

Allometry and Developmental Integration of Body Growth in a Piranha, *Pygocentrus nattereri* (Teleostei: Ostariophys)

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ABSTRACT Piranhas, like many teleosts, change their diets on both ontogenetic and phylogenetic time scales. Prior studies have suggested that pervasive morphological changes in body form on a phylogenetic time scale may be related to changes in diet, but previous reports have found little shape change in piranhas on an ontogenetic time scale. We re-examine the post-transformational allometry of body form in one piranha, *Pygocentrus nattereri* (Kner), using the method of thin-plate splines decomposed by their partial warps. We find substantial evidence of allometry, primarily elongation of the mid-body relative to the more anterior and posterior regions, elongation of the postorbital and nape regions relative to the more anterior head and posterior body, and deepening of the head relative to the body. In addition to these pervasive changes throughout the body, there are some that are more localized, especially elongation of the postorbital region relative to eye diameter and snout, and an even more localized elongation of the snout relative to eye diameter. Initial dietary transitions are associated with changes in head and jaw proportions, but rates of shape change decelerate through growth, so that the final transition to a diet increasingly dominated by small whole fish appears associated with change largely in overall body size. © 1995 Wiley-Liss, Inc.

Evolutionary morphologists have long attempted to explain the diversification of complex morphological structures. Of particular interest are the ways in which diverse parts of morphology can be modified in a coordinated fashion. Often, changes in parts of the form are associated in ontogeny, a phenomenon termed “developmental integration” (Zelditch et al., '92). Because morphological diversification arises by changes in ontogeny, developmental integration may be responsible for complex, congruent changes in diverse parts of morphology on both ontogenetic and phylogenetic time scales.

Many teleost lineages exhibit considerable diversity of body form, involving modifications of numerous regions of the body. In the case of piranhas, South American freshwater teleosts, these modifications include changes in convexity of dorsal and ventral profiles, in body depth, in bluntness of the snout, and in proportions of the head, snout, and jaws (e.g., Géry et al., '87; Jégu et al., '88, '91; Fink, '89, '93). Diversity of body form has been linked causally to ecological diversification, specifically, to acquisition of specialized diets

(Werner, '74; Werner and Hall, '79; McKaye and Marsh, '83; Moyle and Senanayake, '84; Keast, '85; Winemiller, '89, '91). Head and body depth have been singled out as the aspects of piranha form related to diet (Nico and Taphorn, '88). In particular, most piranhas specializing on flesh reportedly have deeper bodies and heads than those eating primarily fins and scales. Several workers have advocated the concept of “ontogenetic trophic units” (Livingston, '80; Stoner, '80; Stoner and Livingston, '84; Werner and Gilliam, '84; Nico and Taphorn, '88; Winemiller, '89) because morphology, diet, and perhaps intensity of competition and degree of ecological specialization change on ontogenetic as well as phylogenetic time scales.

Ontogenetic transitions in diets have been noted in piranhas (Machado-Allison and Garcia, '86; Nico and Taphorn, '88). Small juveniles of all piranha species feed on small aquatic invertebrates, particularly insect larvae. In the clade consisting of *Serrasalmus*, *Pristobrycon*, and *Pygocentrus* many species add scales and fins to the juvenile diet. Within this clade, adult diets are quite diverse: Some

adults feed on fins and scales, some feed on plant materials, or some combination of plants and flesh; adults of other species, such as *Pygocentrus*, the piranha of myth and folklore (Roosevelt, '14), are nearly restricted to flesh (Machado-Allison and Garcia, '86; Nico and Taphorn, '88). Given the proposed relationship between diet and body form on a phylogenetic time scale, we might expect to see a similar relationship on an ontogenetic time scale. Yet, previous descriptions of the ontogeny of *Pygocentrus nattereri* have detected little ontogenetic shape change, with the exception of a striking negative allometry of eye diameter and a slight enlargement of head and anterior body relative to standard length (Fink, '89, '93). The description of *P. nattereri* as generally isometric is consistent with analyses of other *Pygocentrus* (Fink, '93). It is also consistent with generalizations emerging from studies of other teleosts: Little shape change occurs after the larval period (Fuiman, '83; Strauss and Fuiman, '85).

Given this interpretation of little allometry during post-transformational growth, it appears unlikely that evolutionary changes in this phase of growth could be responsible for the diversity of body forms. It also appears unlikely that developmental integration among changes in form during juvenile growth could be responsible for integration among changes on a phylogenetic time scale. In this study, we re-examine these conclusions by analysis of the ontogeny of body form of *Pygocentrus nattereri*, for which we have a particularly large sample drawn from natural populations. We re-evaluate the ontogenetic association between size and shape and explore the integration of changes throughout the body.

We have a geometric view of integration, discussed in more detail in Zelditch et al. ('92). In the context of this perspective, we would consider body and head form to be developmentally integrated should they exhibit an anteroposterior growth gradient or similar large-scale transformations spanning several anatomical regions. In contrast, we would judge body and head form to be less integrated should most of the shape change be highly localized within small regions.

MATERIALS AND METHODS

Data

Specimens of *Pygocentrus nattereri* used herein are listed in Fink ('93). *Pygopristis denticulata* examined are from the Museo de

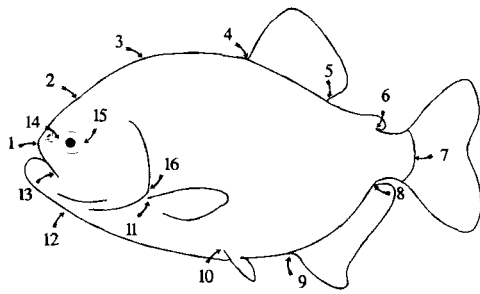
Biología, Universidad Central de Venezuela (MBUCV 10690, spec. 8 and 9) and the Museo de Ciencias Naturales, Guanaré, Venezuela (MCNG 3243, spec. 1). Sizes ranged from post-transformation juveniles with undeveloped pectoral fins (20.5 mm standard length [snout tip to base of the caudal fin]), to large, breeding adults (277 mm SL). We examined a total of 89 specimens. Subdividing these into the size classes for which dietary information are available from Nico and Taphorn ('88) for *P. cariba*, the hypothesized sister group of *P. nattereri* (Fink, '93), we have ten specimens in the 20–39 mm SL class (eating primarily microcrustaceans and aquatic invertebrates), nine in the 40–79 mm SL class (eating primarily fins and scales), 42 in the 80–159 mm SL class (eating primarily chunks of flesh), and 28 in the >160 mm SL class (increasingly taking small whole fish) (these diet data are corroborated for *P. nattereri* by Fink, unpublished).

