Historical Patterns of Developmental Integration in Piranhas

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SYNOPSIS. To test the hypothesis that developmental integration coordinates evolutionary change through history, we dissect the spatial and temporal integration of ontogenetic allometries of piranha body form and examine the evolutionary coordination among ontogenetic features by a phylogenetic analysis. Few of our characters provide evidence in support of the hypothesis. In general, we find that developmental integration is historically labile, being modified at virtually every speciation event. Most of the ontogenetic features are dissociated in their phylogenetic changes and evolve in a mosaic fashion. Indeed, developmental integration is so labile that primitively integrated features of ontogeny usually evolve subsequently as independent characters. Evolutionary changes in developmental integration can result in increased or decreased integration on the ontogenetic time scale. When localized features are deleted from ontogeny, or when spatially integrated features are gained, the derived ontogenies may be more integrated in a spatial sense. The end result of phylogenetic dissociations may be a more highly developmentally integrated ontogeny. Thus, in the piranhas we studied, we find a historically coupled increase in developmental integration caudally and a decrease in developmental integration cranially.

INTRODUCTION

Since the days of Cuvier, many biologists struck by the intricacy and complexity of morphology have wondered how change can occur at all. How can an organized system, comprising many interacting and interdependent parts be transformed into another such system? Developmental integration enters into explanations for coordinated change in two ways. First, an organized, complex adult is not directly transformed into another organized, complex adult. Rather, it is ontogeny that is transformed (e.g., Bock, 1989; Bonik et al., 1979). Second, developmental integration may be a source of evolutionary coordination since parts of an organism develop in a coordinated fashion and thus evolve as a coherent unit (e.g., Rensch, 1959; Frazetta, 1975; Gould, 1977; Cheverud, 1982a; Thomson, 1988; Hall, 1992).

For developmental integration to be a source of long term evolutionary coordination, it must be historically conservative. Developmental associations among characters can hardly coordinate character evolution if the associations fragment and reorganize while morphology evolves. Long term developmental integration may engender coordinated changes regardless of any benefit to an organism and it is for this reason that developmental integration has been regarded as an intrinsic constraint (e.g., Gould, 1977, 1982; Maderson et al., 1982; Zelditch and Carmichael, 1989). Whether this integration is regarded as a source of...
coordination or constraint depends largely on whether the correlations are viewed as adaptive or as necessitated by integration. While this is an important issue, there is a more basic one: does developmental integration, in fact, generate coordinated change? Evaluating evidence for this proposed relationship between developmental and historical integration is our primary aim herein.

We examine the evolution of ontogenetic allometry, a classic example of coordinated evolutionary transformations resulting from coordinated ontogenetic transformations (e.g., Huxley, 1932; Rensch, 1959; Frazzetta, 1975; Gould, 1982). The tie between ontogenetic allometry and developmental integration was clearly expressed by D'Arcy Thompson (1917). As he saw it, changes in shape due to growth gradients would be expressed as a modification of a large number of organs and regions; allometric change would be global and graded across the organism. But we find that growth need not be so highly integrated and simple. Spatially localized, as well as spatially widespread processes, can result in a change in body form, and we have found evidence of both highly localized changes and large-scale, highly integrated changes in the ontogeny of one piranha, *Pygocentrus nattereri* (Zelditch and Fink, 1995). In this case, all changes occur over the same interval of ontogeny, so they are integrated in a temporal sense. In our view, developmental integration refers to these spatially or temporally associated ontogenetic changes of an individual (Zelditch et al., 1992; Zelditch and Fink, 1995). We are particularly interested in exploring the ontogeny and evolution of body shape because much of the diversity of piranhas lies in shape. Adult piranhas differ in numerous features, including profiles of head and postcranial body, depth of the head relative to the body, and also in more subtle features such as fin position and proportions of preand postorbital head. These differences arise from modifications of growth.

We make no attempt to distinguish constrained from beneficial correlations here. The literature on the functional and ecological morphology of piranhas is sparse, so we prefer to avoid speculating about which features may be adaptations. There is evidence that features of body shape are important to locomotory and feeding performance (Alexander, 1967; Webb, 1984), however. Some authors have gone so far as to claim that observations of body shape can be used as a surrogate for direct observation of natural history because body form is so closely tied to ecology (Winemiller, 1991). More relevant to our concerns is the idea that modifications of piranha shape exemplify change of integrated design (Alexander, 1975).

We use two tools in this analysis: A morphometric method for describing shape change, and parsimony-based phylogenetic analysis for inferring historical patterns. The morphometric method, the thin-plate spline decomposed by its partial warps (TPS; Bookstein, 1989, 1991) has a critical advantage for studies of spatiotemporal integration: it explicitly localizes shape change on the organism (e.g., Zelditch et al., 1992). A second advantage, one crucial for our purposes, is that these morphometric features can be analyzed like any other characters, so we can use the basic concepts and methods of phylogenetic systematics to reconstruct their history (Zelditch et al., 1995; Fink and Zelditch, 1995).

