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NOVELTY IN EVOLUTION: RESTRUCTURING THE CONCEPT

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INTRODUCTION

> "In the frequent fits of anger to which the males especially are subject, the efforts of their inner feelings cause the fluids to flow more strongly towards that part of their head; in some there is hence deposited a secretion of horny matter, and in others of bony matter mixed with horny matter, which gives rise to solid protuberances: thus we have the origin of horns and antlers.

This statement by Jean Lamarck (41, p. 122) not only documents how the novelty problem arose immediately with the formulation of scientific theories about the evolution of life, it also exemplifies the early attempt to identify a mechanistic cause for the origin of new organs. It is of little importance that Lamarck failed to identify the mechanism correctly. Later, Darwin (20) also "felt much difficulty in understanding the origin of simple parts" (p. 194) which he thought could have "originated from quite secondary causes, independently of natural selection" (p. 196), and he had recourse to Lamarckian explanations to deal with the problem.

Consequently, the difficulty of how new characters could arise from a process of gradual variation and selection was at the center of the early critique of Darwin's theory (36, 62, 68, 83). At that time, novelty was treated both by its critics and by its advocates (e.g. 108), as a distinct problem of

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organismic evolution. The rise of genetics again refuelled the debate and favored mutationist explanations for the origin of innovations (29, 89). Subsequently, however, with the broad acceptance of the neo-Darwinian synthesis, the issue of novelty became diffused in discussions of the origin of adaptations (31, 90) and in the concept of macroevolution (37, 93, and others). Novelties were seen increasingly as an aspect of the problem of speciation and of the origin of higher taxa and less as a problem of the primary causes responsible for the generation of new anatomical structures. Only Mayr (57, 58) identified novelty again as a distinct and neglected problem of evolutionary biology, but the prevalence of the adaptationist program, characteristic for the past decades of evolutionary research, largely prevented its further analysis.

Spurred by a recent trend toward organismic approaches in evolutionary biology, the issue of novelty has again come to the fore. Several recent publications and meetings were devoted to the problems of innovation (70, 107). The present understanding of novelty, however, is characterized by remarkable heterogeneity. The issue is linked on one hand to the character discussion in taxonomy and on the other hand to the Lamarkism-mutationism, microevolution-macroevolution, and gradualism-punctualism debates. These historical polarities in effect obscure the real problem. Therefore, the primary objective of this chapter is to liberate the novelty issue from its historical burden and to provide a new conceptual foundation for its analysis. After a brief review of traditional concepts and their deficiencies we proceed to analyze the empirical evidence for novelties at the character level. Based on this analysis we redefine the problem and investigate the possible generative mechanisms underlying the origin of new morphological structures. Particular emphasis is placed on the distinction between the generation of new characters and their fixation, which may eventually lead to the formation of novel body plans. In conclusion, we propose that an empirical approach to the problem of novelty has to focus on the organizational principles of developmental systems and their ability to generate new structures.

CONCEPTS OF MORPHOLOGICAL NOVELTY

We restrict our analysis here to the origin of new structures in morphological evolution. Even when limited to the morphological level, very different attitudes are taken toward the problem in current evolutionary biology. The prevailing one is a purely phenomenological treatment of novelty. This is embodied in the discussions of the rates of origination of novel characters (15, 93, 96), their significance as taxonomic characters (111), or their role as key triggers of diversification and adaptive radiation (46, 51). While important for each of these chapters of evolutionary theory, the phenomenological aspect of

novelty is not the central problem and is not dealt with in our further discussion. We concentrate on the generative aspect of morphological innovations in the process of evolution. Although this aspect has figured less prominently in past discussions, it is possible to distinguish three conceptual approaches.

Functional Concepts

That a change of function may initiate the generation of new structures was already expressed by Darwin (20), and the concept was elaborated by Dohrn (23), Plate (73), Sewertzoff (91), and Mayr (57, 58). The basic idea is that environmental and behavioral changes induce the acquisition of new functions which in turn favor the selection of small variations that facilitate the exertion of the new function. This concept is based on a "duplication of function" and "duplication of structure" principle. As noted by Mayr (57), either the organ under question must initially be able to perform two distinct functions simultaneously, or two distinct organs must perform the same function over a transitional period. The classic example for the latter is the coexistence of gills and primitive lungs in the evolution of respiratory organs. Many such duplications of function are known and make a strong case for the change of function concept. Accordingly, Mayr (57, p. 351) defines novelty as "any newly acquired structure or property that permits the assumption of a new function."

Several problems arise both from a functional definition of novelties and from the mechanism proposed for their origination. Mainly when combined with the change of function principle, the definition harbors a danger of circularity. New structures arise from new functions, and new functions from new structures. Thus, it does not seem useful to restrict the definition only to those structures that permit a new function. Such a definition also excludes all those structures that might originate without association to a new function, e.g. exaptations (30).

More importantly, the change of function concept bypasses the generative problem. While the coexistence of old and new functions, as well as that of ancestral and new structures, represents an important principle of functional and morphological transition, it does not explain the first appearance of a new structure. Gills and lungs must coexist for a transitional period to permit the takeover of a new mode of respiration, but what mechanisms generated the lungs, or even the gills? The change of function principle is helpful only in so far as it indicates that a new structure must always arise in a different functional context than the one which eventually represents its adaptive advantage. But what we need to know is, what creates the heritable variation at the site where it is required? And what precisely are the mechanistic causes that are responsible for a specific morphological solution to a new functional

and/or structural problem. And finally, if we accept that new functions are initiating factors for the generation of new structures, is this a necessary prerequisite or can new structures also arise without a change of function?

Genetic Concepts

Although natural selection may act on any kind of heritable phenotypic variation, irrespective of the cause of heritability (59), the majority of evolutionarily important phenotypic variation is ultimately linked to genetic variation and becomes finally established in a population by selection, drift, or genetic drive. Consequently, genetic concepts concerning the origin of morphological novelties have two aspects: first, the kind of genetic change that makes the phenotypic variation heritable, and, second, the population genetic mechanisms that lead to the fixation of these genetic variants.