Specimens from many localities in the Amazon and Paraná/Paraguay rivers are being treated as a single sample, as Fink (1993) found no geographic variation or sexual dimorphism in form among these populations.

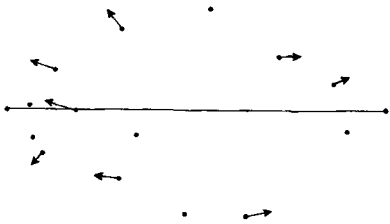
We digitized landmarks, discrete points that can be recognized as "the same" point in individuals at all sizes, and which can be argued to sample homologous parts of all piranhas, on the left side of each individual (Fig. 1A). As these fishes are laterally flattened, little information is lost or distorted when they are projected onto a plane. Landmark locations were transformed to shape coordinates; points 1 and 7 were selected to be endpoints of the baseline and assigned coordinates (0,0) and (0,1) (Bookstein, '86, '91; Tabachnick and Bookstein, '90). All specimens were transformed to the same baseline orientation and length, a transformation that does not change shapes of landmark configurations.

Methods of shape analysis

Figure 1B displays ontogenetic change in shape of an average small *P. nattereri* to an average large *P. nattereri* using these shape coordinates. Each of the shape coordinates can be viewed as a vertex of a triangle drawn to the baseline. The objective of the analysis is to describe spatial organization of the changes in form and where on the organism these changes are localized. We use the method of the thin-plate splines, decomposed by their partial warps (TPS; described more



A



B

Fig. 1. **A:** Landmarks used for description of shape change in *Pygocentrus nattereri*: 1, snout tip, anteroventral junction of anteriomedial borders of premaxillaries; 2, anterior border of epiphyseal bridge bone at the dorsal midline (an insect pin was inserted into the top of the cranium to detect the border, and was left in place for digitization); 3, posterior tip of supraoccipital bone where it lies adjacent to epaxial musculature and the median dorsal septum; 4, dorsal fin origin, not including anterior modified fin rays, marking the anterior junction of the fin and the dorsal body midline; 5, posterior end of dorsal fin base at the dorsal body midline; 6, posterior end of adipose fin base, where it joins with the skin of the posterior back on the dorsal midline; 7, posterior border of hypural bones (identified as the bending axis of the caudal-fin base); 8, posterior end of anal fin base, at the ventral midline; 9, anal fin origin, marking the junction of the fin and the ventral body midline; 10, pelvic fin insertion, where the fin projects laterally from the pelvic girdle; 11, pectoral fin insertion, where the pectoral fin extends laterally from its joint with the pectoral girdle; 12, mandible/quadrates joint (usually marked by an insect pin placed in the middle of the joint), marking the junction between the lower jaw and "face"; 13, posterior border of maxillary bone, where it intersects the third infraorbital (cheek) bone; 14, anterior border of bony orbit, along the horizontal body axis; 15, posterior bony border of orbit, along the horizontal body axis; 16, posterior border of bony operculum, at most posterior point from the snout tip. **B:** Net shape change during ontogeny, as displayed by shape coordinates (relative to baseline drawn between points 1 and 7).

technically below and in Bookstein, '89, '91) because we cannot know in advance of analysis which triangles span developmentally autonomous units and which combinations of triangles extend over developmentally integrated areas. Clearly more than one of the areas circumscribed by the triangles changes shape in ontogeny. The spatial organization of changes cannot be inferred by inspection of the individual triangles. Nor can the separation between changes common to all triangles and those that vary across the form be effected by multivariate analysis of the variances and covariances among shape coordinates. Unlike some methods which require that developmentally discrete units be specified in advance (e.g., finite-element analysis) TPS permits the partitioning of the organism to be determined empirically (Zelditch et al., '92). We prefer the approach taken here because, in our case, we do not know which of the changes are spatially widespread nor which are confined to small regions—this discovery is the aim of the analysis. For a discussion of the comparative merits of alternative methods for analyzing the same landmark data, see Bookstein ('91) and Zelditch et al. ('92).

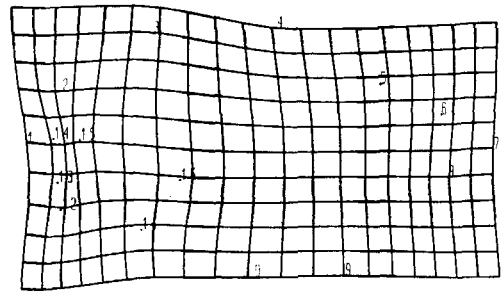
To describe ontogenetic change in body form, we model shape change as a deformation using TPS. This approach, which we use to obtain localized shape variables, employs a physical metaphor, the bending of infinitely thin metal plates, that does not imply any kind of developmental model. The approach can be understood by visualizing the landmarks of one form located on an idealized thin steel plate. Relative displacements of landmarks in the plane of the page are imagined to be vertical displacements of the steel plate. Some sets of the vertical displacements elevate or rigidly rotate the steel plate; these represent affine (uniform) transformations, those in which parallel lines on the two-dimensional starting form remain parallel after deformation. Other sets of displacements require bending of the steel plate, equivalent to bending of parallel lines on the starting form (non-uniform transformations). Steel plates bend in a manner which minimizes both the magnitude of bending and the physical energy required to produce that bending over the whole plate. The formula that describes the conformation of this plate can also be used to describe landmark displacements, in a manner minimizing the implied localized information (Bookstein, '91,

pp. 318–319). The quantity minimized, “bending energy,” “regional distortion” or “localized information,” is not a function of a biological process. This metaphor simply provides the mathematical machinery for decomposing shape change into progressively more localized components, which can then be inspected for their contribution to shape change. We are trying to find areas of the body that change, not to model specific developmental processes.

