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## Transformationalism, Taxism, and Developmental Biology in Systematics

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**Abstract.**—Issues concerning transformational and taxic comparisons are central to understanding the impact of the recent proliferation of molecular developmental data on evolutionary biology. More importantly, an understanding of taxism and transformationalism in comparative biology is critical to assessing the impact of the recent developmental data on systematic theory and practice. We examine the philosophical and practical aspects of the transformational approach and the relevance of this approach to recent molecular-based developmental data. We also examine the theoretical basis of the taxic approach to molecular developmental data and suggest that developmental data are perfectly amenable to the taxic approach. Two recent examples from the molecular developmental biology literature—the evolution of insect wings and the evolution of dorsal ventral inversion in vertebrates and invertebrates—are used to compare the taxic and transformational approaches. We conclude that the transformational approach is entirely appropriate for ontogenetic studies and furthermore can serve as an excellent source of hypotheses about the evolution of characters. However, the taxic approach is the ultimate arbiter of these hypotheses. [Co-option; development; evolution; taxism.]

Developmental biology has a long tradition of comparative studies. The proliferation of molecular-developmental data used to address evolutionary and systematics questions (e.g., Abouheif, 1997, 1999; Averof and Cohen, 1997; Bolker and Raff, 1996; Damen et al., 1998; Damen and Tautz, 1998; De Robertis and Sasai, 1996; Gilbert et al., 1996; Gould, 1997; Lowe and Wray, 1997; Panganiban et al., 1997; Patel, 1994; Patel et al., 1992; Popadic et al., 1996; Quiring et al., 1994; Raff, 1996; Shubin et al., 1997; Sordino and Duboule, 1996; Telford and Thomas, 1998a, 1998b; Tomarev et al., 1997; Wray, 1999) warrants a reexamination of methods of data analysis and interpretation. In recent years, as more has become known about the molecular basis of development and morphogenesis of model organisms, developmental biologists have made attempts to answer longstanding evolutionary questions. In these instances, there has been a tendency to address these questions concerning the origin of particu-

lar morphologies in a traditional, transformational epistemological framework (Eldredge, 1979; Patterson, 1982; Reippel, 1988). Regardless of the kind (e.g., morphology of fossil or extant taxa, DNA sequences, gene expression patterns, embryonic tissue types, ontogenetic sequences, behavior) or quality of data, a logically defensible and consistent methodology for interpreting them must be adopted to be scientifically meaningful. A brief review of the transformational and taxic (Eldredge, 1979; Patterson, 1982; Reippel, 1988) comparisons that can be made in comparative biology are given, followed with two examples from the developmental biology literature that promulgate explanatory hypotheses for insect wing origin (Averof and Cohen, 1997) and dorsal-ventral body axis inversion in animals (De Robertis and Sasai, 1996). A very brief review of the traditional hypotheses for insect wing origin is presented, not as a focus of this paper, but rather, to equip the reader with context for a topic that is somewhat arcane for nonentomologists. The wing origin and dorsal-ventral body axis inversion examples are

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presented as modern cases that illustrate the intrinsically equivocal nature of transformational hypotheses.

#### TOPOLOGICAL CORRESPONDENCE AND TRANSFORMATIONAL BIOLOGY

Biological features can be compared in terms of similarity—an approach that determines what features seem alike or as a variation on a theme. This consideration of topological correspondence, or similarity of corresponding parts of organisms, can be in terms of the relative size of a feature, its shape, its presence or absence, percent similarity of nucleotides or amino acids, and so forth, and constitutes descriptive comparison. The significance of the observation of similarity is not inherent in the data itself; epistemological constructs must be specific to attach significances in a biological sense (Reippel, 1988; Nelson, 1994). The following three underlying assumptions are apparent in many of the molecular-development-based evolutionary explanations:

1. Two taxon comparisons of molecular developmental data (most visibly the use of *in situ* hybridization and antibody staining patterns) allow observation of evolutionary character transformations.
2. Similar gene functions in the developmental precursors of corresponding morphological structures indicate direct evolutionary relationship between the morphologies.
3. Similar gene function, as demonstrated in developmental studies, has primacy over other kinds of character data in determining evolutionary relationships.

Characteristic of most of the evolutionary conclusions found in the recent molecular developmental literature, transformational biology "seeks to document, within an evolutionary lineage, the continuity of morphological change" (Reippel, 1988:96). Transformational biology attempts to infer the processual link between discrete forms in terms of a graded transition true to the Darwinian tradition, thus equating historical and topological transformations (Brady, 1994a:21–22).

