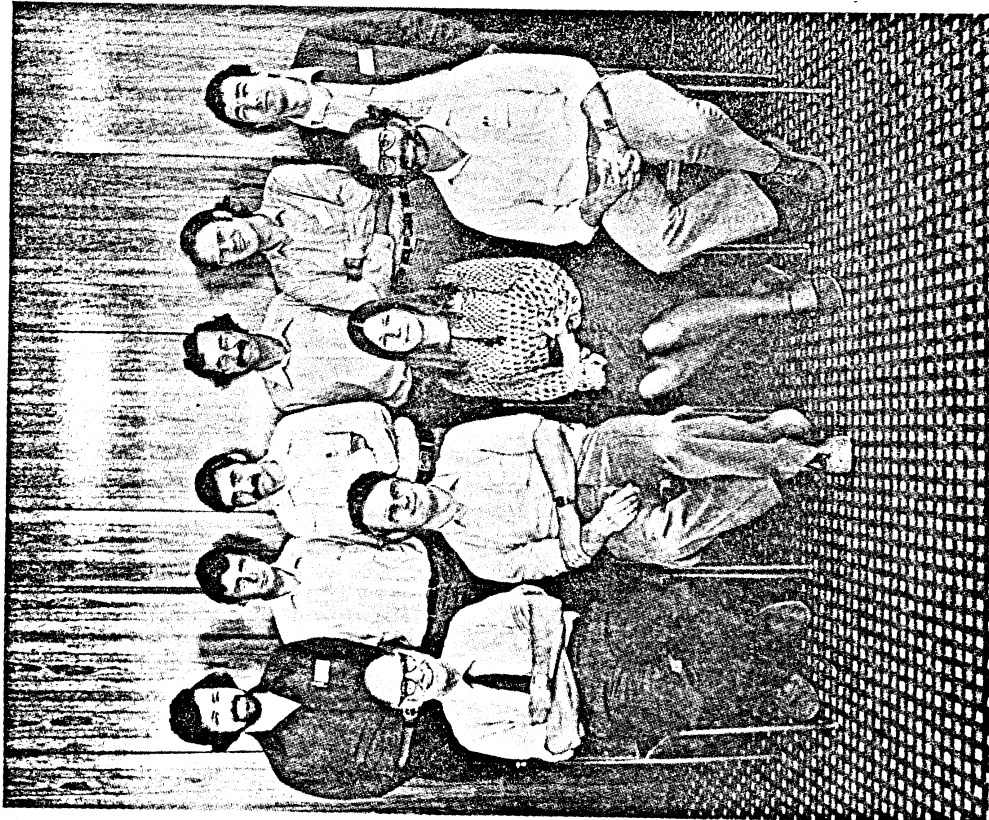


Group on Adaptive Aspects of Development

Evolution and Development, ed. J.T. Bonner, pp. 215-235. Dahlem Konferenzen 1982. Berlin, Heidelberg, New York: Springer-Verlag.



Standing, left to right: Henry Horn, Hans Meinhardt, Rudolf Raff, Dick Strathmann, Wolfgang Dohle, Mike Katz. Seated: John Bonner, Wolf Reif, Mimi Koehl, Stephen Stearns.

Adaptive Aspects of Development Group Report

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INTRODUCTION: ADAPTATION AND CRITICAL COMPARISON

We start with the premise that some changes in development are adaptive and that some are inevitable consequences of physical constraints, developmental architecture, or ancestral legacies.

Any discussion of adaptation is in danger of going around in circles unless the inherently comparative nature of adaptation is fully recognized at the outset. An adaptation is a "better" way of doing something, usually something that has a direct influence on survival and reproduction. "Better" is a comparative term; one must ask, "Better than what?" The answer will vary, but examples involving development usually take one of the following forms. The adaptive developmental pattern in a given environment is better than any other of a range of possible or available developmental patterns that are consistent with the rest of an animal's natural history. In this context, different developmental patterns are similarly adaptive to different natural histories, so a variety of developmental patterns may be adaptive in a given environment. An alternative comparative

statement is that the adaptive developmental pattern is better in a particular environment than in any other of a range of environments that a given beast can or does occupy. An adaptive argument then states that, if adaptation occurs, a given developmental pattern should be found in one type of environment, and another specified kind of development should be associated with another environment.