THE KIND OF GENETIC CHANGE A recent critical review of the molecular concepts concerning the origin of morphological novelties was provided by John & Miklos (38) under the title "The Unsolved Problem." Below we briefly discuss their major conclusions. A number of specific molecular mechanisms have been proposed to explain the origin of novelties, including structural gene mutations, changes in genome size, chromosomal rearrangements, and regulatory mutations caused by diffusion of repeated sequences (9, 16, 24, 25, 54). However, the main problem is that no conclusive evidence is available to demonstrate a specific role of any of these molecular mechanisms in the origin of morphological novelties. There are at least two reasons for this situation, one biological, the other methodological.

The biological reason is that metazoan development is realized via the interaction between cells that communicate by utilizing their gene products. This self-referential structure of metazoan development (72) makes impossible a clear distinction between regulatory and structural genes (16, 74). Possibly the best example is found in the role of the extracellular matrix. Hyaluronic acid, laminin, and fibronectin, all products of structural genes or of secondary metabolism, play an important role in regulating the migration of neural crest cells and thus have a regulatory role in vertebrate development (34). Therefore, it is not sensible to expect genetic changes, responsible for the heritability of a novel morphological feature, to be of a particular molecular type. This means: Certain specific structural gene mutations are as plausible candidates for the genetic basis of a novelty as are changes in gene regulation networks or chromosomal rearrangements.

The methodological problem is critical for all problems of evolutionary genetics, namely, the question of how to distinguish between those genetic changes that are causative in the origin of novelties and those that merely coincide with the observed change. The short answer to this question given by

John & Miklos (38) is negative: "We won't know for certainty"—but this is true for all empirical sciences. On the positive side, their discussion clearly indicates that the way out is to study the role of gene products in development, i.e. to determine the biological role of observed genetic differences in the developmental mechanisms responsible for the realization of morphological differences.

POPULATION GENETIC PROBLEMS Once a heritable phenotypic change has been achieved by a mutation, it has to be integrated into the gene pool of the species. Two problems arise in this area: (*a*) If one assumes, as the neo-Darwinian orthodoxy does, that major changes are realized by the accumulation of many mutational steps with individually small effects, one is confronted with the problem of whether natural selection can deal with such a multitude of pleiotropically and functionally interrelated changes. (*b*) If one believes that new adaptations are initiated by a major genetic mutation (or threshold effect), then one has to deal with the question of how such drastic changes can be accommodated in a genetic background unprepared to compensate for unavoidable and possibly deleterious pleiotropic effects.

The general conclusion is that natural selection is easily able to produce phenotypic changes much faster than has been observed in the fossil record (16, 42). This has also been confirmed by recent studies on the evolution of functionally constrained phenotypes (i.e. the interaction of directional and stabilizing selection on two or more characters), although adaptation by natural selection does not appear as inevitable as in simpler models of selection (12, 101, 103). These studies are based on the assumption of additive genetic effects. In the case of strong epistatic effects, it is generally concluded that a combination of drift and selection (shifting balance) is sufficient to explain new adaptations (6, 17, 19, 45, 114).

Several concepts are available to explain the integration of discontinuous variation into the gene pool. One is the concomitant selection of modifier genes that can compensate for the deleterious pleiotropic effects of a discontinuous variation (44)—this selection works fine under certain conditions. The other concepts are less orthodox. According to West-Eberhard (109), the integration of a discontinuous variant has to pass through a stage in which a stable polymorphism exists with the original condition. This would allow coadaptive fine-tuning of a new structure while a working alternative is maintained. Erwin & Valentine (25) have suggested that horizontal gene transfer may increase the frequency of a new variant to a level where homozygous genotypes become available for selection in spite of a selective disadvantage of the heterozygous genotypes. Arthur (3) has suggested a magnitude effect of phenotypic change, where large changes are viable with a higher probability than changes with intermediate effects. Finally, molecular

drive may be an alternative mechanism to natural selection to explain the first steps in the integration of a novelty into the gene pool (24).

In summary, the origination and fixation of a new genetic variant can be achieved via a multitude of mechanisms and does not appear to be an unresolved question with respect to the origin of morphological novelties.

Developmental Concepts

The currently most popular concept of how development relates to evolution is *heterochrony*—phylogenetic changes in the timing and rates of ontogenetic processes. Heterochrony has particularly been associated with the origination of structural novelty in a number of recent publications (2, 64, 75, 106). Earlier, De Beer (21) paid detailed attention to the ways in which changes of developmental timing can affect the appearance of embryonic structures and the introduction of novel characters, and recent studies demonstrate the pervasiveness of heterochronic alterations in the phylogeny of a large variety of taxa (61). We may safely assume that heterochrony is a fact in evolutionary biology, but not all heterochrony observed is necessarily causal in morphological evolution. Much of it could be a consequence of alterations that do not primarily affect the timing of developmental processes. Including these passive effects would rob the concept of heterochrony of its explanatory value (76). Therefore, ways must be found to distinguish between causal and secondary heterochrony. Also, the occurrence of heterochrony is rarely distinguished from the mechanistic processes through which changes of timing could generate new structures. This however is the central problem if a generative role is to be assigned to heterochrony.

In several instances heterochrony could be related to specific processes of development and to the appearance of novel morphological features. Raff et al (75, 76) and Wray & Raff (113) were able to relate the evolution of direct development in sea urchins, which involves the appearance of several novel larval features, to heterochronic events in early development. Changes in the timing of cell lineage segregation in blastomeres of the direct developing embryos lead to novel forms of nonfeeding larvae, in which some of the features of the primitive pluteus larva are eliminated and other features make a very early appearance. These and other derived features of direct developers such as changes in cleavage pattern and mitotic rates are dependent on the heterochronic changes in developmental mode and not on adaptations in the traditional sense.

The sea urchin example shows that heterochrony can lead to the production of novel features through alterations in the timing of very early ontogenetic processes. But heterochrony is not confined to early ontogeny, and empirical evidence suggests that heterochronic alterations of the processes of pattern formation and morphogenesis are also causal in the generation of novelty. For

instance, truncations of skeletal patterning processes, at the level both of chondrogenesis and of osteogenesis, underlie the transformations of skeletal patterns in vertebrate limb evolution. Nonsegmentations of mesenchymal arrays and secondary fusions of chondrogenic condensations, occurring at advanced stages of the embryonic period, result in the generation of novel skeletal elements (65).