DEVELOPMENTAL INTEGRATION OF PIRANHA BODY FORM

Figure 1 depicts the shape changes during juvenile growth for five species of piranhas; *Pygopristis denticulata* and *Serrasalmus gouldingi* are the outgroups for our study of *Pygocentrus cariba, P. nattereri* and *P. piraya* (description of the landmarks, list of the specimens analyzed, justification for choice of outgroups, and other characters analyzed are given in Fink and Zelditch [1995]).

It is visually obvious that there are differences in ontogeny among these species. Our first aim is to localize change on the organism (technical details are given in Bookstein [1989, 1991]; less technical accounts are in Zelditch et al. [1992]; Swiderski [1993]; Zelditch and Fink [1995]; Fink and Zelditch [1995]). First, net change is decomposed into uniform and nonuniform components;
in a uniform change, each small square on
the grid is transformed into the same paral-
lelogram in the same orientation. Nonuni-
form change varies from region to region.
The nonuniform component can be decom-
posed into a series of components at pro-
gressively smaller spatial scales; changes de-
scribed at smaller spatial scales refer to those
not already described at larger scales. Figure
2b illustrates the component at the largest
spatial scale, which resembles a U-shaped
gradient of growth rates; a more localized
component (Fig. 2c) describes elongation of
the region between dorsal and adipose fins
relative to the caudal peduncle; another quite
localized feature (Fig. 2d) describes elon-
gation of the postorbital region relative to
the eye and snout.

We can draw ontogenetic trajectories for
each component. We could depict the tra-
jectory in terms of change in each direction
(antero-posterior, dorso-ventral) relative to
body size, or, as we do here, by the change
in the antero-posterior relative to the dor-
so-ventral directions (Fig. 3). We draw a line
connecting the expected value for shape at
smallest and largest sizes analyzed. In our
outgroup taxa, *Pygopristis denticulata* and
*Serrasalmus gouldingi* there is change in
both directions, as indicated by the arrows.
However, there is no ontogenetic change in
species of *Pygocentrus*; since this feature

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**Fig. 1.** Ontogenetic shape change in five species of piranhas. Top left: Landmarks sampled for shape analysis. Others: Ontogenetic shape change depicted as Cartesian deformations. Each depicts the change from a juvenile of about 20 mm SL (from tip of snout to base of caudal fin) to an adult of about 250–300 mm SL.
FIG. 2. Three progressively more localized spatial scales of shape change. Right: Shown by vectors depicting relative landmark displacements. Left: Shown as a Cartesian deformation.

has the same expected value for adults and juveniles, no lines are drawn.

We summarize ontogenetic trajectories for each feature (Fig. 4; for descriptions of the particular features summarized here, see Fink and Zelditch [1995]). The length of the trajectory is proportional to its contribution to net ontogenetic change, so we can see which are dominant by comparing their relative lengths. By our definition of developmental integration, the most highly integrated pattern would be one in which the features at large spatial scale dominate. Although the uniform and three largest-scale components contribute substantially to developmental integration, more localized features also do. We conclude that these ontogenies are not highly integrated spatially. But since the changes occur over the same range of sizes, they are highly integrated temporally.
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Fig. 3. An ontogenetic trajectory for a localized shape feature. This is the component shown in Figure 2c, oriented as in *Pygopristis denticulata*, and shown here as vectors of relative landmark displacements (a). (b) Ontogenetic trajectories for shape change at that spatial scale; species are symbolized by the first letter of their specific epithet.

THE EVOLUTION OF DEVELOPMENTAL INTEGRATION

We examine the evolutionary change of these features by inspecting their distribution on the cladogram. For information on all characters used in our analyses, and the methods for coding the characters, see Fink and Zelditch (1995). Briefly, we code the trajectory by whether shape change is present or absent in each direction at each spatial scale. If present, but in different directions, such as relative head deepening in one case and relative head shallowing in another, we code them as different states. Analysis of all characters results in a single most parsimonious cladogram (Fig. 5), the same one implied by osteological, myological and meristic data. We have categorized the novelties according to whether an ontogenetic transformation was gained, lost or reoriented; reorientation here means evolutionary change in the direction of ontogenetic change.