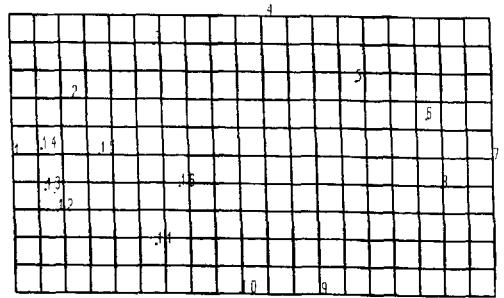
The net shape change (Fig. 2A) can be decomposed into *uniform* (Fig. 2B), and *nonuniform* (Fig. 2C) components; for detailed descriptions of these changes, see the Results section. The uniform component describes changes that are geometrically uniform over the body: Every small square of a starting grid superimposed on the starting form would be transformed to the same parallelogram in the same orientation though ontogeny. This is the most spatially integrated change possible—the whole form would be changing as if it were a single part. In terms of these triangles, all those drawn from each shape coordinate to the same baseline would agree in the principal directions and strains of the shape change.

The nonuniform component describes transformations that differ in different *regions* of the body. This nonuniform component can be further decomposed into a hierarchy of components (principal warps) ordered by bending energy, which is inversely related to spatial scale. Those with low bending energy describe features at large spatial scale because little energy is required to bend the (metaphorical) steel plate between widely spaced landmarks. In contrast, it takes relatively more bending energy to bend the plate between closely spaced points, thus the components with high bending energy describe more localized features of shape change, those confined to closely spaced landmarks.

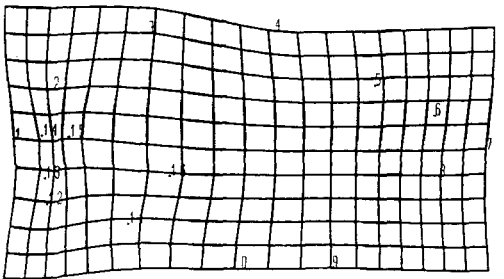
Figure 3 shows three such components in order of decreasing spatial scale. Figure 3A shows a large-scale feature, elongation of the mid-body relative to the head and more posterior body. In the middle (Fig. 3B) is one at a smaller spatial scale, expansion of the postorbital head, nape, and post-pelvic belly relative to the anterior head and pre-pelvic belly. At the bottom (Fig. 3C) is one at small spatial scale, elongation of the snout relative to eye diameter. Changes described at progressively smaller spatial scales are those not already described by a change at a higher spatial



A

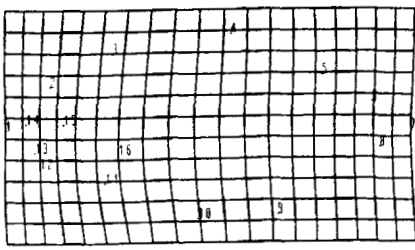


B

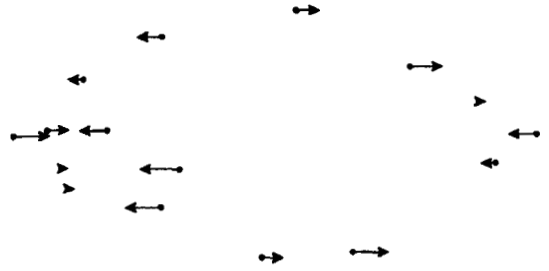


C

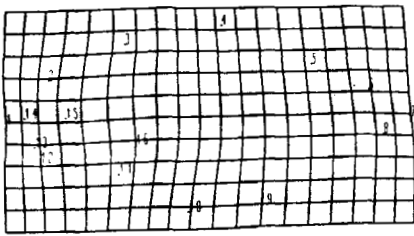
Fig. 2. *Pygocentrus nattereri*. Ontogenetic shape change depicted as Cartesian deformations. A: net change; B: uniform (affine) component; C: nonuniform component. For detailed descriptions of these changes, see the Results section.



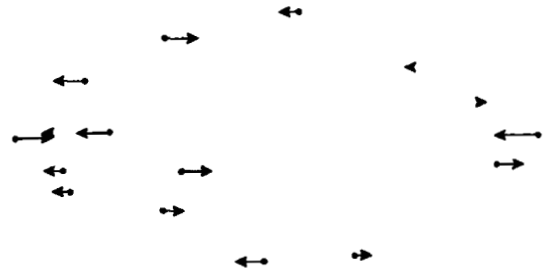
a.1



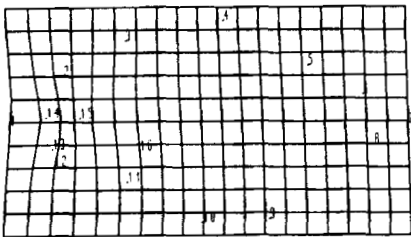
a.2



b.1



b.2



c.1



c.2

Fig. 3. *Pygocentrus nattereri*. Three components of shape change of body form. a.1 describes the change at a large spatial scale (PW3), with relative landmark displacements depicted as Cartesian transformation; a.2: the same change depicted by vectors. b.1 and b.2 present a component at intermediate spatial scale (PW7), depicted as above; c.1 and c.2 present the most localized of the three components (PW11), as above.

scale. Thus, the elongation of the snout relative to eye diameter refers to a change not already described by the changes in head and nape proportions, or in head and midbody proportions at higher scales.

The biological signal does not lie in the number of these components, nor in the pattern of landmark displacements they describe—both are entirely a matter of the location of landmarks in the starting form,

the form to which all others are compared. Each principal warp represents the canonical form, or "mode," of relative landmark displacements for shape changes at that scale of localization.

The signal comes from inspection of the vectors multiplying each of these principal warps, the *partial warps*, which express the contribution each principal warp makes to the realized landmark displacements. Thus, principal warps are geometric terms in which morphological differences *can* be described while the partial warps describe *realized* changes in those terms.

Most real biological shape changes incorporate both uniform and nonuniform components. We estimated the uniform component by the factor-approximation given in Bookstein, '91, p. 279. We used F.J. Rohlf's program TPSPLINE, available with Rohlf and Bookstein ('90) to do the analysis by thin-plate splines (we used the Format Conversion program, also available with Rohlf and Bookstein '90, for converting digitized coordinates into the format required by TPSPLINE). For instructions on how to obtain the current versions, write rohlf@ssbiovm.bitnet. Additional programs for computing TPS (JSpline) or visualizing the vector displacements (Vector Specter) are available from Julian Humphries (jmh3@cornell.edu).

