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MORPHOMETRICS, HOMOLOGY, AND PHYLOGENETICS: QUANTIFIED CHARACTERS AS SYNAPOMORPHIES

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Abstract.—It has been claimed that quantified features are inappropriate for phylogenetic analysis. We consider that claim to be true under most conditions for characters discovered by commonly used morphometric methods, including outline-based and conventional multivariate methods. The most important reason these characters are unsuitable is that one of the tests of homology, the test of similarity, may be difficult to apply to them. This test is not even possible if the methods for comparing forms, such as outline-based techniques, do not ensure that the characters are located in the same part of the anatomy. Conventional methods, including principal components analysis, have no explicit basis for localizing characters. In addition, unless the transformation between forms is homogeneous, conventional methods cannot dissect transformations region by region to discover characters. However, one morphometric method, the thin-plate spline decomposed by its partial warps (TPS), finds characters that can be subjected to the same tests of homology (conjunction, similarity, and congruence) that we would apply to all other characters. Among available methods, TPS is unique in being able to locate the center and spatial extent of regional differences in shape and ensures that the same regions are compared among forms. We provide an example using the teleost fishes piranhas, in which tests of homology are applied to a synapomorphy found by the method. [Morphometrics; homology; synapomorphy; thin-plate spline; character analysis; piranha; *Pygocentrus*; *Pygopristis*; *Serrasalmus*.]

Shape similarities among organisms have long been recognized as having systematic value. Whether shape features in quantitative form can be a source of information about phylogenetic relationships is more controversial. This doubt is reflected in the literature, particularly in the claims that quantitative shape features cannot be subjected to the same tests of homology that other characters must pass (Pimentel and Riggins, 1987). This position strikes directly at the use of morphometrics as a class of tools for phylogenetic analysis. Herein, we argue that at least one morphometric method is both suitable and useful in phylogenetic analysis because characters found by it can be treated in the same way as can characters from any other source. However, we also contend that many methods currently in use are indeed inappropriate because they cannot generate results meeting the criteria applied to phylogenetic characters.

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Because much of our argument depends on our meaning of homology, we begin with a brief foray into semantics. Following a discussion of the definition of homology, we examine several morphometric methods and judge their potential for yielding characters appropriate for phylogenetic analyses.

HOMOLOGY

Patterson (1982), like Rieppel (1980), distinguished between taxic homology, a feature of a monophyletic group, and transformational homology. The evidence of taxic homologies is synapomorphies that have passed three tests: conjunction, similarity, and congruence. Systematists who use the term "synapomorphy" for shared derived states, whether or not shown to be congruent, qualify this definition by restricting it to "corroborated synapomorphies." Systematists who use terms such as "putative synapomorphy" to refer to the coded characters prior to testing their congruence and use "synapomorphy" specifically for those found to be congruent equate homology with synapomorphy.

Transformational homologies refer only to characters, i.e., a particular feature interpreted as transformationally homologous to another feature. In Smith's (1990) terms, transformational homology refers to the vertical relationship among characters. A classic example of a hypothesis of transformational homology is the assertion that the incus is homologous to the quadrate. This is a relationship between characters and provides no information about relationships among taxa.

In general, statements of transformational homology can be rewritten in taxic terms. The example of the incus and quadrate can be written as "the incus and quadrate are homologous as palatoquadrate ossifications of osteichthyans" and "the incus is homologous as the intermediate middle ear ossicle in mammals." There are two claims made in statements of transformational homology thus rewritten: (1) the features (incus + quadrate as palatoquadrate ossifications; incus as the intermediate middle ear ossicle) each characterize a monophyletic group (Osteichthyes; Mammalia), and (2) the features comprise a transformation series, i.e., a nested set of synapomorphies. These are two distinct and different kinds of statements, and we agree with Patterson that only those features that characterize monophyletic groups should be called homologues. The second kind of statement presumes that the variant characters are modifications of the symplesiomorphic feature and are thus comparable.

Many long-standing debates regarding particular homologies are about transformational rather than taxic homology. It is the comparability of the structures, rather than their status as synapomorphies characterizing monophyletic groups, that is often in doubt. For example, if we were to observe a trapezoidal frontal bone in one taxon and a trapezoidal parietal bone in another, we would not judge trapezoidal form as a potentially homologous feature of the group comprising both taxa, even if these taxa form a monophyletic group, because these are not variant shapes of a symplesiomorphic bone. The shapes cannot be homologous when the parts are not phylogenetically comparable. This comparability is one aspect of the test of similarity. There are two distinct components of the test of similarity: (1) features must be judged comparable as modifications of a symplesiomorphic character and (2) features must be judged to resemble each other "in sufficient detail" to code them as sharing a common derived condition. In our example of the two trapezoids, even if they pass the test of similarity (of shape), they fail the other, the comparability of the parts.

