structural/systemic) and the magnitude of the phenotypic effect. Revolutionary changes in the developmental system may bring about trifling changes in adult phenotypes. This is the case of some parasitic polyembryonic wasps, where the whole machinery of the first phases of embryogenesis have been completely transformed, but this is not mirrored by novel adult morphologies (Grbić et al., '96).

On the other hand, important structural novelties can emerge quite abruptly, caused by simple changes at the level of cell properties. This may happen, for instance, when cell sorting is involved, as a consequence of differential adhesion properties of neighbouring cell populations. A substantial body of experimentation (summarized in Steinberg, 2003) demonstrates that no molecular specificity, i.e., no self-recognition code, is required to ensure cell sorting from a mixed-cell assemblage. Simple differences in the number of cell-adhesion molecules expressed on the cell surface are potentially sufficient to the job. It would certainly be rewarding to explore from this perspective the origin and evolution of coeloms and other body cavities. These cavities rank among the key features of the corresponding animal groups, not so much for the large (and disputed) phylogenetic signal with which they have been generally credited, as for the functional importance they have for the animals that possess them. What has been observed in the artificially produced mixed aggregates is probably mirrored by all those developmental events in which compartmentalization is observed (Dahmann and Basler, '99). We may even suggest that compartmentalization, a kind of local cell-lineage restriction due to the immiscibility of neighbouring cell populations, can be regarded as a developmentally favourable exaptation deriving from a much more generally widespread behaviour of basic cell biology. By definition, an exaptation comes from the new use of an already existing trait, another way in which novelty and conservation can be combined.

## CONCLUSIONS

Since the time of Jacob's famous metaphor: "Evolution behaves like a tinkerer" (Jacob, '77: p 1164), almost thirty years of advances in biology have shown how deep into the constitution of genetic and developmental systems this tinkering can go. The remoulding of pre-existent features, genetic networks, or developmental trajectories,

can occur at any level of organization within the living being. Moreover, this remoulding can overcome structural and functional boundaries between subsystems—of any kind—within an organism, by exploiting the pattern and processes of one system to the use of other systems. No matter how sophisticated the modes of change prove to be, evolution nevertheless is always a matter of tinkering. Evolutionary change does not follow our preconceived schemes for the construction of animal form in development and its variation in evolution. In the same way as two phylogenetically independent structures in two organisms can exploit the same genetic toolbox at some level, or the same physical properties of living matter in producing new variants, any possible change in an available ontogenetic pathway has the potential to generate novelties.

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