In our analysis of piranha form and ontogeny, we use an average small juvenile *Pygopristis denticulata* (Cuvier) as our starting form (the average specimen is based on MBUCV 10690, specimens 8 and 9 and MCNG 3243, specimen 1). *Pygopristis* is the presumed sister-group to the clade comprising *Pygocentrus*, *Serrasalmus*, and *Pristobrycon*. A single starting form ensures homology of the regions of the body, to the extent that the points sampled are homologous in this clade. We are thus able to extend the analysis to other piranhas, exploring the modifications of ontogeny that gives rise to the diversity of piranha shapes. In this analysis of the ontogeny of *P. nattereri*, the changes we describe refer to features of that species only—differences between large and small *P. nattereri*—as the choice of starting form determines only the geometry of the principal warps. Thus it is only the particular ways in which changes are localized that are effected by the starting form choice.

Measurement of size

In the case of poikilotherms, size may be an estimate of biological age more closely tied

to growth than chronological time (Strauss, '87). For our size measure we use root centroid size (CS), the square root of the summed squared distances of all landmarks to the center of the form. CS is the only size variable uncorrelated with shape in the absence of allometry (Bookstein et al., '85; Bookstein, '91). Of the diet/size classes discussed above, the 20–39 mm SL class is approximately equivalent to 29–57 mm CS; the 40–79 mm SL size class is approximately equivalent to 58–116 mm CS; the 80–159 mm SL class is approximately equivalent to 117–233 mm CS; and the > 160 mm SL class is approximately > 234 mm CS. Because centroid size increases by more than a factor of 10, and most shape change occurs over initial stages of growth, our shape variables are more nearly linearly related to the log transform of centroid size (LCS) than to CS; we thus used LCS as the size variable in our statistical analyses. However, untransformed CS is more easily interpreted in terms of the familiar SL, as these are linearly related, so our graphics present ontogenetic changes associated with CS.

We analyzed the association between size and shape by multiple regression of log centroid size on the two-dimensional partial warps, to determine if the aspects of shape described at that scale changed ontogenetically. Those partial warps with a table-wide statistically significant association with size (judged by a sequential Bonferroni test [Rice, '86]) were interpreted as exhibiting ontogenetic change. Coefficients describing the size-related change in shape along the two body axes (anteroposterior, dorsoventral) were obtained by simple regression of each dimension on log centroid size.

To depict the relative magnitudes of shape change at each spatial scale, in each direction, we present the regressions for those judged statistically significant drawn to the same scale (Fig. 5). Thus, the contribution each component makes to the overall change can be seen by the magnitude of change along the y-axis.

RESULTS

There is substantial evidence of allometry in these piranhas. The regression of the partial warps on log centroid size is highly significant ($P < .0001$; $R^2 = 0.967$). In the descriptions below of non-uniform shape change, each paragraph is arranged by a spatial scale, with potential shape changes, as described by the principal warps discussed first, followed

by discussion of realized shape change, if any, described by the partial warps.

Uniform shape change

A uniform transformation would be visible in antiparallel displacements of shape coordinates on opposite sides of the baseline (for example, dorsal points displaced anterodorsally while ventral points are displaced posteroventrally) with the magnitudes of these displacements proportional to the distance of each point from the baseline. As is evident in Figure 2B, ontogenetic change in *P. nattereri* does not appear to have a large uniform component, although there is a statistically significant association between uniform change and size ($P < .0001$). Most of this change occurs in the dorsoventral direction, as uniform body deepening; lesser change in the anteroposterior direction reflects a slight anterior shift of dorsal landmarks and dorsad shift of ventral landmarks.

Nonuniform shape change

Following the numbering convention of Zelditch et al. ('92), we number the warps in order of decreasing spatial scale. We report analyses for all the localizable features, whether or not shape change occurs in that region.

At the highest spatial scale, PW1 describes a contrast between the mid-body points and those at the anterior and posterior of the form. Depending on orientation, this warp would describe a gradient of either anteroposterior elongation or shortening, a classic axial growth gradient (if oriented along the x -axis here), or associated changes in dorsal and ventral profiles (if oriented dorsoventrally, along the y -axis here). Although we find considerable variability in *P. nattereri* at this scale, we do not detect an association between change in form and size ($R^2 = 0.031$).

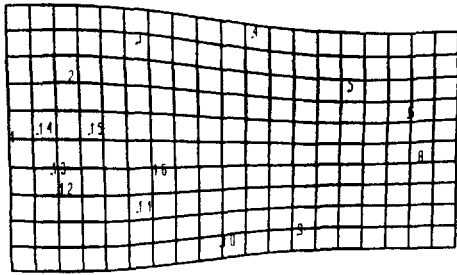
At the next lower spatial scale, PW2 describes contrasting displacements of the landmarks at the anterodorsal and posteroventral "corners" and the landmarks at the anteroventral and posterodorsal "corners" of the form. This resembles the "square-to-kite" transformation discussed in detail in Bookstein ('91), the transformation of a square to trapezoid by relative elongation of one side of the form. The "square" comprises the region posterior to the snout and extending to below the dorsal fin termination; these areas are represented by points 2, 12, 5, and 9. When the partial warp is oriented horizon-

tally, this suggests a relative shortening or lengthening of the dorsal relative to ventral body profile. When oriented in the vertical direction, this suggests a deepening or shallowing of the head and anterior back relative to the sub-dorsal fin region. Ontogenetically we observe dorsoventral expansion of the head and anterior back, with a lesser, not separately significant lengthening of the dorsal relative to ventral body profile (Fig. 4). Relative deepening of the head is the dominant feature of shape change in the dorsoventral direction (Fig. 5).