This form of adaptive argument is discussed more fully by Horn (8) and particularly for adaptive morphology by Reif (21), and it explicitly avoids many of the pitfalls caricatured by Cuppy (5), and catalogued by Lewontin (10). It may also narrow the range of alternative interpretations that must be considered to heed the anti-Panglossian warnings of Gould and Lewontin (6). Other qualifications may be added to this definition of adaptation, and such qualifications were added by various members of our group. Adaptation may be viewed as an intuitive functional statement about an efficient way of doing something, independent of any inference about evolutionary history. As a lineage goes from one environment to another in evolutionary time, the changes in developmental pattern needed to survive at all in the new environment may define an adaptation. The term adaptation may be reserved solely for properties that arise historically by evolution, even though an adaptive pattern, in the sense previously described, could conceivably arise by the competitive sorting of species with fixed developmental patterns into the environments where each pattern was best relative to the others. Each of these restrictions, if used alone to define adaptation, raises epistemological difficulties like circularity, teleology, or unfalsifiability. However, with or without these restrictions, the critically comparative form of adaptive argument may be predictive in the sense of suggesting that we should find surprising associations of traits with environments and with other traits, associations that had not previously been looked for. Furthermore, the comparative adaptive prediction, in this

sense, provides an observational setting that is the logical equivalent of experiment and control.

The notion of comparison and contrast of different adaptations pervaded our discussions. We were dazzled by the variety of developmental patterns displayed by the animals and plants most beloved by our conferees. Whereas other groups could explore the properties of concrete, general mechanisms and patterns of development, we could be neither particular nor general. Instead we explored the ways in which developmental patterns vary over a range of organisms that live in different environments or that share different taxonomic affinities. Every time that someone mentioned a "constraint," someone else reinterpreted it as an "evolutionary opportunity" for a switch to a new mode of life, and a third person would bring up the subject of the complementary "flexibility." To the casual listener, our discussions must have appeared at least irresolute, perhaps contentious, and at best dualistic. However, a thoroughly constructive attitude prevailed. The resulting construction was usually a qualitative statement about the adaptive relation between developmental evolutionary processes at two different levels of organization. Some of these statements are found in the literature, some were invented for the workshop, some were identified as specific and critical areas of ignorance, and some were intriguing, but still hazily formulated. A few could even be expanded into a two dimensional tabular form, with a variety of processes at one level listed across the top and a variety at another level listed down the side, with adaptive predictions filling out the table. To be most useful to the student of life histories, such statements and tables should refer explicitly to survival and reproduction (Stearns, this volume). However, some of our examples were related to these components of fitness only indirectly.

We present these diverse comparative statements and tables below, in all their variety of topics, completeness, and

rigor. The topics are so broad and overlapping that the overall organization is artificial. The rubrics are a) a pattern of patterns of pattern formation, b) developmental processes and evolutionary history, c) constraints as such and as evolutionary opportunities, d) complexities of life cycles, and e) unsettled problems and a wish list.

Most members of our group share several philosophic prejudices that must be kept in mind throughout. There can be no universal optimal pattern of development; evolution can be defined as a heritable change in the way things are done. When "adaptation" is treated as more than an intuitive fact, it is an inherently comparative notion. And a thoughtfully designed comparative-contrastive study of adaptation can have the essential elements of "experiment-control," "falsifiability," "alternative hypotheses," or any other modern method of doing rigorous science.