Although such examples document the possibility of novelties being introduced through heterochrony at all stages of ontogeny, and although the specific processes affected by heterochronic alterations can sometimes be identified, as yet few concepts suggest why paedomorphic or peramorphic changes to developmental processes should result in new structural characters. Two kinds of solutions were recently proposed.

In a study based on an evolutionary analysis of visual-neuronal control, functional morphology, and development of the feeding system in plethodontid salamanders, Wake & Roth (106) suggest that novelties are generated through ontogenetic repatterning. Ontogenetic repatterning refers to the establishment of new sets of morphogenetic processes through dissociation and recombination of compartmentalized subsets of the developmental system. Heterochrony is seen as the process initiating the dissociation and recombination events, thus being ultimately responsible for the foundation of new patterns of developmental interaction that give rise to new morphological arrangements of the phenotype.

Another approach is based on the system properties of development (64). According to this concept, heterochronic and nonheterochronic mechanisms of evolution have a quantitatively modifying effect on developmental parameters, but the magnitude of these modifications is limited by system-specific thresholds. Modifications that go beyond such thresholds can cause nonlinear effects, e.g. by interrupting developmental interactions or by initiating new ones. The kind of resulting morphological effect depends on the developmental reaction norms of the affected cell populations and tissues. Initially inconspicuous structures arising from such a process may first assume an embryonic function and become fixated in the developmental network. In a possibly much later step such "caenogenetic" structures can be moved heterochronically into the postembryonic period and can be further elaborated. The threshold origin and the embryonic preexistence of novel structures is thought to underlie their often rapid phenotypic appearance in a phylogenetic lineage. According to this hypothesis, the first rudiments of morphological novelties appear as neutral by-products of evolutionary alterations to developmental processes. The causality for their appearance is thus proposed to lie in the system properties of development, which can transform gradual and quantitative evolution into qualitative phenotypic effects.

An approach that differs greatly from the two previous ones was taken by

Buss (14) who considered the origin of novelties as resulting from conflicts between levels of selection. Each multicellular organism is composed of units capable of self-replication. The primary evolutionary function of developmental interactions is to solve this conflict between levels of selection. Major developmental innovations are thus expected at those points where a transition between levels of selection occurs. But the fact that new organs and new anatomical elements can originate in the phylogeny of well-established multicellular organisms (e.g. vertebrates) indicates that this cannot be the only mode for the origin of morphological novelties.

In summary, although a number of attempts were made to conceptualize the contributions of developmental systems to the origin of novelties, the developmental concepts are the least elaborated. They also have a common weakness, which is their formulation rather independently from population genetics.

APOMORPHIES VERSUS NOVELTIES

We intend here to set the stage for a reformulation of the problem of novelties. The point of departure will be the least theory-laden definition of a novelty available in the literature. The definition consists simply of the statement that all traits characteristic of a supraspecific taxon were a novelty at some point in the evolution of that group (18, 27).

To obtain an objective picture of the kinds of characters that have been identified as apomorphies of supraspecific taxa, we listed the morphological apomorphies of the higher taxa of mammals (Table 1). The table is based on a recent summary of mammalian characters, used to illustrate the cladistic approach (4). From the list of characters in Table 1, it becomes immediately clear that this set of apomorphies comprises a number of traits whose origin is quite unproblematic and easy to explain on the basis of known evolutionary mechanisms. For instance, a number of characters are negative traits, i.e. the absence of certain structures is characteristic for a clade. Negative characters are legitimate apomorphies in cladistic analyses (4). Among these are the reduction of the nucleus in the erythrocytes (Mammalia), the loss of teeth (Monotremata), the reduction of the coracoid bone (Theria), and the reduction of the marsupial bone in the Placentalia. Although there is no conclusive evidence concerning the causes of reductive evolution, little doubt exists that it can be explained by Darwinian mechanisms because the genetic basis of reduction is largely additively polygenic (112).

Another class of apomorphies that are quite unproblematic are shape characters. For instance, a bent cochlea is apomorphic for the class of Mammalia, but these characters are rare among those characteristic of higher taxa. The great majority of apomorphies is less easily classified with respect

to the kind of processes underlying their origin. A tentative but by no means exhaustive classification would include (*a*) characters that result from differentiations of repeated elements, (*b*) new elements, (*c*) change of context, and (*d*) differentiations caused by the synorganization of plesiomorph traits. Others are hard to classify, such as the differentiation of trophoblast and embryoblast (Placentalia), or the appearance of prismatic enamel (Theria). To determine whether there are specific difficulties in explaining the remaining novelties, some examples are discussed in detail below.

Differentiation of Repeated Elements

A key innovation of mammals with profound functional and adaptive consequences is the differentiation of the teeth. The plesiomorph status is homodont conical teeth that all look basically the same. Tooth differentiation allows the use of a broader spectrum of prey and is considered as one factor responsible for the tremendous success of mammals (39). From a morphological point of view the origin of heterodont teeth is a differentiation of serially homologous elements. Other characters of that kind are the differentiation of the cervical vertebrae (Mammalia) and the origin of whiskers, which are apomorphic for the taxon Theria. Differentiation must be considered to be a major mode of morphological evolution (54, 79, 80).

The explanation of these characters appears similar to simple shape changes, especially when the result is of such obvious adaptive value as are heterodont teeth or whiskers. Adaptively sensible shape changes should be easy to explain given the extensive amount of heritable phenotypic variation available for almost every quantitative character (16, 63). However, the differentiation of homonomous (iteratively homologous) elements is not as easily explainable. Repeated anatomical elements are most probably due to the repeated expression of the same genetic instructions (80, 84, 99). There is no reason to expect that two hairs from the head or two erythrocytes from the blood are due to the activity of different sets of genes.

If the development of repeated elements is only controlled by identical sets of genes, their genetic variation will be highly, if not perfectly, correlated. However, it has been shown that correlation caused by early developmental events can be repatterned during later developmental stages (115). To what extent repeated elements are genetically correlated in species belonging to a taxon that is ancestral to a species with differentiated homonomous structures is an empirical issue. Of relevance would be measurements of genetic and phenotypic correlations of corresponding elements from the left and the right side of the body, of segmentally repeated but undifferentiated structures such as fish vertebrae, or any other class of repeated elements, such as scales and fin rays of fishes.

