STASIS, CHANGE, AND FUNCTIONAL CONSTRAINT IN THE EVOLUTION OF ANIMAL BODY PLANS, WHATEVER THEY MAY BE

G.A. WRAY[1], R.R. STRATHMANN[2]

[1]*Department of Biology, Box 90338, Duke University, Durham, NC 27708-033, USA*
[2]*Friday Harbor Laboratories and Department of Zoology, University of Washington, 620 University Road, Friday Harbor, WA 98250, USA*

gwray@duke.edu rrstrath@u.washington.edu

BODY PLAN
BAUPLAN
DEVELOPMENT
FUNCTION
CONSTRAINT
EVOLUTION

ABSTRACT. – The phrase "body plan" or "bauplan" has been used to mean (1) the characteristic features of a phylum or other taxon of high rank, (2) architectural features of animals (such as symmetry; modular units; types of body walls, body cavities, body openings, and body subdivisions; types of supporting structures; position and structure of organ systems), (3) traits characteristic of an especially invariant stage in a life history (phylotypic stage), or (4) patterns of gene expression that first indicate the development of regions of the body. Multiple meanings of bodyplan within one argument can be misleading, but under all four meanings, body plans of animals have changed after stasis for long periods and after stasis during divergence of other traits. Change in body plans is often associated with an identifiable change in a functional constraint. Examples include decreases in body size and changes in requirements for feeding or locomotion. These observations support the hypothesis that functional constraints contribute to stasis in body plans. There is evidence that ancestral developmental processes constrain directions of evolutionary changes in body plans. There is little evidence that developmental processes prevent changes in body plans, but evidence for developmental constraint is more difficult to obtain than evidence for functional constraint.

PLAN DU CORPS
"BAUPLAN"
DÉVELOPPEMENT
FONCTION
CONTRAINTE
ÉVOLUTION

RÉSUMÉ. – L'expression "plan du corps" ou "plan de construction [bauplan]" a été employée dans le passé pour désigner (1) les caractéristiques d'un phylum ou d'un taxon de rang élevé, (2) les caractères architecturaux des animaux (exemples: la symétrie; les unités modulaires; les types de tégument, de cavités du corps, d'ouvertures du corps, et de subdivisions du corps; les types de structures de renforcement; la position et la structure des systèmes d'organes), (3) les propriétés d'un stade ontogénétique particulièrement stable (stade phylotypique), ou encore (4) des motifs d'expression de gènes qui indiquent déjà le développement des différentes régions du corps. Des significations multiples de « plan du corps » à l'intérieur d'une même argumentation peuvent générer des erreurs, mais dans toutes les conditions évoquées de (1) à (4), les plans du corps des animaux ont été modifiés après de longues périodes de stase et après des stases accompagnées d'une divergence au niveau d'autres traits. Une modification du plan du corps est souvent liée à un changement identifiable dans le contexte d'une contrainte fonctionnelle. Parmi les exemples, on peut citer la réduction de taille du corps et les modifications des conditions requises pour l'alimentation et la locomotion. Ces observations confortent l'hypothèse selon laquelle les contraintes fonctionnelles contribuent à la stase d'un plan du corps. Il y a de très bons indices montrant que les processus ancestraux du développement sont contraignants quant aux directions possibles des changements évolutifs de plans du corps. Il y a très peu d'indices pour que les processus du développement empêchent tout changement de plan du corps, mais les preuves d'une contrainte du développement sont plus difficiles à trouver que les indices de contraintes fonctionnelles.

INTRODUCTION

The potential for confusion from multiple meanings of "body plan"

The term body plan (often used as a synonym of ground plan and *bauplan*) has been used with quite different meanings. The use of "body plan" in studies of evolutionary stasis and change can produce mistaken inferences when disparate meanings are mixed within an argument. As an example, stasis in body plans of animals has been inferred from the fossil record because first appearances of taxa of high rank are early in the Phanerozoic fossil record rather than scattered through the Phanerozoic. Animal phyla with fossilization potential appear as fossils in the Cambrian and not subsequently. Similarly, many of the animal classes are known from the Cambrian or Ordovician. If all members of a phylum or class share the same body plan, then about 500 million years of stasis in body plans is implied. This apparent stasis has prompted the question: Why have no new body plans originated since the Cambrian ? The answer depends in part on the definitions of body plan that are used and how they are combined. Not all members of a phylum or class have the traits that are used to characterize that group. They are classified with it because of evidence that they belong to the same clade. If the traits of animals rather than the traits that are used to characterize clades as taxa are considered, then the answer is that new body plans have originated since the Cambrian.