According to the hypothesis we are testing, developmentally integrated features evolve as integrated units. Interpreted strictly, we would expect to see the same patterns of integration on both ontogenetic and phylogenetic time scales; that is, we would expect the full complement of ontogenetic transformations to be modified together in history. In the context of a cladogram, then, we would see ontogenetic transformations of the features changing together at the same node. However, as is evident from the

Fig. 4. Ontogenetic trajectories of shape change in two outgroup species, and in *Pygocentrus cariba*. The trajectories are ordered from highest to lowest spatial scale, with the highest spatial scale at the top. The horizontal axis is aligned with the anteroposterior body axis; the vertical axis is aligned with the dorsoventral body axis. The uniform and nonuniform components are drawn at incomensurate scales; all nonuniform components are drawn to the same scale. PW = partial warp.
cladogram, these two time scales exhibit different patterns of associations. Subunits of the primitively integrated ontogeny dissociate and evolve independently. At a single node, some primitive ontogenetic transformations may be lost, some novel ontogenetic transformations may be gained, and some may be regained but reoriented (see the novelties of *P. nattereri*, Fig. 5). At virtually every speciation event, developmental integration is modified.

If we interpret the hypothesis less strictly, we can see some evidence of coordinated evolution due to conserved developmental integration. Two primitively integrated features of ontogeny (PW2Y, PW4Y) are lost at the origin of *Pygocentrus*. Together, they are regained but reoriented, in *P. nattereri*. These features describe the primitive deepening of the posterior body relative to the head (PW2Y), and increase in the curvature of the back associated with an increase in the convexity of head and posterior body profiles (PW4Y). In *P. nattereri* we see a *shallowing* of the posterior body relative to the head and anterior back, and a *reduction* in the curvature of the back associated with a *decrease* in the convexity of the head and posterior back profiles. One other pair of features is also coordinated in both ontogeny and evolution, but only through one transition (PW9X, Y). Primitively, the region between dorsal and adipose fins is elongated and deepened relative to the caudal peduncle during ontogeny, and both these aspects of ontogeny are lost together at the origin of *Pygocentrus*.

We also find another kind of developmentally integrated evolutionary modification. Ontogenetic transformations that are highly integrated in a spatial sense represent a form of developmental integration. When these are primitively present, and modified in evolution, they result in a spatially widespread modification of the body. We have an example of this, the body-wide uniform deepening that is a primitive feature of piranha ontogeny. As evident in Figure 3, there is a substantial increase in the rate of uniform deepening in *Serrasalmus gouldingi*. This deepening does not produce an exceptionally deep-bodied adult, however, because the juvenile of *S. gouldingi* is exceptionally shallow-bodied. Here the mechanism that produces a homologous feature of adult form, body deepening, is novel. But only the timing is novel, as the integrated deepening of the body is a primitive feature.

Despite these few examples of developmentally integrated novelties, the dominant pattern in these piranhas is dissociation and decoupling of developmentally integrated features. The general pattern is a sequential, stepwise accumulation of novelties, a pattern classically termed "mosaic evolution" (De Beer, 1954). But the correlations among evolutionary novelties do not result from conserved developmental integration. Rather, as a result of mosaicism, derived ontogenies are made up of components that have different histories. For example, in the ontogeny of *P. nattereri* we find some retained primitive features, such as the ancient combination of the U-shaped gradient (PW3X) and relative elongation of postcranial head + nape (PW7X). In addition to these features, which are at least as old as
piranhas, other features of *P. nattereri* ontogeny, such as elongation of the snout relative to the eye (PW12), are as old as *Serrasalmus + Pygocentrus*, and others, such as elongation of the postorbital region relative to the eye + snout (PW11) are as old as *Pygocentrus*.

Modifications of developmental integration, like conservation of developmental integration, can produce coordinated evolutionary changes. Some novelties of development have pervasive effects on morphology, e.g., loss of a large scale spatially integrated feature has consequences distributed throughout the body. Some other novelties, when acquired together but localized to smaller areas, can also be pervasive because they affect several regions of the body in a temporally integrated manner. In both such cases, evolutionary coordination arises from changes in integration, not from an inherited pattern of integration.

It is possible that even on short time-scales we would see the stepwise mosaic pattern. Our temporal resolution does not permit the tracking of changes generation by generation. The novelties we regard as simultaneous in their origin might be acquired piecemeal, each added sequentially generation by generation. By placing several novelties at the same node, we do not claim that the whole suite of novelties arose by a single saltation. Given the evidence that these arose in a mosaic fashion over long time-scales, we see no reason to doubt their stepwise accumulation over short time-scales as well.