The available evidence is equivocal. In a study of genetic correlations

Table 1 Apomorphic characters of the major mammalian taxa classifies according to the evolutionary transformation underlying their origin.[a]

Type of change	Apomorph character	Plesiomorph character	Taxon
Loss of elements	Erythrocytes without nucleus	Erythrocytes with nucleus	Mammalia
	Teeth absent	Teeth present	Monotremata
	Coracoid absent	Coracoid present	Theria
	No oil droplets in retinal cones	Oil droplets in retinal cones	Placentalia
	Marsupial bones absent	Marsupial bones present	Placentalia
Change of shape	Lateral temporal skull opening	No lateral temporal skull opening	Mammalia
	Cochlea bent	Cochlea straight	Mammalia
	Cochlea coiled	Cochlea not coiled	Theria
	Penis simple	Penis forked	Placentalia
Differentiation of repeated elements	Teeth heterodont	Teeth homodont	Mammalia
	Qualitative differentiation of cervical and thoracic vertebrae	Only gradual difference between cervical and thoracic vertebrae	Mammalia
	Some hairs specialized as whiskers	No whiskers	Theria

New elements	Marsupial bones	—	Mammalia
	Hair	—	Mammalia
	Muscular diaphragm	—	Mammalia
	Lips and facial musculature	—	Mammalia
	Glans penis	—	Mammalia
	Thigh glands	—	Monotremata
	Pseudo vagina	—	Marsupialia
	Corpus callosum	—	Placentalia
Change of context	Centrum of first vertebra fused to second	Centrum of first vertebra a part of first vertebra	Mammalia
	Secondary jaw joint	Primary jaw joint	Mammalia
	Angular (tympanic) fused to temporale	Angular part of lower jaw	Mammalia
	Yolk sack attached to uterus (placenta)	Yolk sack not attached to maternal body	Theria
	Separate opening of gut and urogenital sinus	Common opening of gut and urogenital sinus	Theria
	Scapular origin of supracoracoid muscle	Coracoidal origin of supracoracoid muscle	Placentalia
Combination of plesiomorph elements	Secondary palate	Separate maxillary processes and palatines	Mammalia
	Nipples	Dispersed external orifices of milk glands	Theria

[a] The list of characters is based on Ax (4). Several characters could not be classified, especially the physiological ones, such as homeothermy, sucking movements, vivipary, and the type of tooth replacement. Further, the histological type of enamel, the sweat glands, the phalangeal formula, the yolk content of the egg, and the location of the embryoblast relative to the trophoblast were not taken into account.

between bilaterally represented nonmetric cranial traits of rhesus macaques, McGrath et al (60) found high correlations between left and right characters and no significant heritability of directed asymmetry in 11 out of 13 traits. Phenotypic correlations between osteometric traits from fore- and hindlimbs of *Myotis sodalis* are higher among corresponding (homologous) structures within and between limbs, while the overall correlations were rather low (5). Repeated elements were also measured in fossil specimens of the teleost *Knightia* (length of centra of four vertebrae and three neural spines). The average pooled nonparametric correlation of these characters is 0.921 (centra) and 0.903 (neural spines), while the overall average correlation was 0.876 (calculated from data in Olson & Miller; 71). However, there are also less convincing results, e.g. about antennal segments of alate *Pemphigus populitransversus* (82, 95). Hence, some evidence suggests that repeated elements are strongly correlated, but the data are far from conclusive. This question will have to be examined with especially designed experiments, comparing species that have undifferentiated repeated traits with species in which differentiations of these traits have occurred.

If we assume that repeated characters are most probably highly correlated genetically, it becomes more difficult to explain the origin of new characters by differentiation of repeated elements. Technically speaking, the problem is that differentiation of repeated elements is a multivariate process, for which the univariate measures of heritability are inadequate to predict the evolutionary potential. Even if the heritability of each trait were positive, differentiation would be difficult as long as the characters are highly correlated genetically. This was shown by Maynard Smith & Sondhi (56) who demonstrated that it is impossible to select for directional asymmetry in laboratory strains of *Drosophila melanogaster*. All that selection led to was an increase in the level of fluctuating asymmetry; no stable difference between left and right could be achieved. Whether this result is representative of repeated elements in general needs to be tested with other characters, such as snake vertebrae or teleost fin rays.

An interesting fact is that the directional asymmetry of the internal organs in mammals can be converted into fluctuating asymmetry by a single autosomal recessive mutation in mice (47). This shows that specific mechanisms are necessary to realize directional asymmetry in addition to the genetic information required for the development of the traits themselves. The developmental mechanisms are unknown, but see Brown & Wolpert (10) for a recent hypothesis. It is at least not self-evident that there is always ample genetic variation, allowing selection to differentiate repeated elements. To what extent genetic variation is available in natural populations for independent heritable variation of homonomous traits needs to be examined.

New Elements

Often apomorphic characters are anatomical structures that have no predecessors as repeated elements in the plesiomorphic state. Examples are the corpus callosum of the placental mammals, the so-called marsupial bone of the mammals (which became reduced in the Placentalia), and glands, such as sweat glands and sebacous glands (Mammalia). At lower taxonomic levels examples are equally frequent. They include, to name a few, the famous thumb of the giant panda or the horns and antlers found among artiodactyl placentals. Again, these characters are of obvious functional and adaptive significance, but the main problem is whether one can expect significant amounts of heritable phenotypic variation for these characters in the ancestral lineage. For two characters, namely, the corpus callosum and new bony elements, extensive developmental data are available and are discussed below.