#### TAXIC BIOLOGY AND PHYLOGENETIC RECONSTRUCTION OF CHARACTER TRANSFORMATION

Transformational biology offers a first approximation of the identities of organismic features (Brady, 1994a, 1994b). It is useful for determining categories of kinds, for example, limbs, and subcategories, for example, wings. It is not capable of determining the evolutionary relationship of the subcategories—whether the arm or the wing came first or whether they uniquely share an origin—without making evolutionary assumptions. To make this determination requires taxic comparative biology. Taxic biology (taxism) summarizes all relevant available data for a group of relationships of organisms in a treelike topology (assuming life arose once). This is especially advantageous over transformational analytical techniques because it enables the distinction between features that have a unique origin from those that may have arisen more than once (Fig. 1). Figures 1a and 1b show that, for a given occurrence of a character or character state, taxic and transformational approaches have the potential to describe the evolution of the character opposingly. Taxic biology uses the hierarchical arrangements of taxa to infer that the character has arisen twice (Fig. 1a). Transformational biology uses the apparent continuity of morphological change of two taxa to interpret the character as conserved (Fig. 1a). For given occurrences of other characters, taxic and transformational biology may converge on a similar interpretation of character evolution (Fig. 1b).

Two typical examples among many in the literature, the origin of insect wings (Averof and Cohen, 1997) and dorsal-ventral axis inversion (De Robertis and Sasai, 1996; Hogan, 1995; Kimmel, 1996) are discussed in the following sections. These examples demonstrate how some molecular-developmental data have been used in evolutionary studies. (Other examples include eyes—Dickinson, 1996; Gehring, 1996; Hanson and Heyningen, 1995; Quiring et al., 1994; Roush, 1997; limbs—Panganiban, 1994; Panganiban et al., 1995, 1997; Shubin et al., 1997; Sordino and Duboule, 1996; segmentation in arthropods—Averof and Akam,

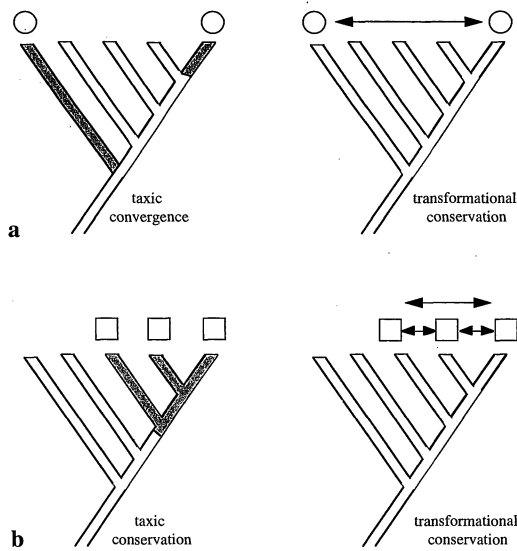


FIGURE 1. Comparison of detection of convergences in taxic and transformational approaches in comparative biology. Taxic biology is capable of uncovering convergence, whereas transformational biology cannot. (a) Taxa with the occurrence of a particular character or character state are indicated by the circle above the terminal. Double-headed arrow indicates apparent discovery of continuous change by the transformational method. Shaded parts of the tree indicate inferred origin of the character by the taxic method. (b) Taxa with the occurrence of a second character are indicated by the square over the terminals. Arrows indicate the three possible inferences of continuity when using the transformational approach. Shaded areas of the tree indicate the single origin of the character inferred using the taxic method.

1995; Damen et al., 1998; Damen and Tautz, 1998; Patel, 1994; Patel et al., 1992; Tautz and Sommer, 1994; Telford and Thomas, 1998a, 1998b; and insect mandibles—Popadić et al., 1996). As we suggest below, both examples utilize the transformational approach to make claims for the origin and evolution of morphological features based on localization of gene products.

#### INSECT WING ORIGIN

Several hypotheses have been proposed for the persistent problem of insect wing origins. None of these has been supported by direct evidence—no wing intermediate-stages have yet to be unambiguously identified in any proto-pterygote taxa. Averof and Cohen (1997) have suggested that,

based on gene expression patterns, the problem has been solved. The following is a brief overview of the competing hypotheses and the developmental data.

The tergal lobe derivation, or paranotal, hypothesis is indicated by fossil evidence. Small, flat pronotal lobes suggestive of wings project from the prothoracic tergum, as well as other thoracic, and head, tergites of Carboniferous insect fossils. Wings are thus postulated to have developed from similar lobes from the other thoracic segments (Snodgrass, 1935); Wooton (1976) suggests that meso- and meta-thoracic paranotal lobes of extant insects show topological similarity to the prothoracic lobes of a Permian Ephemeropteran and the extinct insect orders Paleodictyoptera, Protodonata, and Protorthoptera. Both of these hypotheses depend on the interpretations of the fossils and require inference of a transformation of these lobes into wings.