The straw-man premise for the question "Why have there been no new body plans ?" was flawed, but it must be admitted that many ancestral traits characterizing animal phyla and classes have been retained for more than 500 million years. Thus some traits do exhibit remarkable stasis. These observations prompt questions that are not so easily dismissed. Why do body plans remain unchanged over such long periods ? Given such extended stasis, what enables them to change ? Such questions are being answered by functional and developmental biologists, but to interpret the answers one must consider the differing uses of the term "body plan."

Diverse meanings of "body plan"

1. The body plan often means the distinguishing morphological characteristics of a phylum or class. Under this definition, it would not be surprising that the traits that comprise a body plan are ancient and conservative. In so far as the hierarchical arrangement of taxa represents a sequence of evolutionary divergences, the traits that characterize higher taxa must have originated early. To be useful as diagnostic characters for descendants within the clade, the traits must change rarely. For more than two centuries zoologists have been searching for these ancient and conservative traits and redefining the animal phyla, and they are not done yet (Nielsen *et al.* 1996). Higher level systematics of animals has been an enduring source of controversy, and many zoologists are hoping that molecular evidence will help resolve questions about homology and homoplasy of traits that have been used to characterize taxa of high rank. Thus, even under this definition of body plan, one can find aspects of body plans that have changed in descendant lineages. Some of the traits characterizing a phylum vary within the phylum. We recognize the animals as members of a phylum or class because some indication of relationship remains. The observation that there are no new phyla since the Cambrian does not imply that there are no new body plans. It only implies that the animals with good potential for fossilization that originated later can be assigned to one of the clades known from the Cambrian. Similar observations apply to animal classes, with few new ones since the Ordovician, and to other ancient animal clades given high taxonomic rank. Nevertheless, there does appear to be a phenomenon to be explained. Many traits have remained unchanged for the majority of animals in a phylum or class. Groups characterized by these traits, if possessing readily fossilized parts, can now be traced as separate clades back to the Ordovician or Cambrian. For this meaning of body plan, observations of stasis and change in body plans are observations on traits that are considered to be persistent synapomorphies (shared derived characters) of clades of ancient origin.

These traits gained the attention of biologists because they are ancient and persistent. The bias in the biologists' choice is for prolonged stasis. With choice from a large number of traits, what is the probability that some would be so persistent by chance alone ? An estimate of that probability might be based on a null hypothesis of random change in traits during speciation and extinction, but we shall not attempt such an estimate here.

2. Body plan can also refer to architectural features of animals, such as types of body cavities, body walls, types of epithelia (Rieger 1994), organ systems, and skeletal support. Also included are arrangement of parts, as in segmentation, symmetry, position of mouth relative to nerve cords, or colonial versus solitary habit. Sometimes cell lineages (as in spiralian development) or cell movements (as in schizocoely and enterocoely), or cell types (such as choanocytes) are included as features of body plans. When body plans are defined as features of body organization rather than traits characterizing higher taxa, biases in selection of traits are eliminated (Fitch & Sudhaus 2002). The traits do not depend on relationships among clades, and other changes qualify as changes in body plans.

3. The traits of a phylotypic stage (Sander 1983, Raff 1996) have been suggested as the definition of the body plan, at least for those phyla or classes for which a phylotypic stage can be identified. Attention to phylotypic stages arose from the observation that some intermediate stage of development has diverged less than both earlier and later stages. For vertebrates the pharyngula has been considered to be a phylotypic stage, despite its variation among taxa (Ballard 1976, Richardson 1995). Most generally, a life-history stage has been considered to be phylotypic if it is the least varying stage of development in the most inclusive clade. To our knowledge there have been no attempts at a quantitative application of these dual criteria. Should greater weight be given to inclusiveness or to constancy in the identification of phylotypic stages? Phylotypic stages are a special case of persistent synapomorphies. Like other persistent synapomorphies, they are selected by biologists for their stasis out of a large and uncounted set of traits. One explanatory hypothesis suggested for such especially conserved stages is that necessary interactions among developing body parts constrain evolutionary changes in this stage of development (Raff 1996).