The corpus callosum is a massive fiber tract that connects the two telencephalic hemispheres of placental mammals. It is autapomorphic for the taxon Placentalia. In subplacental mammals, the telencephalic hemispheres are connected only via the anterior commissure. This commissure is also present in placental mammals, but the majority of cortical areas are connected via callosal connections (87). Embryologically, the corpus callosum is not derived from the rudiment of the anterior commissure (crossing the medial plane via the lamina terminalis) but is a new structure that bridges the interhemispheric fissure (77). The first cellular elements that bridge the gap between the hemispheres are a specific population of glial cells, called glial sling (92). If these glial cells are experimentally destroyed, the majority of callosal fibers fail to reach the contralateral side, and they never compensate by entering the anterior commissure (49, 50). Acallosal states are also known as congeneric malformations in humans and mice (28, 92). The independent embryological origin, its dependency on a specific set of radial glial cells, and the lack of regulation of the anterior commissure in acallosal brains speak for the fact that the corpus callosum is a true novelty and not simply a part of the anterior commissure.

The development of the corpus callosum passes through a critical stage, a kind of epigenetic needle's eye, where a certain population of glial cells must be present after the septal regions of the telencephalic hemispheres become fused (92). The glial sling is not known from marsupials and acallosal strains of mice. It is not reasonable to assume great amounts of heritable variation for the presence or absence of fibers that cross the interhemispheric fissure in species ancestral to the placentalia. Of course, at some time in the phylogeny of the placentals such a population must have existed, but it is not evident that the presence of the glial sling is within the range of variation typical for subplacental mammals. Some special but unknown conditions must have been

attained in the placental lineage that allowed the expression of these characters.

A similar needle's eye situation has to be realized in the ontogeny of new bony elements. These conditions are best known from the fibular crest that appears in the archosaur lineage and are discussed later in this paper.

Other Nontrivial Novelties

Much less is known about the genetics and development of other characters that originate from a change of context (such as the separation of the angulare from the dentals and its fusion with the temporale in mammals), or from the synorganization of elements already present in the plesiomorph state. Few structures listed by Ax (4) are combinations of plesiomorphic characters, but such characters can be found in all higher taxa. For instance, multicellular epidermal mucous glands are rare in teleosts. In fish, mucus is usually produced by singular mucous cells. The multicellular glands seen in ripe male blennies are composed of goblet cells (40), a cell type usually found dispersed within the epidermis of fish (110). It would be highly interesting to know more about the developmental conditions necessary to realize these traits.

Common Features of Nontrivial Novelties

Differentiation of repeated elements and new elements such as new bones or new fiber tracts are certainly innovations with profound adaptive value. Hence, there is every reason to think that the fixation of these characters in the population was due to natural selection. This, however, does not solve the problem completely. In all these cases the main problem is to explain why and how heritable phenotypic variation for that character became available in the first place. Independent genetic variation of repeated elements is not always present and the critical embryological features necessary for the development of the corpus callosum are absent in primarily acallosal mammals.

Common to nontrivial novelties is their origin in spite of strong developmental constraints against their realization in the ancestral taxon. Developmental constraint on natural variation is a prevailing feature in morphological evolution (1, 55), but shifts of developmental constraints are quite common (81). For instance, in each salamander species the majority of carpal variants are due to one or two fusions between neighboring elements. But which of the fusions prevails is more or less genus specific. For instance, the fusion between the distal carpal 4 and 3 is a common variant in *Bolitoglossa* species and is even a fixed trait in at least two *Bolitoglossa* species (105), but it is completely unknown in natural populations of *Plethodon cinereus* from Maine and Virginia, and is very rare in the highly polymorphic Nova Scotian population (35). The ultimate causes of these apparent shifts of constraints are unknown.

Nontrivial novelties appear to become realized in spite of developmental constraints in the ancestral lineage. If one is willing to accept this premise, one must conclude that an adequate explanation of the origin of anatomical novelties has to account for the fact that these constraints were overcome at some stage of the phylogeny of the group.

A REFORMULATION OF THE NOVELTY PROBLEM

In this section we discuss a definition of morphological novelty that meets two objectives: (*a*) the definition is not based on assumptions about the mechanistic bases of novelties, since we are not in the position to provide an empirically justified and general explanation as yet; (*b*) the definition has to be specific enough to highlight the important unsolved biological problems.

If we consider the table of apomorphies discussed in the last section, one realizes that some of the apomorphies can hardly qualify as novelties. For instance, negative characters that result from the loss of certain elements cannot be considered as novelties. The same is true of size and shape characters. On the other hand, it is quite obvious that new elements, like the corpus callosum, or new bones and cartilages, are proper novelties. But there are other phenotypic variations that are difficult to classify as novelties or nonnovelties. This is the case with variation in the number of repeated elements, such as bristle number of an insect, or the number of vertebrae and fin rays. If a species has two more pectoral fin rays than the parental species, the two additional rays are something new. But do we want to call these additions novelties? In a certain sense they are, but one may also consider this meristic change as a case of quantitative variation (i.e. more of the same). What is then the difference between the additional digit of the panda and an additional bristle of a drosophila? The following definition is an attempt to avoid this dilemma.

DEFINITION *A morphological novelty is a structure that is neither homologous to any structure in the ancestral species nor homonomous to any other structure of the same organism.* This definition is less restrictive than previous ones (57, 64). In accordance with our considerations above, it excludes simple quantitative variation or negative traits. In addition, it allows a distinction between meristic variation, e.g. additional bristles or fin rays, and novelties like the marsupial bone or the panda's thumb. Additional bristles are both homologous to the bristles already present in the source population and homonomous to all other bristles on the same fly. But there is nothing that can be meaningfully identified in reptiles with the marsupial bone or in subplacental mammals with the corpus callosum.

The situation is more subtle with regard to other kinds of apomorphies classified in Table 1, e.g. the differentiation of repeated elements. Molar teeth are both homologous to the conodont teeth of reptiles and homonomous to the other tooth types of mammals. However, in these cases the hierarchical nature of homology (80) must be taken into account. The molars are homologous to conodont teeth of reptiles, but nevertheless, reptiles do not possess teeth that can be identified as molars. Hence, a "molar tooth" in mammals is a new anatomical entity that originated from the differentiation of preexisting repeated elements and thus counts as proper novelty.

The same argument holds for new structures that are composed of elements already present in the ancestral lineage. For instance, the main body parts (tagmata) of insects (head—thorax—abdomen) consist of segments already present in the annelid-like or myriapod-like ancestors of insects (94). But tagmata are units that result from the synorganization of several segments and cannot be identified with any body part of an annelid or a myriapod (102).