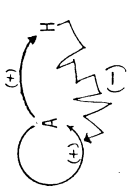
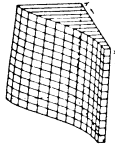
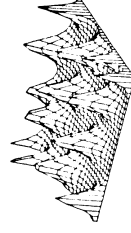
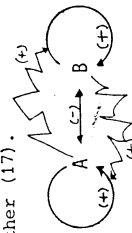

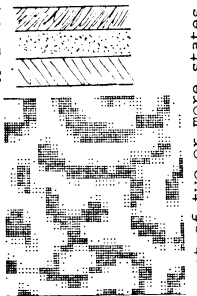
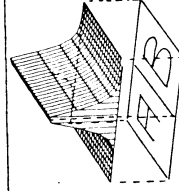
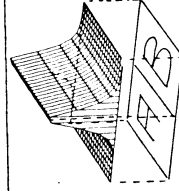
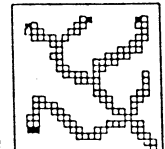
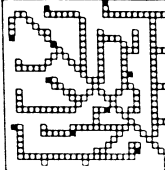
A. PATTERN OF PATTERNS OF PATTERN FORMATION

Although the work of Meinhardt (15-17) belongs properly in the purview of the report by Gerhart et al. (this volume), it is an instructive exercise to view it from our perspective. Table 1 shows the kinds of patterns that are generated by mathematical models of the behavior of substances that are postulated to affect differentiation. This table teaches two important and general lessons. Many patterns typically seen in development can be generated by a few simple and realistic models. Furthermore, different patterns can be produced by changes in the parameters of one model. Compilation of the regulatory features of pattern-forming systems in different species suggests that very few basic mechanisms have evolved. The enormous variety of forms, shapes, and sizes of organisms results more from processes that follow after the basic pattern has been laid down.

DEVELOPMENTAL PROCESSES AND EVOLUTIONARY HISTORY

Katz, Lasek, and Silver (in preparation; see also (26,27))

TABLE 1 - Reactions which lead to pattern formation (15-17).

Type of reaction	Pattern which can be generated
<p>1. Local autocatalysis and long-range inhibition (15).</p> 	 Graded concentration profiles  Bristle-like pattern
<p>2. Long-range activation of states which locally exclude each other (17).</p> 	 Stripe-like arrangement of two or more states.  A pattern centered over the common boundary is formed. Used to organize subfields such as limbs
<p>3. Cooperation of compartments. Cell type A produces, e.g., a precursor, cell type B the final product (16).</p>  Long elongated structures such as veins, tracheae or nerves	 A pattern centered over the common boundary is formed. Used to organize subfields such as limbs
<p>4. Local elongation (15), see type 1, and: local maximum causes cell differentiation, differentiated structure repels the maximum.</p>  A pattern centered over the common boundary is formed. Used to organize subfields such as limbs	 A pattern centered over the common boundary is formed. Used to organize subfields such as limbs

describe the sudden appearance of the dorsal corpus callosum, an intercerebral nerve axon tract found only in placental mammals, as an example of the evolution of a novelty. They argue that because permissive developmental mechanisms were already present, a small number of heritable changes could

immediately produce a dramatic change in phenotype. Katz (this volume) discusses the crucial role that such ontogenetic buffers play in the evolution of novel structure and function; a novelty is of no use unless it can be functionally integrated with what is already there.

Patterns of development are in general more conservative than structures of adults. For example, most mollusks and annelids share a strikingly similar embryology, with spiral cleavage and similar cell fates, but of course their adults differ markedly in form. However, there are many counter-examples, in which development is varied and the adult is conservative. For example, the species of onychophorans, which share affinities with both annelids and arthropods, are difficult to tell apart as adults. Yet their early development differs remarkably among the species; some have yolky eggs and ovoviviparity, others trophic organs, and still others placentation (3).

Biased directions of evolutionary changes in development may lead to persistent developmental maladaptations. For example, crinoids, relatives of the starfish and sea urchins, apparently lost those features that allow relatives to feed as larvae. Crinoids of many species currently live in habitats where most species of sea urchins and starfish have feeding larvae, so there is reason to suspect that a feeding form of larva would be advantageous in crinoids as well; yet no living crinoid has developed a feeding larva (30).