4. A new use of the phrase "body plan" is its application to patterns of gene expression in embryos. Of particular interest are genes that establish the organization of developing embryos, including those that pattern general architectural features of body plans (body axes, germ layers, etc.) and distinguishing characteristics of particular body plans (notochord, segmentation, etc.). Most of the genes that pattern these features in embryos encode regulatory proteins such as transcription factors and intercellular signaling systems (Gerhart & Kirschner 1997, Carroll *et al.* 2001). The phrase "body plan" is increasingly used in association with the embryonic expression patterns of these genes (Fig. 1). Although there is clearly a relationship between regulatory genes and body plan features, gene expression profiles are not the same set of traits that have been used to distinguish phyla or classes, and they do not include all the features that distinguish types of body organization. As discussed in a later section, the phylogenetic distribution of most embryonic gene expression patterns does not match specific phyla and classes particularly well.

The term "body plan" seems to gain special significance for biologists when disparate meanings are combined in one argument. Confounding several meanings in one argument can produce a false impression of stasis. Not all traits that characterize higher taxa are architectural. Clearly not all architectural features of animals are useful in characterizing higher taxa. Homologous genes may be expressed in a similar pattern yet quite different structures result in subsequent development, and similar structures can develop via rather different patterns of gene expression. By using the term body plan (or ground plan or *bauplan*) ambiguously, one can attribute properties of one set of traits to another. When the attributes of the traits that characterize taxa of high rank are applied to the architectural features of multicellular animals or to the patterns of expression of homologous genes, or *vice versa*, confusion is likely. Use of "body plan" with double or triple meanings can bias assessment of the frequency or causes of stasis and change.

What one means by evolutionary stasis or change in "body plans" clearly depends on the traits considered to be part of a body plan. Nevertheless, for all of the meanings listed above, there are examples of changes in body plan following change in a functional constraint. In contrast, it is more difficult to demonstrate developmental constraint as a cause of stasis in body plans. In selecting examples, we examined correlates of change because they are easier to examine than correlates of stasis. We selected examples that met one of two criteria. For some cases, the inferred phylogeny, the distribution of traits, and the fossil record indicated that the change occurred after prolonged stasis. In other cases there was little evidence on the duration of stasis or time of the change, but differences in body plan within taxa of low rank indicated that a trait remained unchanged during the evolution of marked morphological disparity but nevertheless changed subsequently (the alternative and unparsimonious hypothesis for examples in this second category is that the trait represents the ancestral condition and traits in all other members of the clade were convergently derived from it).

CHANGES IN FUNCTIONAL REQUIREMENTS

One explanation for stasis is stabilizing selection, with the explanation of change being a change in functional requirements. The functional requirements that may account for stasis and change in body plans are varied. Here we emphasize ancient synapomorphies and architectural features of animals.

Nutrition from symbionts

A variety of free-living animals with chemoautotrophic symbiotic bacteria have lost the gut lumen and in some cases the mouth and anus. As a change in the construction of the body, the loss of a gut may be considered a change in body plan. Indeed the absence of a recognizable gut in the adult contributed to the Pogonophora being considered a phylum, although morphological and molecular ev-

idence now nest them within the annelids (George & Southward 1973, McHugh 2000).

A gut has been lost within families or genera within a number of clades (Gustafson & Lutz 1992, Krueger *et al.* 1992). The distribution of gutlessness within clades indicates extended stasis in which a gut was present followed by loss of a gut. Such distributions of gutlessness are found among species of protobranch bivalves, oligochaetes, and nematodes (Giere & Langheld 1987, Fisher 1990, Ott *et al.* 1982). As an example, the bivalve *Solemya reidi* has a stomach rudiment as a larva but lacks a functional gut. At metamorphosis, the larva ingests its own test cells, but the material enters the lumen of the perivisceral cavity (Gustafson & Reid 1988).

Nutrition by parasitism

The evolutionary transition from a free living habit to parasitism can involve extensive changes in body plans as ancestral structures for feeding and locomotion are lost and other structures elaborated. An extreme example from the crustacean arthropods illustrates the magnitude of possible changes. Rhizocephalan barnacles are allied to other cirripede crustaceans (Høeg 1995), but as adults the rhizocephalans lack such arthropod traits as segmentation and jointed appendages and in some cases are colonial. The female develops from a vermiform slug of cells injected into the host (Glenner *et al.* 2000). It becomes an interna, a set of branching roots with an epithelium and a cellular core. The externa, the reproductive part of the female, develops from the system of roots and extends outside the host. In one group of rhizocephalans, multiple externas develop from a set of rootlets (Høeg & Lützen 1993), thus achieving a colonial construction, with tissue connections and nutrient exchange maintained among morphological individuals. Thus the arthropod body plan has been so modified that it has been possible for coloniality to evolve as a novel feature of the body plan. The male rhizocephalan develops into a gametogenic structure hyperparasitic on the female. The multicellular structures of postlarval rhizocephalans give no morphological evidence of relationship to arthropods.