More problematic is the last category of apomorphies, those that result from a change of context. One may argue that the fusion of the centrum of the first cervical vertebra with the second cervical vertebra leads to an anatomical element that is a new unit of the phenotype, comparable to the case of multisegmental body parts. On the other hand, the fusion of the angular (tympanic) with the temporale does not change the character of the latter, since the angular simply becomes integrated into the preexisting unit. Without further information, these cases must be accepted as gray areas in the range of application of the above definition, but the difficulties point to interesting biological problems.

Although the definition helps to clarify the terminological question of what one may want to call a proper novelty and what is just a modification of the given design, it also leads to conceptual costs because of the reference to homology. The biological basis of homology is still a matter of debate and unfortunately of little positive evidence (85, 99, 104). But it is not necessary to wait for a solution to the homology problem. It is sufficient to rely on the accepted methods to establish homology between body parts on the basis of structural and developmental similarity (78, 80). Note that the homology concept used in this definition is more restrictive than the one used in systematics. In systematics, any discernable structural difference may be homologized. In evolutionary biology it is more useful to restrict the homology concept to anatomical units (104). This excludes merely quantitative variation, changes of proportion, and topological relationships among body parts.

To identify the relevant research questions, it is useful to recall that the set of characters described as novelties is, according to the above definition, the same as those apomorphies that became realized in spite of apparent developmental constraints in the ancestral lineage. In the light of this con-

cordance, the most obvious questions in relation to the study of morphological novelties are the following:

1. What is the generative potential of the developmental mechanisms in the members of the ancestral taxon? Only in rare cases does the ancestral species still exist, but the conservatism of developmental mechanisms justifies the comparative analysis of species that are members of the same supraspecific taxon as the supposed ancestral species. Hence, it is appropriate to examine crocodilian development to learn about the generative potential of the ancestral bird lineage, or to study salamander development of the genus *Plethodon* to understand the preconditions for the evolution of more derived plethodontid taxa.

2. What are the critical changes in generative mechanisms of development that allowed the realization of the derived feature, i.e. the novelty? This can be achieved by comparative experimental studies of derived and ancestral ontogenies (66).

3. Which genetic changes were the reason for the heritability of morphological novelties? This is essentially the same question as raised by John & Miklos (38), but with an important methodological difference. We propose that we first need to understand the biological context in which the genes play a role, before a sensible distinction can be attempted between causally relevant genetic changes and genetic changes that simply happened to occur at the same stage of phylogeny, but that were not causative in the transformation to be explained. The least understood context of genetic change, but obviously the most relevant, is that of its developmental expression.

GENERATIVE MODES FOR THE ORIGIN OF MORPHOLOGICAL NOVELTY

Given that the emphasis of the open questions lies on developmental biology, we propose that the study of the developmental modes associated with the appearance of new characters is the critical step for further elucidation of the novelty problem. We have already presented the arguments for why this approach now seems more relevant than a genome-centered one. Here we identify particular properties of developmental systems that could promote the origination of novelty. Our approach, however, resides in a strictly neo-Darwinian frame, assuming that morphological evolution proceeds through gene substitutions that primarily affect cell behavior in developmental processes, leading primarily to changes in relative proportions and positions of embryonic characters. If these classic processes can produce novelties in the anatomical structure of organisms, one is led to hypothesize that the causality for their appearance lies in very basic and general properties of developmental systems that are affected by gene substitutions. We briefly review the evidence in support of this assumption.

Hierarchical Organization

It is commonplace to understand organisms as a hierarchy of building blocks from molecules to organs. However, with few exceptions (3, 7, 69, 74), evolutionary concepts rarely take into account that development, as the process of deployment of this hierarchical order, is itself organized largely hierarchically. Underlying are geometric hierarchies of cell and tissue organization, but also, and most importantly, hierarchies of stepwise successions of qualitatively different kinds of processes. The products of each step form the starting point for the next, and modifications introduced at one level of the developmental hierarchy can be assumed to have profound effects at very distant levels. For instance, the studies of sea urchin development mentioned above (75, 76, 113) show that the novelties in the larvae of direct developers are a consequence of very early modifications in cell lineage segregation, an alteration much higher up in the hierarchy of developmental decisions than the level of anatomical effect.

A similar and equally well-documented example comes from detailed comparative and experimental studies of spiralian development in protostomes. In some spiralian lineages novel larval types appear, such as the veliger of molluscs or the setiger of annelids. The work of Freeman & Lundelius (26) indicates that the origination of the derived larval types is dependent on a change of mechanism in early blastomere specification, the first major event in spiralian embryogenesis, establishing the axis of bilateral symmetry. This process is determined by the specification of the "D quadrant," the blastomere responsible for the formation of large parts of the mesodermal and endodermal structures of the embryo. In primitive forms the D quadrant is specified by inductive interactions between certain macromeres and micromeres that result from several sets of cleavages. In the derived forms the D quadrant is specified through cytoplasmic inheritance from the vegetal pole causing unequal cleavage and resulting in one of the first four macromeres being larger than the other three. This macromere invariably becomes the D quadrant, a sheer effect of size, which could be mimicked experimentally (26). The cytoplasmic specification of the D quadrant occurs earlier in the developmental sequence than the inductive specification, and it has a series of consequences down the hierarchy. The larger macromere gives rise to larger micromeres, and these lead to a further acceleration of development, which in turn results in the appearance of larvae with adult features in some lineages, while others lose the larval stages completely and become direct developers. Thus, in effect, larval morphology is profoundly altered through the acquisition of a mechanism that modifies the sequence of cell specification. The acceleration of D quadrant specification through cytoplasmic inheritance seems to have played a causal role in the origination of novel larval forms during spiralian evolution.

It is obvious that heterochrony has been an initiating factor in both examples, but the specificity of its phenotypic consequences depends on the hierarchical arrangement of the processes that were affected. However, the generative qualities of hierarchical organization lie not only in its cascading and amplifying effects. The hierarchical succession of processes also contains the possibility of changing qualitatively the patterns and structures of previous levels of organization. Each switch-over from one mechanism to the next represents an opportunity for structural change, a principle that has been proposed to underlie many qualitative transformations in morphological evolution (64). In avian limb development, for example, the switching from chondrogenesis to osteogenesis generates the unique tarsometatarsal bone from the cartilaginous rudiments of one tarsal and three metatarsals. Thus, the basic mechanisms of ontogenetic patterning can remain conserved in the evolution of an organismal lineage while the final phenotypes can be substantially altered through the expansion of secondary and tertiary level processes.