CONSTRAINTS AS SUCH AND AS EVOLUTIONARY OPPORTUNITIES

A given constraint, be it physical, phyletic, or developmental, may have two very different effects. It may constrain the course of evolution, or it may explain a pattern in nature that would otherwise provoke adaptive, functional, or historical speculations. When discussing developmental constraints on evolution, we do not intend to imply that there is a limitation on the genome that prevents it from producing a particular phenotype. What is implied, rather,

is that a certain pattern of development that is characteristic of a taxon restricts the range of that taxon's future adaptations.

Developmental constraints on evolution vary in their severity from difficult, perhaps insurmountable barriers, to constraints that are removed immediately when some other part of the system changes. The evolutionary "choice" of a particular developmental pattern early in the evolution of the body plan of a group of organisms limits the range of future adaptations in a lineage. Yet it may provide unique opportunities for adaptations that are not open to other groups with other body plans. A particularly instructive example, where much is known about both evolution and development, is the five-part radial symmetry of starfish and their relatives, which imposes severe limitations on development and on body form, yet allows extensive adaptive radiation (19). Strathmann (29) notes that the usual structure of echinoderms shows a one-to-one correspondence between units of the water vascular system, including the hydraulic tube feet, and the skeletal plates of the body wall. The one-to-one association has rarely been broken in 500 million years, though the form and number of units varies greatly. The sand dollars have broken this rule, however, with spectacular results; their form requires extensive growth of a limited number of plates, while their feeding requires numerous podia. Hinegardner (7) has found mutants of varying symmetry among sea urchins, apparently controlled by a small number of loci. Therefore there is some hope that the experimental methods of genetics and developmental biology might reveal the mechanisms that produce the podial-skeletal match in living echinoderms and thus suggest the changes needed to break this constraint. In several lineages of echinoderms in the Paleozoic there are indications of an evolutionary trend toward increasing specification of form (28). Skeletal plates in the body wall become definite in number and assume highly specific shapes. Modelling the

growth of these forms, as Raup (20) has done for echinoids, requires increasingly elaborate specification of the generating process. It is not clear whether this specification restricts the permissible forms, or whether, as Vermeij (31) suggests, by permitting a greater potential variety of solutions to adaptive problems, it allows even more finely tuned forms.

An example of much wider scope is the elegant review by Reif and Robinson (22), who classify the mineralized skeletons of animals according to their developmental programs. They define a minimal list of seven qualitatively different mechanisms for the geometrical development of both external and internal skeletons; give appropriate examples, and briefly discuss their value in framing morphological questions.

Constraints directly related to survival and fecundity are difficult to find at our present level of ignorance, but some simple constraining mechanisms can be found. An example comes from the work of Rivest (23). In the snail *Searlesia dira*, which lays its eggs in batches in little capsules, development of some eggs is blocked, and these eggs are eaten by their brother and sister gastrulae. The mother appears to be incapable of controlling the relative numbers of blocked and unblocked eggs that she puts in an egg capsule. So hatching size and hence vulnerability to predators varies greatly and at random within her total brood. A few capsules even get no unblocked eggs with a resulting reduction in fecundity that appears to be maladaptive.

The vital functions of developing and adult organisms are constrained by physical laws that limit the range of possible forms and behaviors. A simple and yet elegant set of such physical constraints has been compiled by Koehl in Table 2. Many different aspects of an animal's relation to its physical environment are affected by change in any dimension, be the change

TABLE 2 a - Physical effects of dimensions of organisms.