Nutrient content of eggs

Loss of a feeding larval stage has occurred numerous times within diverse phyla (Thorson 1950, Strathmann 1978, Hanken 1992). The transition from feeding to non-feeding development is often accompanied by loss or reduction of larval structures and accelerated development of postlarval structures. Loss of the larval mouth is common and loss of the entire gut has occurred in bryozoans, with development of the gut delayed until metamorphosis. These are substantial changes in the larval body plan. In some cases the loss has occurred after a demonstrably long period of stasis (Wray 1996). Cases of facultatively feeding larvae demonstrate that nutrient rich eggs and independence of exogenous food have evolved prior to evolutionary changes in the larval body (Hart 1996). Such changes are in part the result of loss of a functional requirement for obtaining food during the larval stage and as such could result from release from stabilizing selection (Strathmann 1975), but some of the changes may result from selection for improved performance of the non-feeding larva in swimming (Emlet 1994) and more rapid development to competence for metamorphosis (Wray & Bely 1994) and therefore could result from new directional selection. The changes in size of eggs and larval morphology and accelerated development of postlarval structures are associated with changes in cell fates that are evident early in development (Wray & Raff 1990).

Among the most dramatic developmental changes are the transitions from holoblastic cleavage to incomplete (meroblastic) early cleavages. Such changes have occurred in both directions with increases and decreases in size of eggs, as in arthropods. The processes establishing developmental fates of portions of the embryo can differ between syncytial embryos, in which nuclei share cytoplasm without diffusion barriers, and embryos composed of separate cells.

Other nutritional change

A radula is characteristic of most classes of molluscs and is a plesiomorphic trait for gastropods, but it has been lost independently in several lineages that diverged since the Paleozoic (Oliverio 1995). These animals have been assigned to families or genera in which other species have a radula and they are easily identified as gastropods, but they have lost part of the gastropod body plan. Losses may be concentrated in a clade in which the radula had become specialized for delivery of toxin and the losses may be associated with a shift in diet (Kantor & Sysoev 1989).

Changes from microphagous suspension feeding to macrophagy have occurred in several clades, with the derived macrophagous animals often occupying habitats that are poorer in suspended food. Sponges in the Cladorhizidae have lost the aquiferous system and choanocytes that are used in suspension-feeding and that are characteristic of sponges. These sponges trap larger prey, such as crustaceans. The condition is inferred to be derived rather than ancestral. "Such a unique body plan would deserve recognition as a distinct phylum, if these animals were not so evidently close relatives of Porifera.

Their siliceous spicules resemble those in several families of poecilosclerid Demospongiae" (Vacelet & Boury-Esnault 1995).

The small ctenophore *Ctenella aurantia* lacks the colloblasts characteristic of Ctenophora and also lacks the peripheral canals (Carré & Carré 1993). It appears to be a highly modified cydippid, with functional changes associated with exogenic cnidocysts and small size.

Motility and habitat selection

Notochord, dorsal nerve cord, and postanal tail are chordate features that have become restricted to a non-feeding larval stage in ascidians. Their functional role is thus restricted to habitat selection and perhaps other kinds of dispersal. This restricted role has preceded loss of the larval tail and thus most of the chordate body independently in several lineages. A restricted functional role preceded their loss. Taillessness appears to have evolved more times within molgulids than in other ascidians, which raises the possibility of a developmental predisposition for tail loss in molgulids and by implication a greater developmental constraint on tail loss in other ascidians (Huber *et al.* 2000). Nevertheless, mutations resulting in loss of most of the body axis are known for other chordates, as in the floating head and no tail mutants of zebra fish (Halpern 1997). Stasis in the vertebrate body axis has not been from an absence of mutations. Most of the body posterior to the head can be removed by a mutation, but whereas some ascidians thrive without axial or appendicular locomotion, no vertebrates have adopted a mode of life that permits such a loss (Strathmann 2000).

Adult size

Evolution of smaller adults is often associated with changes in body plans. The annelids offer examples of changes in several components of the annelid body plan. In marine annelids, smaller size is associated with an interstitial habit and can be associated with loss of parapodia, loss of setae, and acquisition of rings of cilia in the adult (Westheide 1985). Reduction in size can also be associated with an acoelomate condition (Smith *et al.* 1986, Fransen 1988). Such divergences in body plan occur within families, as in the Hesionidae and in the Dorvilleidae together with the allied Dinophilidae.