Kukalova-Peck (1978, 1983, 1991), presenting a hypothesis of wings as leg derivatives, argues that the proto-wing originated from a flattened, first segment (epicoxa) of the euarthropodan upper leg and its exite. This suggests that coxal endites found in basal fossil arthropods and in some extant arthropods have given rise to insect wings, but only if the early insects have the equivalents of these leg segments. No extant or extinct taxa do. But Kukalova-Peck (1983) hypothesizes a total of 11 segments in early insects and that the modern number of 6 leg segments is a product of fusions, subdivisions, and incorporation into the body wall, based on contentious interpretations of fossils. This hypothesis, like those discussed above, also depends on inferring a transformation, in this case of an appendage that would have been derived from a leg segment that has not even been demonstrated to have an equivalent leg segment in any known extant or extinct insect taxa.

The styli/endite hypothesis proposes that wings are derivations of thoracic styli of a terrestrial, apterous insect that would have resembled a machilid, of the most basal insect (*sensu strictu*) lineage (Wigglesworth, 1973). This hypothesis relies on the morphology of basal, extant insects rather than fossil insects or fossil arthropods. Again, this hypothesis depends on in-

ferring a transformation, in this case of thoracic styli into wings.

A final hypothesis argues for wing derivation from breathing organs. Classical work suggests that wings were derived from tracheated external branchial lamellae of the air-breathing "Ancylozoa," whereas Gegenbauer (1870) postulates their derivation from tracheal gills of an aquatic ancestor. As in all the others discussed previously, these hypotheses require an inferred, not observed, transformation of the putatively ancestral structure into the insect wing.

Averof and Cohen (1997) present data in support of the hypothesis of derivation of insect wings from gills. This conclusion is based on the gene expression patterns of two *Drosophila melanogaster* genes, *nubbin* (*pdm1*) and *apterous* (*ap*), and their *Artemia franciscana* (brine shrimp) counterparts, *Af-pdm* and *Af-ap*, respectively. *pdm1* is expressed throughout the prospective wing and in a set of rings in leg primordia in *D. melanogaster*. *Artemia Af-pdm* shows expression over most of the developing limb bud. At a later stage, when the limb shows signs of regionalization, the expression is sequestered to distal epipodite primordia, in which expression is maintained, and from which a gill eventually develops. Averof and Cohen (1997) also document *Af-pdm* in *Pacifastacus leniusculus* (Class Malacostraca: Decapoda), expressed in the epipodite lobe as well as in rings along the length of the leg; *Af-pdm* expression is not detected in the endopods of the first thoracic segment of *Pacifastacus*.

*Apterous* is expressed on the dorsum of developing wings as well as in a ring in the fourth tarsal segment of *D. melanogaster* legs. In *Artemia Af-ap* is expressed in a similar pattern to plain *Af-pdm*. The authors stress that *Drosophila* leg primordia expression patterns are less like *Drosophila* wing primordia patterns, which are more like the crustacean epipodite patterns. Averof and Cohen (1997) thus depict a transformation involving an epipodite gill of a hypothetical ancestor of crustaceans, insects, and myriapods into a wing, with a retention of the gill in the larvae of mayflies, and indicate four independent losses of the epipodite gill. But because observations of the expres-

sion of these genes were not made in myriapods (which do not have a single origin themselves) or mayflies, it is difficult to make a determination of unique origin of either wings/gills or *ap/pdm*. Effectively, Averof and Cohen present a pairwise comparison of Crustacea and *Drosophila*. The data indicate similar expression patterns of two genes, not any observation of a morphological transition. It is also not evident, based on these data, whether these features are convergent or not. Their conclusion is dependent on many assumptions: (1) The most recent common ancestor of crustaceans, insects, and myriapods had multi-branched appendages and epipodite gills; (2) the groundplan for Crustacea includes biramous appendages with epipodite gills; (3) Crustacean gills share a unique evolutionary origin with mayfly larval gills; (4) larval mayfly gills can be transformed to *Drosophila* wings; (5) similarity of crustacean epipodite molecular patterning to *Drosophila* wing patterning necessitates the two morphological features as derived from a common ancestral structure; (6) all crustaceans, myriapods, and insects have *ap/pdm* expression in some leg-related structure. The molecular-patterning data do not address assumptions 1–5. The final assumption remains to be substantiated, but would not be sufficient to override the evidence supporting what is known about the phylogenetic relationships determined from a large number of other characters. Perhaps the authors have defined the presence of embryonic *ap/pdm* expression as a gill, so that anything having *ap/pdm* expression must be defined as a gill—although the appearance of *ap/pdm* expression in *Artemia*, *Pacifastacus*, and *Drosophila* leg primordia and fourth tarsal segment of the adult are not discussed with respect to wing identity. The fact that the leg primordia should show ring-like expression patterns of *ap/pdm*, whereas transcripts of *ap/pdm* are also observed in the fourth tarsal segments of *Drosophila* legs, are interesting observations that warrant further investigation.