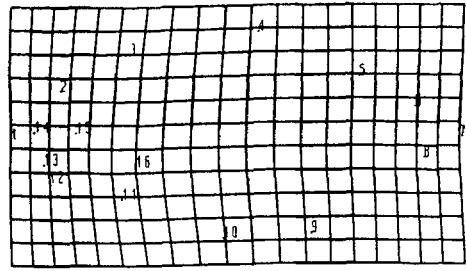
At an almost equally high spatial scale, PW3 describes a contrast between points within the mid-body region and those in the anterior and posterior ends of the body. When oriented horizontally, this warp suggests a shortening (or elongation) of the mid-body with resultant steepening of the anterior head profile; when oriented vertically, it implies a shallowing (or deepening) of the mid-body. At this scale, shape depends substantially on size ($R^2 = 0.826$). While change occurs in both directions (Fig. 4), only lengthening of the mid-body relative to the head and peduncle regions is separately significant and makes a substantial contribution to shape change (Fig. 5). This relative elongation of the mid-body is the dominant feature of body-form ontogeny in *P. nattereri*.

At the next smaller spatial scale, PW4 describes a contrast between points 4, 7, and 15 with the anterior points 2 and 15 and points 5 and 6 on the posterior back. When oriented in the horizontal direction, this partial warp describes an elongation (or shortening) of the dorsal fin and, to a lesser extent, the ventral head, relative to the anterior back and the dorsal caudal peduncle. In the vertical direction, the warp describes a reduction (or increase) in the curvature of the back, and deepening (or shallowing) of the suborbital head, with a resulting reorientation of the fin base to align it more nearly parallel to the anteroposterior axis. We find ontogenetic reduction in the curvature of the back (Fig. 4), making a moderate contribution to net shape change (Fig. 5).

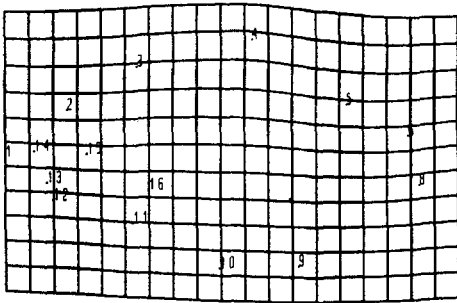
At the next lower spatial scale, PW5 describes the contrast of points 9, 12, 13, and 15 versus 1 and 10. When oriented horizontally, this partial warp describes a blunting of the snout and contraction of the belly between the pelvic and anal fins relative to the ventral head and anterior belly (or a relative contraction of the ventral head and anterior



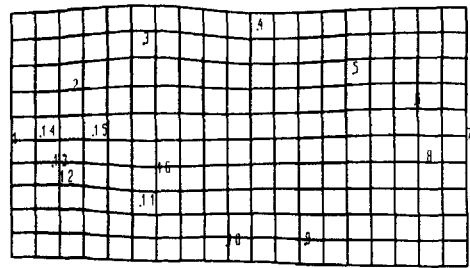
PW2



PW3



PW4



PW6

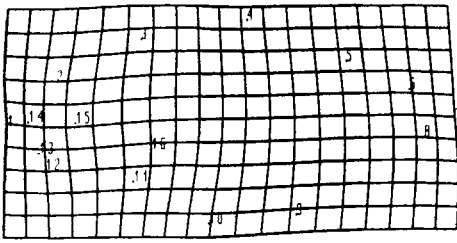
Fig. 4. *Pygocentrus nattereri*. All partial warps (PW) statistically significantly associated with increase in body size, depicted as Cartesian transformations.

belly). Oriented vertically, this partial warp describes a deepening of the anterior head profile and a decreasing convexity of the belly near the pelvic-fin base (or lessening of the relative depth of the anterior head profile and lessening convexity of the belly). Ontogenetically, we find slight evidence of size-related change, primarily a deepening of the anterior head profile, but this is not statistically significant table-wide.

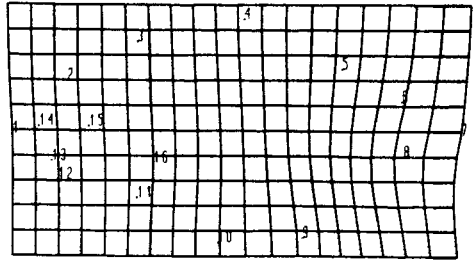
At the next lower spatial scale, PW6 describes the contrast of point 3 versus 4 dorsally, and point 12 versus 16 ventrally. When oriented horizontally, this warp (dorsally) suggests an elongation of the anterior back and steepening of the head profile posterior to the epiphyseal bar, as well as (ventrally) elongation of the ventral head and deepening of the ventral head profile. When oriented

vertically, this warp (dorsally) describes a lessening of convexity of the anterior head and back and a steepening of the dorsal-fin base (or the converse changes), as well as (ventrally) a deepening of the ventral head profile (but more posteriorly than when projected in the horizontal direction). Ontogenetically, we observe changes in the dorsoventral direction, decreasing convexity of the head and back, decreasing steepness of the dorsal fin, and decreasing depth of the posterior ventral head profile (Fig. 4), but this makes a minor contribution to net shape change (Fig. 5).

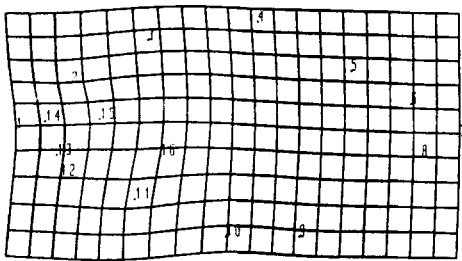
The next most localized partial warp, PW7, describes a contrast between points 1, 3, 8, and 16 vs. points 2, 7, 10, and 15. Oriented horizontally, this suggests expansion (or contraction) of the postorbital head, nape, and



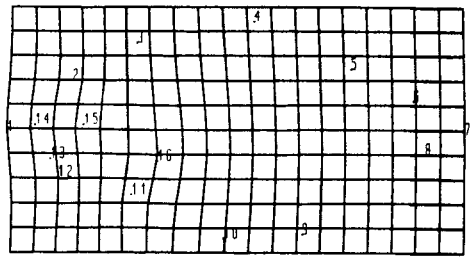
PW7



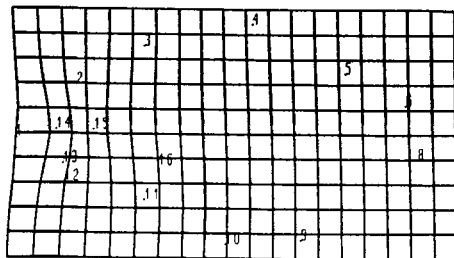
PW8



PW10



PW11



PW12

Figure 4 (continued)