Loss of a blood vascular system and changes in excretory systems are also associated with reduction in size. In the hesionid polychaetes, small species that are apparently derived from larger ones have lost the blood vascular system and reacquired protonephridium-like excretory organs (Westheide 1986). This trend conforms to a broad correlation among multicellular animals (Ruppert & Smith 1988). In animals with a blood-vascular system, muscle-mediated filtration from blood vessels through podocytes into the coelomic cavity produces the filtrate. The filtrate is then modified as fluid passes through an open duct from the coelom to the outside. In contrast, in animals without a blood vascular system, cilia-mediated filtration of fluids occurs from the coelom into the excretory duct from coelom to the outside. The cilia extend into the duct, and fluid is filtered through a weir formed by extensions of cells at the inner ends of the ducts. Ruppert and Smith note that development of these protonephridia-like and metanephridia-like systems does not conform to germ lines, and they question homology among protonephridia. An example of consequences of divergent size of adults within a species is provided by *Bonellia*, an echiuran with large females and minute parasitic dwarf males (Schuchert 1990). The females have a blood vascular system and open ducts between coelom and the outside. The males lack a blood vascular system, and have protonephridia-like excretory organs. The excretory organs of the male do not develop from a larval excretory system but rather as a new structure. Body plans can diverge between sexes within a species in association with different functional constraints.

Skeletons and requirements for support, defense, and density

Accretionary growth of a shell, as opposed to molting, has evolved in several arthropods. A bivalved carapace (as in conchostracans) or sessile habit (as in barnacles) appear to have been the preconditions for this change. Presumably the zoologists who initially classified barnacles as molluscs considered a permanent shell and mantle cavity to be important parts of a body plan.

A particular form of calcite skeleton is the most consistent distinguishing feature of living and fossil echinoderms. Each skeletal element is composed of a latticework of anastomosing rods, the whole element optically like a single crystal of calcite. Skeletal elements are absent in the Pelagothuriidae, a family of elasipod sea cucumbers, although they belong to a clade of undoubted echinoderms and their inferred sister group within the suborder has skeletal ossicles (Hansen 1975). This condition may be associated with their pelagic life at great depths. Reduced skeletons, of which this is an extreme, carry consequences for buoyancy, structural support, flexibility, and defense.

Protection of embryos

Protection of gastropod embryos is associated with especially long cell cycles for the cells that will form trochoblasts and apical ectoderm, and the specification of the mesentoblast and dorso-ventral body axis occurs when the embryo has fewer cells

(van den Biggelaar *et al.* 1997). As a consequence, trochoblasts and other ectodermal cells can depart from a radial arrangement of cell fates and diverge in differentiation when the embryo has fewer cells. For example, fewer cells form prototrochal cilia and some instead form the head vesicle in pulmonate gastropods (van den Biggelaar 1993). Protection has led to modified cell interactions and cell fates to modify the trochophore. In addition to changes in ancient synapomorphies and architectural features, these are changes in what could be considered to be a phylotypic stage and presumably also in gene expression in the cells that do or do not form trochoblasts in the divergent clades.

Conclusion on functional constraints on ancient synapomorphies and body structures

The foregoing examples suggest that stasis in body plans (as architectural features of animals) results from stabilizing selection for performance of certain activities. Change results from changes in selection on performance. The foregoing examples include change and stasis in body plans under other definitions as well, with different subsets concerning traits characterizing major groups, body architecture, and changes at nearly all stages, including some that could be candidates for phylotypic stages.

Functional requirements are, by themselves, sufficient to account for many instances of stasis and change in traits that are considered parts of body plans, but support for a hypothesis of functional constraint does not in itself exclude developmental constraints in these or other instances. A hypothesis of functional constraint emphasizes that high performance of some function is maintained by stabilizing selection. Developmental processes may influence the effect of mutations on performance and thus affect selection for or against the change. Our examples simply indicate that changes in body plans are associated with changes in the need to perform certain identifiable tasks. We now turn to meanings of "body plan" that are explicitly developmental.

CHANGES IN DEVELOPMENT

The two definitions of body plans that are based on development produce a somewhat different perspective on stasis and why it might occur. Here too, however, changes in body plans are clearly possible in post-Cambrian time and are commonly associated with shifts in functional constraints.