Interactivity and Dissociability

Developmental systems are characterized not only through sequential hierarchies but also by the interactivity between parts of different hierarchies, a condition described by the terms "epigenetic cascades" (34, 97) and "ontogenetic networks" (86). It is generally thought that an increase in the number of interactive events in which a morphological character takes part leads to an increasing phylogenetic stability of this trait. This forms the basis of the concepts of "burden" (80) and of "epigenetic traps" (104). With regard to the origin of novelties it is crucial whether and how interactive networks can be dissociated and whether new sets of interaction can be causal in the generation of new structures. We restrict the discussion to the cellular level.

The best understood epigenetic cascades lie in the domain of epithelial-mesenchymal interactions that are involved in the differentiation and patterning of a great number of anatomical structures, such as the inductive cascades leading to the formation of vertebrate eyes, limbs, and epidermal appendages (88). The variety of epidermal structures, all developmentally initiated by a similar sequence of inductions, is a good example of how the progressive elaboration of a primitive mechanism of integumental differentiation has led to the generation of greatly different structures, such as hair, glands, or teeth. This indicates that it is not so much the establishment of new kinds of interactions that is generatively important for the formation of new structures but the change of context in which the conservative and long established interactive mechanisms take place.

Not many empirical examples are available for the kind of contextual change that could have provoked new routes of interaction. Nevertheless, some of the few cases of novelty that were analyzed from a developmental

perspective are instructive. One is the origin of the turtle carapace. The carapace is a unique association of ribs and vertebrae with a specialized dermis. This arrangement also represents a profound deviation from the tetrapod Bauplan because the elements of the limb girdles lie inside the rib cage, as opposed to an outside position in all other tetrapods. Studies of the developmental events that generate this arrangement indicate that epithelial-mesenchymal interactions, which when primitive produced only integumental features, were expanded to affect deeper layers of the mesenchyme (13). Through this mechanism the prospective costal cells are oriented toward a more lateral pathway than in other tetrapods, causing the superficial position of the ribs. The primary contextual change in this process seems to have been the timing of the epithelial-mesenchymal interaction. It takes place much earlier than the primitive interactions that lead to purely dermal differentiation and thus affects a much smaller embryo. Burke (13) suggests that the precocious inductive activity in a smaller embryo would have a relatively deeper penetration into the mesenchyme, reaching the skeletogenic cells that migrate from the somites, reorienting their pathway and causing the ribs to form superficially to the limb girdles.

A second instructive case is the origin of external cheek pouches in pocket gophers and kangaroo rats, a novelty in the evolution of rodents (52). In contrast to the primitive internal cheek pouches known from other rodent taxa, the external pouches open outside of the mouth cavity and their inner surface is not covered with buccal epithelium but with fur. Both pouch types arise from an invagination of the buccal epithelium of the oral cavity, close to the corner of the mouth. A detailed comparison of these processes shows that the externalization of the derived pouch types is initiated developmentally by a slight anterior shift of the invagination, leading to the inclusion of the lip epithelium (11). As a consequence the pouch not only acquires an external opening, but the epithelium of the pouch rudiment grows into a dermal environment which has the capacity to induce hair follicle formation. Fur-lining of the pouch is thus a consequence of a change of context, i.e. a shift of invaginated epithelium into an area with inductive capacity. The shift itself is possibly a mere allometric consequence of evolutionary modifications in facial proportions.

Both examples illustrate that a change of context, initiated by temporal or spatial shifts, can lead to the formation of novel morphologies on the basis of preexisting interactive capacities. The historically established networks of developmental interactivity, in particular those of epithelial-mesenchymal inductions, thus not merely constrain morphological evolution, they also represent an important generative source for the origination of new structures.

Equilibria and Thresholds

Ontogenies can be understood as systems of temporary equilibria or steady states between developmental entities (7, 53, 69, 100). This is not the place to discuss the various formalisms that were developed in this regard, but we want to emphasize the principal importance of these properties for the origin of novelty. They explain why continuous variation of developmental parameters can result in discontinuous phenomena. Upon transgression of certain thresholds a developmental system can fall into a different steady state resulting in different phenotypic expressions. Thresholds must and do exist at all levels of development and have been demonstrated in a variety of experiments (e.g. 8, 22, 32, 98). Conceptually, the realization of discontinuous forms of morphological variation has been attributed to thresholds in development (48), and polygenic models of digital reduction have been based on threshold concepts (43). Only recently, however, has it been proposed that threshold effects may represent a generative factor in the origination of morphological novelties (64, 66).

Developmental thresholds can lie in molecular and physical parameters of pattern formation, in critical cell number or blastema size, in inductive or spatial relationships, in physiological or biomechanical factors, etc. A spatial threshold effect, for example, was proposed to have initiated the formation of external cheek pouches discussed above (11). Here, we shall focus on simple biomechanical changes that are associated with continuous developmental variation. It is well known that embryonic movement is required for the formation of sesamoids and of secondary cartilage (33). We can assume that evolutionary changes in the proportions of embryonic structures also modify pressures and tensions that arise from embryonic movements. As a consequence, when these biomechanical forces transgress a threshold intensity, we should expect the appearance of sesamoid cartilages in connective tissue structures or of secondary cartilage in the vicinity of dermal bone. These reactive structures provide an important source of skeletal novelty and can be elaborated during the further course of evolution. That this is indeed the case is supported by a large number of cases in which skeletal neomorphs are based on sesamoids or on secondary ossifications (Table 2).

An example studied in more detail is the fibular crest of theropod dinosaurs (67). The fibular crest is a neomorph on the tibia that appears first in theropod dinosaurs and is synapomorphic in birds. Developmentally, the formation of the osseous crest is based on a separate cartilaginous sesamoid that is later ossified and eventually becomes incorporated into the tibia. Paralysis experiments in bird embryos demonstrate the dependence of the sesamoid's formation on embryonic movement and the consecutive loss of the crest in paralyzed embryos. Müller & Streicher (67) propose a scenario in which the

Table 2 Examples of skeletal novelties in vertebrates that are based on reactive cartilage and bone formation.