Processes & Attributes	Dimensions related to attributes by physical laws
Flow of air or water	$\propto \text{Length} \times \text{Velocity}$
Drag force at small Re^*	$\propto \text{Area} \times \text{Velocity}^2$
Drag force at large Re	
Force of accelerating fluid at large Re (e.g., waves, swimming bursts)	$\propto \text{Volume}$
Thickness of boundary layer of fluid "stuck to" an organism	$\propto 1/\sqrt{Re}$
Surface & exchange properties	
Transport time for diffusion	$\propto \text{Distance}^2$
Transport time for stirring, convection, or circulation	$\propto \text{Distance}/\text{Velocity}$
Force exerted or resisted by surface tension of a liquid	$\propto \text{Length}$
Molecular or electrostatic cohesion	$\propto \text{Area}$
Gravity	
Weight, or force of impact when moving	$\propto \text{Volume}$
Static compressive or tensile stress	$\propto 1/\text{Transverse area}$
Bending stress (Stress is force/area)	$\propto \text{Length}/\text{Diameter}^3$
Stress to buckle a hollow cylinder	$\propto 1/\text{Diameter}$
Muscle	
Maximum force exerted	$\propto \text{Transverse area}$
Maximum power	$\propto \text{Volume}^{3/4}$
Maximum velocity of contraction	$\propto \text{Length}$

* Note: $Re = \text{Reynolds number} = \text{ratio of inertial to viscous forces} = (\text{Length} \times \text{Velocity})/(\text{kinematic viscosity of fluid})$. So small Re implies some combination of small size, low speed, and a viscous medium; large Re implies large size, high speed, and a nonviscous medium.

TABLE 2 b - Crucial physical parameters and structure for small versus large organisms.

Function	Small organism	Large organism
Swimming or flying	viscosity	inertia & streamlining
Locomotion & support	surface tension, molecular & electrostatic cohesion	gravity
Structure (non-aquatic species)	exoskeleton	endoskeleton with tensile elements
Physiological transport	diffusion	convection, stirring, & circulation

during development of an individual or during evolution of a lineage. The shopping list of parameters to be measured is quite small. Yet the few basic ingredients can be combined in many quantitative recipes to yield a rich variety of transitive laws that relate physical structure to biological function, like the laws reviewed by Bonner and Horn (this volume). Since the laws are expressed in quantitative form, they can be used to show how changes in size, shape, and material can compensate for changes in each other or for changes in habitat or behavior. These and other physical rules, such as those discussed by Alexander (1) and McMahon (14), should be consulted as both aid and restraint in theorizing about developmental and evolutionary patterns of size and shape. An important general result from biomechanics is that it often produces alternative, physical explanations for trends that could also generate speculations about comparative embryology or adaptive ecology and life history. Thus biomechanics may provide either an adaptive interpretation of a given pattern or a nonadaptive alternative (6).

The simultaneous conflict and synergy of physical and adaptive interpretations are best shown by examples. Large fan corals are normally oriented perpendicular to the currents that bear their food, and Leversee (9) has shown that this orientation maximizes their interception of food. Yet Wainwright and Dillon (32) have shown that a perpendicular orientation to current is the only dynamically stable position for a stiffly pliable fan, and that young sea fans, initially oriented at random, are "blown" into this position by local currents, and that they then reinforce their new orientation as they grow. The physical interpretation here may be either the mechanism by which adaptation is achieved, or it may be a nonadaptive alternative interpretation of the uniform orientation of sea fans in a current. A converse example is the interpretation of why slow aquatic snails have morphologically ornate shells and faster snails have

streamlined shells. Linsley (12) argues plausibly that this is an adaptation to the relative importance of shape-induced drag when crawling at maximum "snails' pace" in water. Palmer (18) argues that much of this pattern has to do with other adaptations to habitat. Many of the slower snails live in the open, have spines and callosities for protection against predators, and move by slow muscular contraction; the faster snails have streamlined shells to burrow in sand and mud, and they move by rapid ciliary actions. The streamlining indeed reduces frictional drag, but in a semi-solid medium. Other features of shells that facilitate burrowing are discussed by Seilacher (25). He points out the advantages of imbricate ridges like those on clams, he lists the kinds of mechanisms that form them, and he reviews the taxonomic and environmental distribution of these mechanisms. They are found adaptively among burrowers, but also among non-burrowers where the sculpturing of the shell may be yet another example of a nonadaptive consequence of a particular mechanism of morphological development, an epiphenomenon of the sort discussed by Gould and Lewontin ((6), also Gould, this volume).