The overall pattern of developmental integration in these piranhas is labile but many of its components are homologous over a variety of hierarchical levels. Our findings are contrary to other studies which explicitly compared patterns of integration, because their conclusions were that there is no hierarchical, phylogenetic pattern in the evolution of integration (e.g., Riska, 1985; Lovsfold, 1986; Kohn and Atchley, 1988; Cheverud, 1989; Wagner, 1989; Zelditch et al., 1990; Atchley et al., 1992). Differences among taxa were explained by random factors, independent of evolutionary relationships. That we come to a different interpretation is probably due to major methodological differences between our study and those others. One major difference is that we have analyzed patterns of ontogenetic transformations rather than patterns of static inter-individual covariation, as done in the studies just referenced. These are different notions of "integration" altogether, and since the relationship between ontogenetic and static allometries can be complex (Cheverud, 1982b), it is possible that the contrast in our interpretations may be due to the variant concepts of integration. Also, we are using a different technique for describing integration. But, most importantly, we have used a different method for comparing patterns of integration. Typically, comparative studies of integration have looked for phylogenetic patterns by asking if there is greater overall similarity among covariance matrices of closely related taxa than among those of more distantly related taxa. These are comparisons of overall similarity. Our analysis is the first to compare patterns of integration from the perspective of phylogenetic systematics.

The decoupling and dissociation of developmentally integrated features described here is consistent with findings from numerous studies of heterochrony. Dissociation is commonly found when studies look at multiple features (e.g., Alberch and Alberch, 1981; Fink, 1982; McKinney, 1986; McNamara, 1988). In addition to dissociated modifications of temporally integrated features, the form of dissociation typically detected in studies of heterochrony, we also find dissociation of spatially integrated features. This may be an example of what Wagner (1996) termed "parcellation." This parcellation is indicated by subdivision of spatially integrated features into more localized ones. For example, we see the acquisition of localized change in the postorbital region (PW11X) at the origin of *Pygocentrus*. Primitively, all change in the postorbital region was due to processes at a higher spatial scale, but at the origin of *Pygocentrus* there appears to be a gain of a localized change (PW11X). This implies a gain of a localized region-specific growth rate. It is possible that some of the instances of dissociation reported in the literature on heterochrony are also instances of dissoci-
ated spatial integration, what we have called “heterotopy” (Zelditch and Fink, 1996). Because studies of heterochrony look exclusively at changes in temporal pattern, they neglect this other form of dissociation.

Dissociations can also result in more integrated ontogenies. For example, primi
tively in piranhas there is localized ontogenetic change in the caudal peduncle region. In Pygocentrus, all change in that region is due to processes at higher spatial scale. This implies a loss of a region-specific growth rate. In this case, the phylogenetic dissociation results in an increase in the ontogenetic integration of the caudal body. An important consequence of analyzing spatial scale is the potential for identifying those dissociations that increase ontogenetic integration.

The regular discovery of dissociation argues against the hypothesis that the epigenetic nature of development impedes mosaic evolution. According to that view, organisms will undergo coordinated evolutionary transformations because of developmental integration (e.g., Thomson, 1988; Hall, 1992). Gould challenged the view of organisms as integrated; he considered that mere prejudice dictates the perception of organisms as integrated systems (Gould, 1977, p. 234). He proposed an alternative view of organisms, emphasizing their dissociability. In the case of piranhas, the dissociation we see on the historical time scale may be due to the developmental dissociability of growth processes. Most of the ontogenetic integration we have detected in these piranhas is temporal. This could mean that many processes regulate growth and that their integration reflects no more than that growth occurs during a particular phase in the life-cycle. Taxa exhibiting more spatially integrated ontogenies might exhibit less mosaicism in evolution. For example, skull growth of the cotton rat Sigmodon fulviventer is highly integrated after weaning (Zelditch et al., 1992). Virtually all postweaning skull growth can be described by an anteroposterior gradient of growth rates. Transformations in that gradient would result in a coordinated change of skull proportions throughout the skull. If most of mammalian skull growth is due to a small number of highly integrated processes, there could be a developmental basis for skull-wide changes in proportions.

In contrast to widespread assumptions about the conservatism of development, and consequent invocation of developmental integration as a stabilizing force in evolution, we find that developmental integration itself evolves. Such a finding is perhaps not surprising, but the frequency with which integration changes may be. Our results show changes in integration at every speciation event examined, sometimes leading to more highly integrated ontogenies, sometime to less integrated ones. While our study is of a limited sample of the history of piranha evolution, the diversity of body forms within the group suggests that further investigation will corroborate our results.

We have found features which are correlated during ontogeny, but which have different histories; and there are features which are historically correlated, but which are not developmentally correlated. We have also shown that the ontogeny of any particular species is a complex of features with different histories, including changes that have occurred as recently as the immediately preceding speciation event, and as long ago as the origin of the entire clade. Our methods of investigation of developmental integration are the first to allow tracking of changes in ontogeny in a historical framework, so that we are able to tease out developmental transformations that occurred at particular times in the history of this teleost group.

ACKNOWLEDGMENTS

This work was supported, in part, by the ASZ Division of Systematics and Division of Vertebrate Morphology; by NSF funding for the symposium DEB-9406574; and by NSF grant DEB-9220619 to MLZ and NSF grants BSR-8600115 and DEB-8206939 and Horace H. Rackham Research Grant from the University of Michigan to WLF. We benefitted greatly from discussions with participants at the symposium.

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