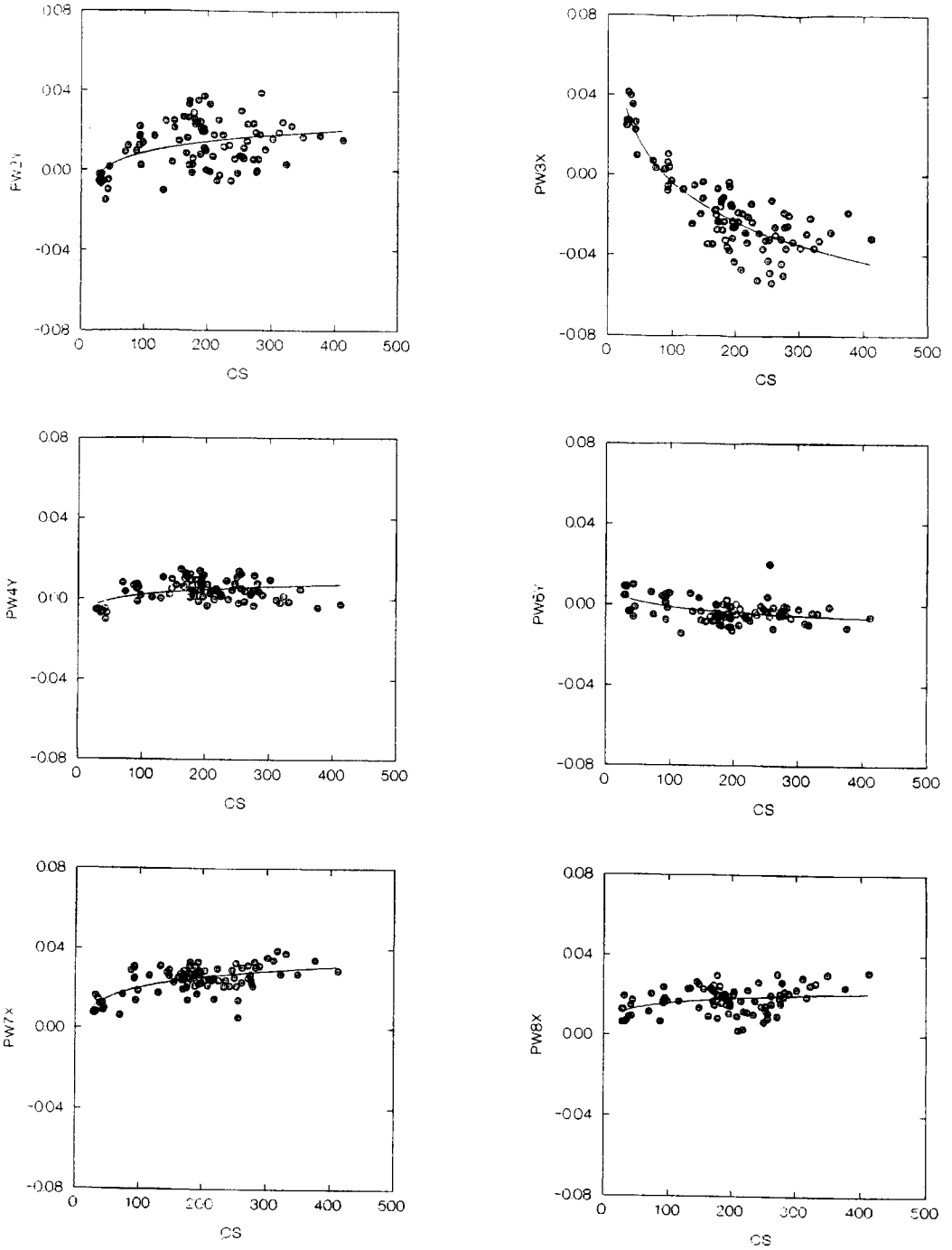


Fig. 5. *Pygocentrus nattereri*. Scatter plots for all partial warps exhibiting ontogenetic shape change, drawn to a common scale. The relative contribution of each warp is evidenced by the magnitude of change along the y-axis. Centroid size (CS) is represented on the x-axis.

For graphical purposes we depict the regressions of shape on CS; as our statistical analyses used the log transform of centroid size, we show the curve fitted by a log smoothing function.