Phylotypic stages and body plans

Only three clades within phyla have been proposed to possess phylotypic stages: vertebrates, insects, and sea urchins (Ballard 1976, Sander 1983, Raff 1996). Within these clades, the phylotypic stage is generally well conserved (although exceptions exist, as described in the next paragraph). Most phyla, however, seem to lack a phylotypic stage. There are few obvious phylum-wide similarities in the embryonic or larval development of (for instance) cnidarians, bryozoans, nemerteans, and platyhelminthes. Either these and most other phyla lack phylotypic stages, or those stages are evolutionarily labile. In either case, a body plan definition based on phylotypic stages does not match the perception that body plans have remained static since the Cambrian.

Modifications in phylotypic stages

Some modifications to the phylotypic stage have evolved within each of the three groups proposed to possess one. Waddington (1956) and Elinson (1987) pointed out that the phylotypic stage of vertebrates is not the beginning of development, but rather a point of convergence that is preceded by more disparate earlier stages and followed by more disparate later ones. Duboule (1994) and Raff (1996) called this the "developmental hourglass" to emphasize the many changes in early (i.e., pre-phylotypic) development, most of which are associated with changes in functional constraints on embryonic nutrition (Elinson 1987, Raff 1996). The famous phylotypic "pharyngula" of vertebrates is itself not as stereotypic as implied by Haeckel's famous figures, with component features often appearing in different sequences (Richardson 1995). The phylotypic stages of insects (germ band) and sea urchins (adult rudiment and juvenile) (Emlet 2000) show similar differences in the order of events and relative size of component structures. Thus, simple modifications to the phylotypic stage are possible. In a few cases, the phylotypic stage has been more extensively modified. The best examples come from sea urchins and other echinoderms with essentially direct development, where formation of the adult body plan shows almost no similarities to that of other species with overall rather similar adult anatomy (e.g., McEdward 1992, Schatt & Feral 1996, Emlet 2000).

Gene expression and body plans

Anatomical and gene expression indices of body plans show rather different patterns of stasis and change. Indeed, if all we had to go on were com-

parisons of gene expression, it seems unlikely that we would recognize the same clades of animals as most distinctive. Many regulatory genes and features of their expression are very widely shared among animal phyla (Slack *et al.* 1993, Gerhart & Kirschner 1997, Carroll *et al.* 2001). Enthusiastic assertions that all animal embryos are patterned in essentially the same manner with the same set of regulatory genes (DeRobertis & Sasai 1996, Holland 1999, Carroll *et al.* 2001) probably overstate the case (Davidson 2001, Wilkins 2002). Nonetheless, some striking similarities exist. Genes of the *Hox* complex pattern position along the anteroposterior axis in all phyla for which the relevant functional information exists (Gerhart & Kirschner 1997). This applies to phyla with body plans on anatomical grounds that are about as different as they come, including cnidarians, arthropods, echinoderms, and chordates (Davidson 2001). Another good example is homologous regulatory proteins that control the differentiation of muscle and neuronal cell types in the same broad set of phyla (Davidson 2001). Most published comparisons of regulatory gene expression among phyla have emphasized similarities rather than differences.

Some features of embryonic gene expression are apparently restricted to particular body plans, however. One is the expression of functionally antagonistic domains of *engrailed* and *wingless* at future segment boundaries in a wide variety of arthropods (Patel *et al.* 1989, Brown *et al.* 1994b). Unfortunately, no data are yet available from other ecdysozoan phyla with metameric or segmented body organization. Superficial similarities in *engrailed* expression have been reported from other phyla (Wedeen & Wiseblat 1991, Holland *et al.* 1997), but these cases do not appear to involve segment patterning, since expression is restricted to only a few taxa and occurs too late to play a role in segmentation (Bely & Wray 2001, Davidson 2001). Another example of body plan-specific regulatory gene expression appears to be the expression of *brachyury* in the notochord of urochordates and chordates. Although this gene has rather different developmental roles in other phyla, its function in notochord differentiation is apomorphic for chordates and appears to be widespread within the phylum.

Additional examples of regulatory gene expression that closely match anatomical body plan features are scarce. This may be due partly to insufficient information. The depth of phylogenetic sampling of embryonic gene expression does not approach that for anatomical data , and for most animal phyla, the expression of not even a single gene has been examined. Four phyla have been extensively studied (arthropods, nematodes, chordates, and echinoderms) and scattered information is available for several others (cnidarians, annelids, mollusks, platyhelminths, and hemichordates). With data from more phyla and from more taxa within each phylum, a closer match between gene expression and anatomical body plans may emerge. For now, however, regulatory genes are primarily remarkable for how many similarities they reveal among phenotypically disparate phyla and for how many changes have evolved within phyla (see below).