COMPLEXITIES OF LIFE CYCLES

Life cycles are discussed by Stearns (this volume), Bonner and Horn (this volume) and Wilbur (34). Despite the number and high quality of recent reviews of this subject, our group continually felt the need for more empirical studies and more critically comparative reviews.

Different periods of the life cycle of an organism are differentially plastic and differentially sensitive to environmental influences. The literature relating to these features is copious but diverse and scattered. Reviews of these aspects of life cycles, comparing both broad and narrow taxonomic groups in qualitative and quantitative form, would surely be profitable. The paper by Stearns (this volume) is an exemplar for such reviews.

Post-embryonic metamorphoses produce complex life cycles in which the radically different life forms usually live in different habitats (Bonner and Horn, this volume). The complex life cycle allows differential adaptation to foraging, reproduction, dispersal, or dormancy. The relative assortment of a major proportion of these functions, each and severally, to particular stages of the life cycle, is another topic that would profit from a broad and detailed comparative review. Interesting patterns are surely there, as the following general observations show. Dispersal may be costly or advantageous depending on circumstances, but it certainly occurs at quite different stages in complex life histories. Most frogs and insects disperse as adults, and bottom-living marine invertebrates disperse mostly as larvae. Among marine invertebrates some larvae both disperse and feed, and others are dispersed but do not eat as larvae. Correspondingly, similar stages in complex life cycles may differ greatly in function. For example, both copepods and barnacles have nauplius larvae, but the copepods are dispersed throughout their life and the adult barnacle is cemented to a rock. Dispersal is probably one of the functions of the barnacles' larvae, but need not be for the copepods' larvae.

While metamorphosis clearly allows adaptive diversification within the life cycle of an organism, it may also be viewed as a mechanism that allows convergence of adult form among species that have divergent larvae. This is nicely illustrated by Wassersug's (33) elegant study of the internal oral anatomy of tadpoles of a variety of frogs. The important pattern that emerges is a variety of larval adaptations to habitat, food, and life cycle, even among species whose adults are all reagent-grade frogs. Of particular interest are the larval adaptations to predaceous habits, which involve much simplified gill structure. In most tadpoles the gills arise as little nubbins that subsequently branch

elaborately and are later resorbed in the process of metamorphosis. In some species of predaceous tadpoles the reduced gills look underdeveloped; in others they look like branched gills after partial resorption. The development of these species has not been studied, but it deserves exploration as a possible example of attainment of the same adaptive result by the alternative pathways of retardation versus acceleration of an aspect of development. It might provide a literal example of "the two faces of heterochrony" (Gould, this volume) making a single facies.

Another potentially interesting case of heterochrony in metamorphosis comes from Raff and Kaufman's (19) reinterpretation of Lynn's (13) classic study of the embryology of the terrestrial tropical frog, *Eleutherodactylus nubicola*. This frog and its many congeners differ in ontogeny from distant relatives. The changes are in such gross features as the actual sequence of developmental events, the retarded development of some skull bones, and the loss of intermediate stages of development that are remarkably conservative in many other amphibians. The adult form is little changed, however, looking superficially like tree frogs that have a free-living tadpole stage. The condensed ontogeny of *Eleutherodactylus* is associated with complete development within the egg, which has allowed the beast to become independent of stable bodies of water for breeding, and thus to invade a new habitat. Lynn (13) suggested that many of the developmental oddities were consistent with precocial activity of the thyroid, but the changes in the very order of developmental events suggest that this is more than a trivial concatenation of embryogeny with metamorphosis. It is not clear whether the unusual features of development in *Eleutherodactylus* have any adaptive significance in themselves, or whether they are non-adaptive correlates (Gould, this volume) of the evolutionary reduction of a complex life cycle to a "simple" one.