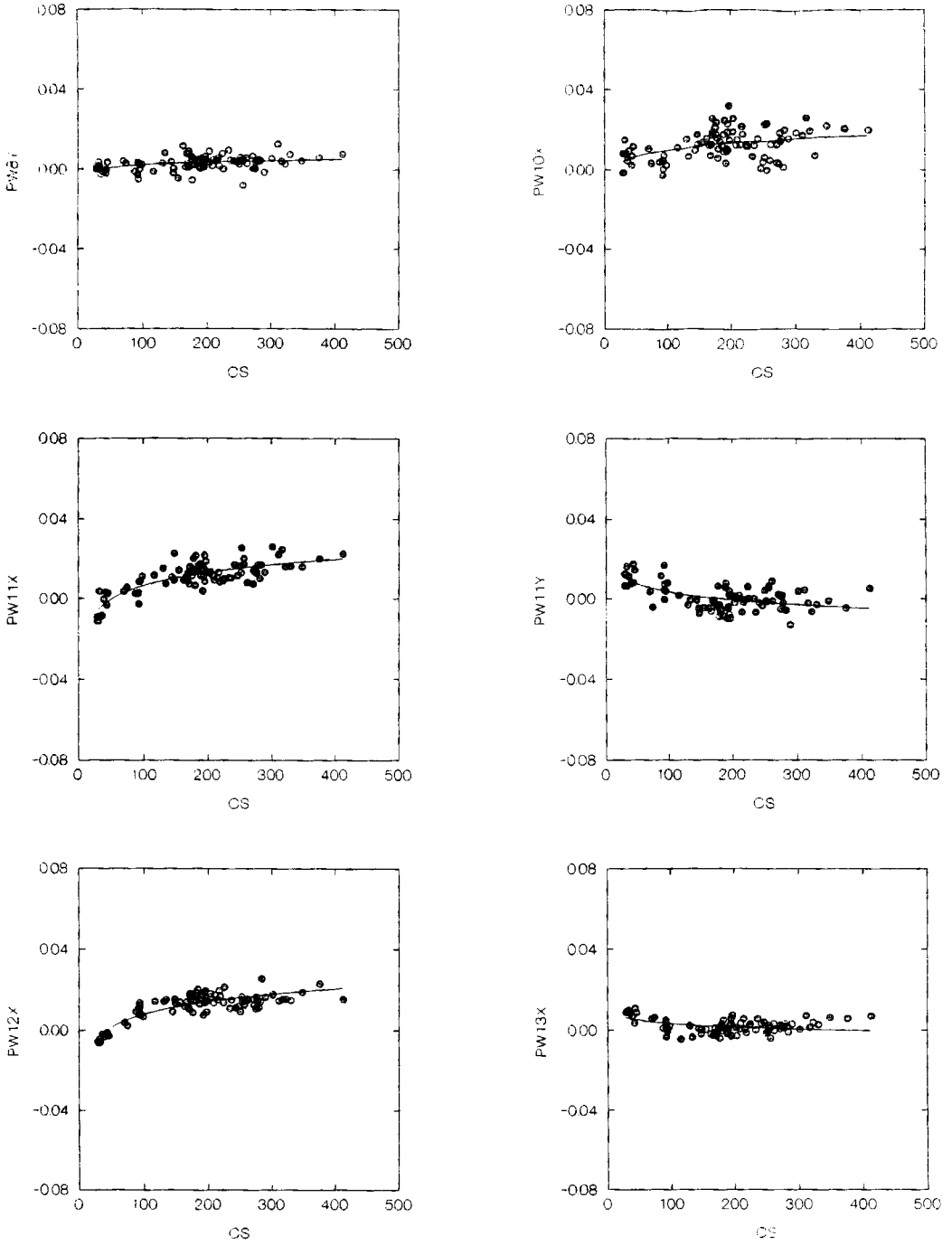


Figure 5 (continued)

postpelvic belly relative to the anterior head and prepelvic belly. In vertical orientation, this implies decreasing (or increasing) convexity of the dorsal head profile, along with relative expansion (or contraction) of the dorsal snout tip, and an increase (or decrease) in depth of the area between the pelvic fin and posterior head. Ontogenetically, we observe relative expansion of the postorbital head, nape, and postpelvic belly compared to the more anterior head and belly regions (Fig. 4); this is one of the dominant features of net ontogenetic shape change (Fig. 5).

At the next lower spatial scale, PW8 describes a contrast between points 7 and 9 to points 8 and 10. These contrasting displacements oriented horizontally suggest shortening (or lengthening) of the anal-fin base, relative to the ventral body anteriorly and posteriorly. Oriented vertically, this pattern implies a relative deepening (or narrowing) of the ventral region of the caudal peduncle associated with a narrowing (or deepening) of the more anterior belly. Ontogenetically we observe slight shortening of the anal-fin base relative to the anterior and posterior ventral body and, to an even lesser extent, relative deepening of the ventral region of the peduncle associated with relative shallowing of the more anterior belly (Fig. 4). In both aspects of shape at this scale, there is considerable variability among individuals; both make minor contributions to net shape change (Fig. 5).

The ninth partial warp describes a contrast between points 5 (and to a lesser degree 7 and 8) and point 6, implying localized changes within the posterior back and peduncle region. Contrasting displacements oriented in the horizontal direction suggest elongation (or shortening) of the caudal peduncle relative to the posterior back. Displacements oriented in the vertical direction suggest steepening (or shallowing) of the profile of the back, along with a narrowing (or deepening) of the caudal peduncle. We find no evidence of change at this scale ($R^2 = 0.001$).

The next most localized partial warp, PW10, describes the contrast between points 2 and 11 vs. 15 and 16. In horizontal orientation, this implies relative elongation and steepening (or shortening and shallowing) of the dorsal head profile along with an anterior (or posterior) displacement of the pectoral fin. In vertical orientation, this suggests lessening (or increasing) of the convexity of dorsal head profile along with ventrad (or dor-

sad) displacement of the pectoral fin. Ontogenetically, elongation and steepening of the dorsal head profile is size-related (Fig. 4), making a moderate contribution to net shape change (Fig. 5).

The 11th partial warp describes a contrast between points 2, 12, and 16 and points 11 and 15. When aligned with the horizontal axis, this implies elongation (or shortening) of the post-orbital region relative to the eye and snout. In addition, the pectoral fin approaches (departs from) the head along the anteroposterior axis. When aligned with the vertical axis, this warp suggests an increase (or decrease) in the convexity of the head profile and a shallowing (or deepening) of the head dorsal to the eye as well as an approach of the pectoral fin toward the head (or departure of the fin away from the head) along the dorsoventral body axis. Ontogenetically, we find relative elongation of the post-orbital region and increase in depth of the head dorsal to the eye with a decreasing convexity of head profile (Fig. 4) associated with change in body size; these are among the dominant features of ontogenetic shape change (Fig. 5).

At an even more localized scale, PW12 describes a contrast between point 14 and points 1 and 15. When this partial warp is oriented horizontally, it suggests an elongation (or shortening) of the snout relative to eye diameter. Change along the vertical axis implies a rotation of the snout relative to the anteroposterior axis of the orbit. We observe an ontogenetic trend of increasing relative snout length (Fig. 4). This localized ontogenetic modification in snout proportions is also one of the dominant contributors to net ontogenetic shape change (Fig. 5).

The most localized principal warp, PW13, describes a contrast between point 13 and points 12 and 14. In a horizontal orientation, this partial warp suggests a shift (anteriorly or posteriorly) of the anterior border of the infraorbital series and maxilla tip. In vertical orientation, the partial warp describes enlargement (or decrease) in extent of the anterior suborbital region relative to the depth of the lower jaw. Much of the observed variability appears to be associated with size, although there is little net change at this scale (Fig. 5).

DISCUSSION

In contrast to previous studies of the ontogeny of body form in *Pygocentrus* (Fink, '89, '93), we find substantial evidence of allometry. The dominant features of post-transfor-

mational growth of these *Pygocentrus nattereri* are the elongation of the mid-body relative to the more anterior and posterior regions (the aspect of shape described by PW3) and deepening of the head and anterior body relative to the posterior body (PW2). We do not find a general deepening of head and body, the shape change previously interpreted as the morphological response to the evolutionary acquisition of a specialized flesh-eating adult diet (Nico and Taphorn, '88). Instead of a head + body deepening, we see a relative deepening of the head, especially postorbitally, compared to the postcranial body.