Skeletal novelty	Taxon	Based on
Fibular crest	Theropods, birds	Sesamoid
Preglossale	Passerine birds	?
Panda's "thumb"	Panda bears	Sesamoid
Panda's "7th digit"	Panda bears	Sesamoid
Rüsselknochen	Boars	?
Calcar	Bats	?
Falciforme	Moles	Sesamoid
Third forearm bone	Golden mole	Ossified tendon
Naviculare	Horses	Sesamoid
Patella	Birds, mammals	Sesamoid

evolutionary reduction of the reptilian fibula leads to an increased mechanical instability during embryonic movement of the limbs, which could have initiated the formation of the sesamoid, on the basis of the reactive potential of connective tissue to form cartilage under pressure stresses. The origination of this novelty is thus based on a number of very specific conditions, such as skeletal proportions, biomechanical changes, and the reactive potential of connective tissues.

We are aware that the formal separation of the three generative modes is to some extent artificial. Most examples would fit into all three categories. However, we do believe that these are three fundamental properties of ontogenetic systems that must be taken into account when we think about evolutionary modifications of developmental parameters and their role in the origination of novelty. Common to all three modes is their potential for rapid morphological transitions, and the fact that their effects have an indirect and removed relation to the level of genome evolution.

FROM NOVELTY TO BAUPLAN

A discussion of evolutionary novelties would be incomplete without mentioning the most profound innovations that occurred in the history of life—the origin of the basic design principles underlying the major supraspecific taxa, i.e. the bauplans of phyla and classes. So far, we have been concerned only with the origin of new morphological characters but not with the origin of supraspecific taxa, even if this is often considered as the same problem (27). While the origin of new body plans and the origin of new characters are linked processes, they are not necessarily the same. This insight is mainly due to Riedl (80), and we discuss his concept below.

The notochord is an axial rod of cells representing the functional precursor

of the vertebral column, both ontogenetically and phylogenetically. In mammals this structure has lost most of its adult function and persists only rudimentarily as the nucleus pulposus of the intervertebral discs. Nevertheless, the notochord is present in all ascidian larvae, in *Amphioxus*, and in the embryos of all vertebrates. The stability of this structure is best explained by its central role in embryogenesis, in organizing the differentiation of the central nervous system and of the axial mesoderm. Originally, however, the notochord was not as indispensable as it is for the derived members of the phylum. This is indicated by the complete lack of a notochord in two orders of the chordate class Thaliacea, which belongs to the subphylum of tunicates. The fact that the members of one order of Thaliacea, the Doliolida, do possess a notochord, indicates that it is most likely secondarily lost in the other orders.

Here the main point is that the notochord is a constant character of the acranian and vertebrate bauplan, but hardly was a bauplan character when it first arose. The essential characteristic of a bauplan is not the degree of similarity or dissimilarity to other forms of life, but the fact that each group of animals has its own characteristic patterns of constraints and opportunities. According to Riedl (80, p. 196), a bauplan (or morphotype) is defined by the "*pattern of freedom and fixations [constraints] formed by the collective of features of a phyletic group.*" From this definition it is obvious that the origin of a new character is not sufficient to change a bauplan. Only if the new character achieves an indispensable function, and becomes epigenetically integrated into the basic body design, does it become a bauplan character. The origin of new body plans requires the origin of morphological novelties, but it also requires the integration of this new character with the other parts of the organism. In this context it is irrelevant whether integration is due to functional necessities or due to epigenetic interdependencies. What counts is that some characters acquire an indispensable biological role that causes their conservation in spite of changing adaptive pressures.

CONCLUSIONS

Morphological novelty has the status of a distinct problem in evolutionary biology. Novelties are not synonymous with all taxonomically relevant apomorphies, and their emergence is not identical with the process of speciation or with the origin of novel body plans. Once new variants have occurred, their fixation by drift or selection is easily explained. But there are problems specific for the origin of novelties that are not the same as in the case of adaptive modifications of existing structures, namely the developmental realization of novelties depends on very specific epigenetic conditions. For these, no significant amounts of heritable variation have been demonstrated in

taxa related to the ancestral groups. To the contrary, novelties apparently arise in spite of strong developmental constraints that generally canalize morphological evolution.

We conclude that the problem of novelty must be considered from a new perspective in order to be able to formulate adequate research questions. At the organismic level, morphological evolution can be described as a process of progressive origination, transformation, and loss of homologs. Therefore, we suggest a definition of novelty that is framed in the homology concept. The main properties of the definition are that it is independent from descriptive or mechanistic qualifiers, that it excludes merely quantitative or negative traits, and that it allows distinction between meristic variation and true novelties.

The new questions that arise from an organismic definition concentrate on the mechanistic basis of their generation. The genetic side of the generative problem does not seem to differ substantially from the classic mechanisms, and does not hold much promise for further advances with regard to the novelty problem. The majority of open questions, and the greatest potential for an increase in our understanding of novelty, lie in the realm of the developmental context in which genetic changes can trigger a change of structure. It is unlikely that explanations for the origin of morphological novelties can be successful without the inclusion of the generative properties of developmental systems.

A preliminary overview of the developmental modes associated with the origination of novelties point to a central role of heterochrony as the primary initiating factor. Heterochrony alone, however, can only modify processes that are already established. The specific morphological composition of novelties that arise as a consequence of heterochronic alterations of a developmental process will depend on the particular organization of the developmental network of which the process is a part. Hierarchical organization, interactive interdependency, and equilibrium conditions are basic properties of all developmental systems that will invariably be affected. Evolutionary modifications of any part of these systems that go beyond specific thresholds can automatically cause morphological effects that are only indirectly related to the causes of the primary modification. By-products of development will be "seen" by selection and can be further elaborated through neo-Darwinian processes. We need to learn through experimental and comparative studies what specific potentials exist in the developmental systems of an organismic lineage, to be able to identify the individual causes that lead to a particular novelty in evolution. In general, however, the available data strongly suggest that side effects of developmental organization represent the kernel of morphological novelty.

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