Changes in body-patterning gene expression

Losses and modifications in the expression of body-patterning genes have occurred within phyla, and some are associated with life history transformations. A well-studied example involves the wasp *Copidosoma*, which is a parasitoid with polyembryonic development. Unlike other wasps and holometabolous insects in general, the earliest body-patterning genes are no longer expressed in this species, including the "gap" genes and those that establish the anteroposterior axis. Later in embryogenesis, however, the conserved network of segmentation and homeotic gene expression is instituted (Grbic & Strand 1998). Another clear example involves the urochordate genus *Molgula*, where reduced larval dispersal has evolved several times independently by loss of the tail (Huber *et al.* 2000). Genes that pattern the notochord, a characteristic chordate feature, are expressed in embryos of species with tailed larvae but not in those whose larvae lack tails (Swalla & Jefferey 1996).

Although these losses of characteristic aspects of embryonic gene expression in *Copidosoma* and *Molgula* both evolved in conjunction with shifts in life history, this correlation is not always evident. Some other dramatic changes in the expression of body-patterning genes have evolved without any obvious connection to functional changes in development or body plan organization. Examples include the role of *bicoid* in anteroposterior patterning of embryos of Diptera but not other holometabolous insects (Stauber *et al.* 2000), the role of even-skipped in pair-rule patterning of holometabolous but not hemimetabolous insects (Patel 1994), and the loss of homeotic patterning functions of *zen* and *fushi-tarazu* in holometabolous insects (Brown *et al.* 1994a, Dawes *et al.* 1994, Falciani *et al.* 1996).

DISCUSSION

Evolutionary changes in body plans abound, under four different meanings of the term body plan. The changes support the hypothesis that stasis in body plans depends on functional requirements. When functional requirements change, widely conserved features with long periods of stasis can be

changed. Extensive modifications in development often accompany these changes. Some of our examples are post-Paleozoic changes in body plans. For others, the variation is found within extant taxa of sufficiently low rank that one can infer stasis for the body plan through repeated evolutionary divergences in many other features prior to the change in the body plan.

Multiple parallel cases are known for changes in body plans. These replicated evolutionary events are associated with parallel changes in functional requirements. Examples include changes in nutrient content of eggs, changes in requirements for motility, changes in nutrition of adults associated with parasitism, and changes in size of adults. Thus functional constraints on body plans are well documented.

We did not, however, tally instances in which there was a change in functional requirements for a body plan but little change in the body plan. The concentration of evolutionary loss of tails in molgulids is consistent with differing constraints on mutational "knock outs" in different ascidians. The comparative evidence on developmental processes is suggestive. Molgulids lack an ankyrin-like protein that is present in the cortex of eggs in other sampled ascidian families, and this trait might be a developmental precondition that results in loss of tails in molgulids more readily than in other families of ascidians (Huber *et al.* 2000). Some sea urchins with large eggs and no apparent requirement for larval feeding, like *Brisaster*, have retained the pluteus form whereas other echinoids with large eggs and no requirement for feeding have lost the pluteus form (Hart 1996, Wray 1996). Also, some sea urchins with a feeding pluteus larva require thyroxine from their diet for development of the echinus rudiment, but at least one sea urchin with non-feeding larval development produces thyroxine (Saito *et al.* 1998). Endogenous production of thyroxine could be a developmental precondition for the evolutionary loss of a pluteus larval form. If so, dependence on diet for thyroxine could be considered a developmental constraint on the evolutionary transition to a non-feeding larva. It therefore remains possible that developmental processes differ in clades in which there have been apparently similar changes in functional requirements but difference in whether there has been a change or no change in body plan. Although hypotheses of developmental constraint have not fared well thus far, differences among clades in incidence of stasis and change raise the possibility of differing developmental constraints in different clades. Such differences offer the possibility of testing hypotheses of constraint by the comparative method.

Despite intense interest, body plan-constraining features of development have yet to be demonstrated. Instead, studies of the *cis*-regulatory elements involved in body patterning have indicated
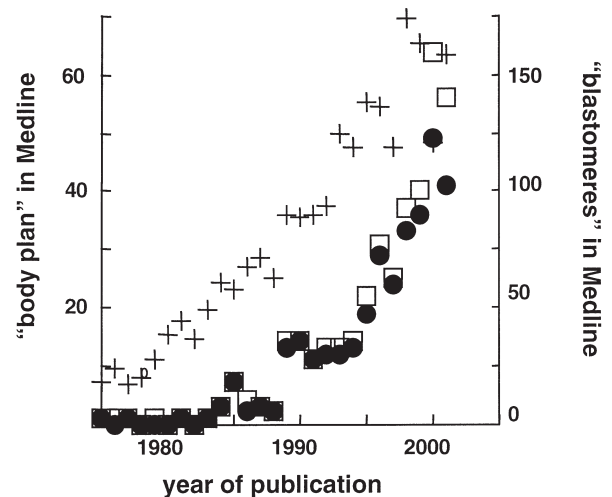