Much of the ontogenetic shape change can be described in terms of spatially widespread modifications, but there also are more highly localized changes of head form. The post-orbital region and anterior nape elongate relative to the more posterior and more anterior regions (PW7) and this expansion of the post-orbital region is further enhanced by a more localized change, elongation of the post-orbital region relative to the anterior head and deepening of the post-orbital region dorsal to the eye (PW11). In addition, the snout elongates relative to eye diameter (PW12). The distinctive shape of the head of *Pygocentrus* is thus formed by a combination of spatially integrated changes of the head and anterior body and the more localized modifications of the post-orbital region, snout, and jaw.

We found little evidence of localized post-cranial changes, such as shortening or lengthening of the caudal peduncle relative to the posterior back (PW9) or shortening of the anal-fin base relative to the ventral body (PW8). Changes in post-cranial shape are generally associated with more spatially large-scale changes of body proportion. The one localized post-cranial ontogenetic change observed was the reduction in curvature of the back and the reorientation of the dorsal fin base (PW6). To some extent, the impression of lesser developmental complexity of the body compared to the head is due to the denser sample of cranial landmarks. It is not possible to localize changes in regions lacking closely spaced landmarks. Yet, we found little ontogenetic alteration in those post-cranial regions where our landmarks did permit us to localize change.

Most ontogenetic shape change appears to occur before small whole fish become a dominant component of the diet of these piranhas, although our sample sizes are too small to

permit us to estimate growth parameters. Nico and Taphorn's ('88) diet information on a congener, *P. cariba*, allows a preliminary analysis of diet and shape change (W.L.F. has unpublished observations corroborating this for *P. nattereri*). During the initial dietary transitions, shape and size are both changing so a variety of shapes are associated with each juvenile and subadult diet. At larger sizes small whole fishes are more frequently present than are chunks of flesh or fins and scales combined; associated with this change in diet there is an increase in overall body size rather than more localized changes of jaw or head proportions. Unfortunately, reports of gut contents are available only for rather coarsely subdivided size classes. It would be particularly interesting to have more finely detailed information for the 80–159 mm SL fish, to determine how much shape change occurs with increase in frequency of the taking of small whole fish. Small whole fish were found in the guts of only 2.5% of the 40–79 mm fish sampled, while 29% of those between 80 and 159 mm SL had whole fish in their guts, as did 51% of those sampled at larger sizes (Nico and Taphorn, '88). Because piranhas bite chunks of flesh, they can take food items that exceed their gape (Irish, '87). When they feed upon whole fish, gape-size might become more constraining, but at the size piranhas are feeding on whole fish, they may be large enough to be only slightly affected by such a constraint.

Regions of the body where we find no evidence of any localized changes (e.g., the posterior back) have no demonstrable developmental individuality during post-transformational morphogenesis. That is not to say that they lack such individuality during earlier larval growth; however, Fuiman ('83) and Strauss and Fuiman ('85) interpreted larval growth to be remarkably integrated as a U-shaped gradient of increasing growth rates toward anterior and posterior ends. We do not yet know if this gradient is characteristic of teleosts, including *Pygocentrus*, or is restricted to the few other ostariophysans, smelt, and percids examined by Fuiman ('83) or sculpins analyzed by Strauss and Fuiman ('85). Nor do we know if this gradient is an adequate summary of larval shape changes. A "U-shaped gradient" of decreasing growth rates toward anterior and posterior ends is the dominant feature of post-transformational growth in these piranhas, but it is not an exhaustive description of post-transforma-

tional shape change. More complete characterizations of the ontogenies of shape are necessary to identify the modifications of development responsible for the evolution of form. Strauss and Fuiman ('85) concluded that adults can be characterized by the same aspects of form as their larvae, suggesting that morphological novelties arise by modification of very early development. Yet piranha species differ in more than the relative size of head and tail compared to mid-body, so there must be evolutionary changes in growth of more localized features. Perhaps these changes evolve by modifications of juvenile growth, but there may be developmentally individualized features of larval growth too subtle for detection by previous morphometric methods. Extending landmark-based comparisons to larval forms is complicated by the small number of landmarks shared among larvae and juveniles, but comparative studies of small juveniles may reveal whether the differences of adult body form result from modifications of earlier development.

Having no measures of any developmental factors, except for size, we cannot tell if juvenile growth of *P. nattereri* has a simple causal basis with a complex spatiotemporal distribution of effects or, instead, is controlled by multiple developmental factors. Any attempt to relate these shape changes to specific developmental mechanisms is premature, given how little is known about juvenile morphogenesis in teleosts. In skull growth of the cotton rat *Sigmodon fulviventer*, all the various localized shape changes result from the same morphogenetic processes (i.e., deposition and resorption of bone), but even when these changes are coextensive in time they appear to be separately regulated (Zelditch et al., '93). Studies of the ontogeny of variability provide a method for exploring one aspect of the developmental associations among features, their joint regulation by common factors in normal growth.

Phylogenetic studies of ontogenies present another way to explore the epigenetic interdependencies among parts of the body. Our analysis dissected spatiotemporal integration and individuality of head and body regions on an ontogenetic time scale. Comparative studies placing these ontogenetic transformations in phylogenetic context can dissect temporal associations on a phylogenetic time scale. Any hypothesis proposing a necessary causal interdependency among parts of the body would be untenable if these

regions were found to be evolving independently. Such comparative studies could show whether ontogenetically integrated parts of the head represent a single complex character, or, alternatively, are made up of several parts with independent histories. Our own comparative studies have suggested that aspects of growth temporally integrated in *Pygocentrus* do appear to have different histories (Fink and Zelditch, in press). The combination of relative mid-body elongation and relative postorbital + nape elongation are features of ontogeny common to all piranhas examined, but localized elongation of the post-orbital region relative to the eye + snout is a synapomorphy of *Pygocentrus*. This particular ontogenetic shape change (PW11) may be one candidate for an aspect of shape associated with the evolution of the specialized diet of *Pygocentrus*.

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