#### DORSAL-VENTRAL BODY AXIS INVERSION

*Bone morphogen protein-4* (*BMP-4*) and *chordin* (*chd*), homologs of *Drosophila de-*

*capentaplegic* (*dpp*) and *short gastrulation* (*sog*), respectively, have been found in *Xenopus* (Francois and Bier, 1995; Francois et al., 1994; Holley et al., 1995; Kimmel, 1996; Sasai et al., 1994, 1995; Wieschaus et al., 1984; Zusman et al., 1988). In *Drosophila*, *sog* is expressed in the venter and suppresses *dpp*, a dorsal morphogen, whereas *sog*'s *Xenopus* homolog is a dorsal organizer that induces dorsal mesoderm and the central nervous system. Injection of *Xenopus* embryos with *Drosophila dpp* and *sog* demonstrates conserved function (De Robertis and Sasai, 1996). Thus some conclude that arthropods and vertebrates share a common ancestor, dubbed the Urbilateria. This conclusion assumes that (1) current *BMP-4/dpp* and *chd* gene function is shared by all taxa between vertebrates and *Drosophila* and (2) current gene function has not been modified since the origin of deuterostomes. The conclusion depends on an abstracted ancestor, defined by *BMP-4/dpp* and *chd/sog* expression data of two taxa, to infer a transformation from Arthropoda to Vertebrata. Thus these authors appear to be suggesting that invertebrates and vertebrates should be recast as sister groups, to form the Urbilateria. Dorsal-ventral axis inversion is plausible only if the body axis is defined as the interaction of *dpp* and *sog* or *BMP-4* and *chd* (which De Robertis and Sasai [1996:39] suggest must be done) and the body organization of all other real taxa that fall between arthropods and vertebrates (including the radially symmetrical echinoderms) is considered secondary.

The demonstration of *sog* and *dpp* activity in *Drosophila* wing vein development complicates the view that a conserved *dpp/sog* and *BMP-4/chd* interaction defines dorsal-ventral axis patterning. Yu et al. (1996) have shown that *dpp* is expressed in vein precursor cells in the pupa, whereas *sog* is expressed in the intervein-cells and suppresses the formation of veins. It would seem that De Robertis and Sasai (1996) have in fact uncovered a part of a signaling pathway (the TGF- $\beta$  signaling pathway) that has been conserved in evolution but co-opted for patterning very different aspects of the body. This observation in itself is extremely interesting. It is unclear why a similar function of a pair of genes, or even a

whole genetic pathway, need take precedence over morphological and phylogenetic evidence (Abouheif, 1997; Jeffries and Brown, 1995; Kimmel, 1996; Peterson, 1995; Romer and Parsons, 1986) that would otherwise support treating dorsal-ventral patterning of flies and frogs as having independent origins. Only with the assumption that convergent features should bear no similarity to each other at the genetic level should one suspect a gross inversion of body plans. But this assumption has not been empirically justified. Even Aristotle (1991 translation) realized that similarity didn't necessarily indicate that two different organisms were of the same stock (in his sense, they did not share the same essence). A commonly postulated mechanism for the evolution of function in organisms is that genes may be co-opted for different functions (Abouheif, 1997; Lowe and Wray, 1997; Roth, 1988, 1991; Wagner, 1989). There is no evidence to indicate that the different functions might not appear similar, and, perhaps, it might be "easier" for genes to retain their functions through evolutionary time and be re-used in different taxa for similar functions as their original ones. Initially assuming that gene expression is equivalent to the body axis precludes the ability to test whether or not this possibility is correct.