Another way of looking at metamorphosis is as a mechanism that isolates different parts of the life cycle and permits independent evolution of each part (Freeman, this volume). Wassersug's (33) frogs, discussed above, are one example. Another comes from the work of Willis and her collaborators ((36), see also (24,35)) on the cuticular proteins of insects, which form important structures in larva, pupa, and adult. At any one stage, a large number of electrophoretically distinct proteins are involved in the formation of cuticle, and most of these proteins are unique to their respective stages. There is substantial evidence suggesting that the electrophoretically different proteins are encoded in different parts of the genome. Thus superficially similar structures appear to be separately encoded for larva, pupa, and adult, with the result that these stages are not constrained to follow totally interdependent courses of evolutionary adaptation.

Complex life cycles spread the development of adaptations to different vital functions over the whole life span. In a sense, some properties like those of embryos are present as metamorphosis and regeneration in the adult stages, just as adult structures and functions may be found in larvae (Freeman, this volume). This offers a special opportunity to disentangle the roles of various mechanisms of morphological change in development. Although the following case does not provide a direct example, it at least provides a metaphor. Pattern formation in early life stages takes place on a scale of millimeters and less ((15-17), also Gerhart et al., Kaufman and Wakimota, and Wolpert, this volume). The resulting patterns then grow up until they are one to several orders of magnitude larger, a scale at which the same chemical mechanisms simply cannot work. The regeneration of the adult pattern following injury, if it occurs, cannot use the deterministic mechanism that originally formed the pattern in the embryo. This may be yet another reason why polar bears do not regenerate lost limbs (cf. Gerhart et al., this volume). As usual, there are instructive counter examples, like Hydra, in which budding

and regeneration are similar in sequence and in details of pattern formation (4), and many other instances in which metamorphosis occurs at a small enough size for chemical and micromechanical mechanisms of pattern formation to function.

Among insects, the higher flies have a particularly interesting mechanism for pattern formation at metamorphosis ((2), also Kaufman and Wakimoto, this volume). During larval life, certain cells are sequestered in a somewhat embryonic state; these cells form the imaginal disks, which at metamorphosis undergo episodes of proliferation, pattern formation on a small local scale, and further differentiation. Anderson (2) makes an eloquent plea for appropriate studies to discover to what extent this segregation of adult rudiments in embryogenesis "is predicated in the embryos of other orders" of insects. More generally among invertebrates with larvae there is great variation in the degree to which larval tissues are carried into the adult stage or instead histolyzed or even eaten! The implications of this variation are surely great, but they have barely been specified, let alone analyzed, either theoretically or empirically. A further related variation, also with important implications for evolution, is the degree of predetermination of cell fates at metamorphosis (Freeman, this volume).

The important question from an evolutionary point of view is whether life histories with radical metamorphoses have different evolutionary potentials and constraints than those with more gradual transitions, and if so, what they are. The possibilities discussed above for such differences include: balance of plasticity versus canalization (Stearns, this volume), specialization to habitat and to life cycle function (Bonner and Horn, this volume), evolutionary independence of larval versus adult stages, consequent conservatism versus radiation of either larval or adult adaptation (Freeman, this volume), patterns of pattern formation (Gerhart et al., this volume), consequent potential for regeneration of lost or injured parts, and speed of the transition between forms that are adapted to very different functions or habitats.

UNSETTLED PROBLEMS AND A WISH LIST

Throughout our discussions we felt the need for more critically comparative reviews of our subject matter, especially the subject of complex life histories. These reviews should explore likely constraints of development and possible adaptive patterns of development. They should further explore the ways in which life histories can be modified by alterations of size, shape, and developmental timing. At a grander level, the reviews should explore the question of: To what extent are changes in life histories important in the long-term changes of evolution, and if they are not important, what additional factors are?