Fig. 1. – Number of articles published between 1975 and 2001 that were identified with the key words "body plan" and "blastomeres" from the data base Medline/PubMed. Open squares are total number each year that were obtained with "body plan" and filled circles are for those articles whose titles indicated that gene expression or pattern specification were part of the study. The latter account for most of the accelerating increase in use of "body plan." The + symbols are numbers of articles obtained with "blastomeres,"which increased during the same period, but only linearly.

remarkably great scope for evolutionary change (Carroll *et al.* 2001). This does not, however, rule out body plan-constraining features of development. It seems unlikely from current evidence that tissue interactions constrain body plan features. It remains possible that gene interactions do so. Technical advances that would allow this possibility to be tested have come into widespread use in model systems and are now being applied in a comparative context.

An extreme hypothesis of developmental constraint on body plans would be that variation in the traits comprising a body plan is impossible. This would mean that there are no mutations that change the body plan. An alternative hypothesis is that stabilizing selection accounts for stasis in body plans. Although changes are possible, they result in poorer performance of some key activity and are therefore selected against. As a functional arrangement of body parts is improved, there may be a decreasing number of routes to further improvements that do not pass through a functionally inferior transitional state. In addition, as ecological "space" is filled by a variety of animals, the minimal functional requirements may become greater and possible transitions between body plans thereby restricted (Frazzetta 1970, Valentine 1973, Strathmann 1978). New features arise very rarely, not because preexisting ones are "optimal" solu-
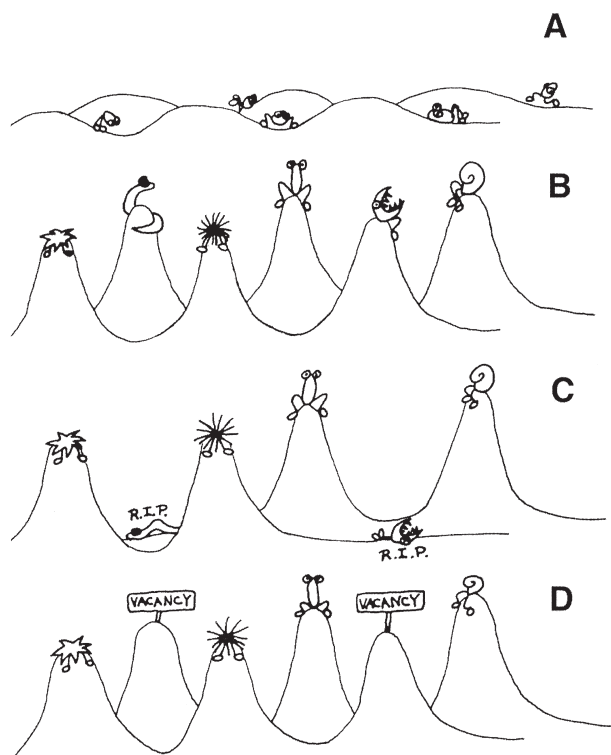
Fig. 2. – A model, based on Sewall Wright's metaphor of an adaptive landscape, that illustrates constraints on evolutionary change in body plans. A, When a new way of life is first entered, clumsy transitional stages can nevertheless be improvements over coexisting forms. Many adaptive peaks may occupied, or at least closely approached. B, In an occupied way of life, reaching new adaptive peaks is less likely because occupation of adaptive peaks has produced deeper maladaptive valleys and perhaps because the adaptive changes involved in reaching the peaks removed traits that provided the initial evolutionary flexibility. C, In a mass extinction, adaptive peaks temporarily disappear, but the valleys between peaks may nevertheless remain steep because of survivors' traits. D, Even when adaptive peaks reappear, they may remain unoccupied. Adaptive body plans may not appear as before because survivors continue to produce deep valleys in the adaptive landscape and because some ancestral traits are no longer represented in the descendents (After Strathmann 1978).

tions (pan-adaptationist hypothesis) but because new features are very unlikely to be better than preexisting ones. Moreover, local optima that were once attained may not be attained a second time. One such situation is modeled in Fig. 2).

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