#### TRANSFORMATIONALISM, TAXISM, AND SYSTEMATICS

The previous examples demonstrate an inherent difference in transformational and taxic comparative biology. Although transformation-based observation is appropriate for ontogenetic study, its propriety in determining the evolutionary history of an attribute or taxon is questionable. The empirical basis of ontogenetic study is in the direct observability of transformations, whereas in phylogenetic study transformation is not observable (deBeer, 1930; Roux, 1895). What can be observed about growth and development of different taxa is inextricably bound with the respective phylogenetic histories of each of the taxa. Thus transformationalism to reconstruct phylogeny, or some part thereof, necessitates the abstraction of the transition states. Prob-

lematic when the sole means for reconstructing phylogeny, transformationalism is invalid when considered the primary basis for redefinition of a morphological feature as a gene expression pattern. The establishment of this identity is common in attempts to redefine the gene expression pattern as the embodiment of an abstracted intermediate of a morphological transformation. There is no evidence that the evolving feature did not cease to exist when being modified through evolutionary time and then reappear in full integrity as a morphological whole again once finished, like some kind of neoplastic transformation. Even full knowledge of what genes were involved, or how they were modified, does not constitute direct evidence for what state the morphology looked like in getting from taxon A to taxon B—if, indeed, the morphological product of taxon A actually has any affinity to that of B, for transformationalism does not allow identification of independent acquisitions of characters. Taxic comparative biology reconstructs ancestral character states on a cladogram to document the transitional states from one ancestral state to other states. It results in explicit statements of hierarchical relationship based on the sum of evidence of relationship, not just one piece, for the taxa of interest.

Transformationalism offers a hypothesis as to whether two features can be comparable and is equivalent to making definitions. Only through reconstruction of history can the degree of comparability be discovered. One can compare anything one wants, but only with other criteria can one determine how comparable those things are. As Reippel (1985) points out, the taxic approach produces stable schemes of order. A stable scheme or relationship is required for determining the point of origin and subsequent modifications of a morphological character or, for that matter, any character.

The two methods are intrinsically different and therefore address different problems. The transformational approach makes definitions about the observed attributes and hence will always result in positive statements about comparability. The taxic approach discovers the hierarchical relationships of taxa and attributes to present the means to obtain both positive

and negative statements about the uniqueness of character origins, depending on the level of comparison, and allows for the testing of hypotheses of the relationships of characters against each other. In a taxic framework the presence or absence of a gene or gene product, or of the kind of function it performs, may be shown to be informative at a higher phylogenetic level but not at a lower one, where morphological or other characters provide evidence of relationship. It follows that each of these levels of organization—the gene, the function of the gene, and the morphology that the gene (and presumably many other genes) mediates—represents different levels of biological information with various degrees of independence (Abouheif, 1997, 1999; Wray, 1999; Wray and Abouheif, 1998). Gene expression patterns cannot universally be equated to morphological features without empirical justification. This empirical justification would be acquired by concurrently analyzing gene sequences, expression patterns, and morphology as well as other sources of characters in phylogenetic analysis (Janies and DeSalle, 1999).

#### CONCLUSION

The preceding discussion impinges on a single concept, homology, still a contentious term in modern biology (Bolker and Raff, 1996; Tautz, 1998; Wilkins, 1998). It should be acceptable to all that the terminology used for biological definitions in reconstructing hierarchical relationships in cladistic methodology be unambiguous, precise, and reflective of empirical observation. If the phylogenetic phenomena to be documented are the origin and uniqueness of a morphological character, then the relationships of taxa must first be established. Thus we must follow Patterson (1982), defining homology as synapomorphy, a shared, derived, unique character, because of its direct relationship to cladograms reflecting phylogenetic relationship and sum of character data available for taxa. Other branches of biology and approaches to phylogeny reconstruction do not necessarily follow or agree with this austere definition of homology.

Molecular-developmental expression studies are sometimes suggested as revealing the evolutionary origin of a given morphological character. This suggestion assumes that similar gene expression is a reasonable criterion for equating or homologizing a set of morphologies. Sometimes they are also treated as though they should supercede other criteria (e.g., morphological, fossil) as infallible markers of history. However, when morphology is defined as gene expression, the ability to discover how closely genes and morphology evolve with respect to each other is eliminated. Indeed, it is not empirically demonstrated, but rather is often assumed, as in the examples discussed above, that there is a one-to-one correspondence between the evolution of a given gene expression pattern and morphology. Gene expression patterns in embryonic tissues reflect yet another aspect of topographical similarity of primordial morphological features. Use of this, or any other, source of comparative data to address questions of unique origins of attributes requires the construction of a cladogram from all available evidence that would approximate the genealogical relationships of the group in question. Only then can characters be traced on the tree to identify analogous or homologous features. Modern, molecular-developmental techniques will eventually be of general interest in systematics. Its use, perhaps, will be most fruitful in reanalysis of convergent characters, analyzing the underlying basis for morphological units of evolution, and discovery of new character systems (DeSalle et al., 1996; Janies and DeSalle, 1999).

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