These comparisons should be carried out at several levels:

a) between genetic variants of a single species, b) between closely related species, and c) between higher taxonomic groups, up to and including phyla. Comparisons of genetic variants are critical because heritability is a central part of the evolutionary mechanism. Closely related species provide developmental patterns that are qualitatively similar enough for similar and consistent description, and perhaps even for a quantitative analysis. More distant taxa provide interesting qualitative differences in developmental patterns, which by the very fact that they are not qualitatively similar, provide evidence of evolutionary innovations. Explicit contrasts between different levels of comparisons may help to discover why developmental patterns are generally less comparable among distant taxa than among close taxonomic relatives, as well as what role microevolutionary changes in developmental patterns may play in the evolution of higher taxa.

Those are the goals. Specific predictions come from theoretical work in biomechanics, adaptive life histories, and adaptive patterns of development. If the data are gathered in an appropriate comparative context, for example, in a group of organisms that has undergone extreme evolutionary radiation

compared with a group that is more conservative, in groups that inhabit different environments, or in groups that appor-tion relative specialization to habitat in different ways through complex life cycles, then such data will both test the predictions and suggest new patterns in need of explanation.

Once the goals are set and the method of comparison is specified, the following list of data required becomes per-functory: adult size and shape, size at birth, rate of maturation, age at maturity, brood size, interbrood interval, longevity, senescence, habitat, ecological role, pattern of growth and differentiation, plasticity of form, degree of genetic control, and degree of environmental control.

On a few important topics, our discussions were severely hampered at the outset by a lack of the most basic information. These topics are in special need of both review and new data. We heartily endorse the lists of problems at the ends of the papers by Bonner and Horn and by Stearns (this volume). In addition, we endorse Wolpert's and Alberch's (this volume) wish for more explicit understanding of geometric models and metaphors involving developmental fields, positional information, induction, and morphogenetic programs; in particular we need to know the physical and chemical machinery responsible for these idealized processes and properties, as well as the way that they may be controlled and changed by genetic mechanisms. There is a distinct gap between the discussion of Dawid et al. and Gerhart et al. (both, this volume) that needs to be filled. A similar gap exists in our knowledge of the comparative variation of hormonal and physiological systems that mediate between development and crucial aspects of life history, such as growth, survival, reproduction, and senescence (Bonner and Horn, and Stearns, this volume). The relative capacities of different species for regeneration and its adaptive significance are clearly subjects worthy of critical review. In fact the whole topic of complex life histories is in need of several reviews, as was mentioned explicitly in the previous section of this report.

Hoary descriptive embryology should not be ignored in the modern reviews that we wish. For example, in a classic descriptive embryology of clams, written in 1895, Lillie ((11), pp. 36-37) presents evidence that can be interpreted in the modern language of Wessells and of Freeman (this volume) as showing adaptive modification, in a supposedly conservative taxon, including: changes in cell fates, changes in relative rates of cell division, changes in cytoskeletal matrix to alter placement of mitotic spindles, and consequent rearrangement of blastomeres (19). Conversely there are many topics for which old-fashioned data and observations are crucial and yet missing. Paradoxically this is the case for many insects (2) and marine beasts, despite the fact that the developmental patterns of so many "off-the-shelf" organisms in these groups are known in exquisite detail. These groups are of particular importance to ideas about the macroevolutionary events involved in the origin of phyla (Freeman, Maderson et al., this volume).

Finally, the reviews should be written in a style that is mutually intelligible to students of many academic fields. For example, developmental biology and paleontological morphology share little common language, but both must communicate their studies of shells and skeletons before one can fully understand the evolution of "novelties" that actually appear in the fossil record.

Acknowledgement, As rapporteur I am very thankful to all participants in this conference, but especially to the members of this group. Their efficient communication of ideas, data, and enthusiasm to a student of ecology and animal behavior was exemplary of the kind of communication that is the ultimate desire in our wish list.

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