One of the reasons Pimentel and Riggins (1987:208) opposed using morphometric characters in systematics is that they claimed it seems "obvious [that] most quantitative variables can lead only to implied homologies, i.e., transformational homologies [and] so are useless for cladistic analysis." This statement implies that morphometric variables can be arranged into transformation series but that they cannot be regarded as potential synapomorphies. However, morphometric variables obtained by some methods (but not all) are not even comparable. In some cases, the comparability of the parts is essentially unknowable, and so there can be no phylogenetic information in their shapes. This limitation is most evident in outline-based methods (those that do not employ landmarks). However, even some ways of analyzing landmark data fail to ensure that comparisons are restricted to phylogenetically comparable parts of the organism. Yet not all methods are suspect; the thin-plate spline decomposed by its partial warps allows discovery of characters that can be assessed for taxic homology.

The term homology as used in morphometrics has a different meaning than it does in phylogenetic systematics. This term has most often been applied to landmarks, i.e., discrete, recognizable points on the organism. When systematists choose particular landmarks, the choice is often defended on the grounds that they sample parts of the organism judged homologous at the most inclusive level being studied. The intent is to identify homologous shape

features of these comparable parts. However, in the usage of morphometrics, homology is not a hierarchical concept. Once we declare landmarks to be homologous at some phylogenetic level, all the shape variables extracted by analysis of these landmarks must be homologous at that level because, technically, landmarks and the features extracted by analysis of patterns of landmark displacements are algebraically equivalent. If landmarks are homologous at the most inclusive level of study, and the features extracted from the comparisons are algebraically equivalent to the landmarks, then we are forced to regard the shape variables as also homologous at the most inclusive level of study. For example, in the semantics of morphometrics, we could not refer to the landmarks as homologous at the level of Mammalia and call a particular shape character homologous at the level of Rodentia. This usage is in clear contrast to the usage of homology in phylogenetic systematics, where one would not oppose viewing the bones and their shapes as forming a nested set of homologies. To avoid misunderstandings due to this semantic inconsistency, we suggest replacing the term "homologous" with "corresponding" or "comparable" when referring to landmarks in a strictly morphometric context.

Outline-Based Methods

Some methods are attractive because they include information about outlines of forms. When landmarks are inconveniently located (or altogether missing), these methods may seem especially appealing. However, currently available methods do not ensure that the corresponding points on the outlines are properly matched. The problem with such methods is demonstrated in Figure 1. Any morphometric method that allows us to compare the scapula, potato chip, and chocolate chip cookie clearly does not insist that the parts being compared are homologous at any level.

Any attempt to compare these forms must rely on something other than biological homology. This something is a distance function. What is deemed corresponding is determined by the particular algebra of the distance function selected. Distance, for example, could be measured as the squared difference of the radial directions of the outlines integrated around the form; the difference is taken between points at the center or at some fraction along the perimeter from some starting point, etc. Correspondence of points would be established by matching forms to minimize this distance. A different distance function would compute a different optimal correspondence of points.

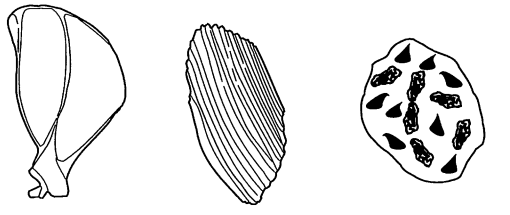

FIGURE 1. Three forms (scapula, potato chip, and chocolate-chip cookie) that can be compared by outline-based methods.

Fourier and eigenshape analysis (among others) are examples of such methods that are inapplicable in phylogenetic systematics, on principle. Advocates of these methods recognize the problem but deny that phylogenetic comparability is a prerequisite for comparative studies. For instance, Ehrlich et al. (1983:203) "make no claim that the use of homologous features has no place in biomorphological studies, but simply suggest that examination of discrete homologous skeletal features is only one of many approaches." We strongly disagree with this statement because we regard this compromise as fatal to comparative morphology.

Landmark-Based Methods

Conventional Multivariate Methods

Conventional multivariate morphometric methods, such as canonical variates analysis (CVA) or principal components analysis (PCA), differ from the outline-based methods described above by assuming the fundamental importance of com-

paring homologous parts. Usually, studies employing these methods begin with measurements of lengths and widths of parts of the organism presumed to be comparable. These size measurements are then algebraically manipulated to produce composites of the measured variables, i.e., linear combinations optimally discriminating between samples or describing what varies most within them. These are the morphometric methods most often applied in systematic studies, partly because of their historical ties with phenetics, which used these combinations of measured lengths and widths to formulate a net phenetic distance between groups. Over the past decade, there have been considerable improvements in this class of methods, such as increasing emphasis on coefficients describing group differences (e.g., Humphries et al., 1981; Strauss and Bookstein, 1982; Bookstein et al., 1985) and decreasing emphasis on inferring relationships by Mahalanobis distances. Yet, underlying all these methods is a concern with distances among taxa. For example, Bookstein et al. (1985) interpreted distance, "taxonomic dissimilarity," as a latent variable, serving as a proxy for evolutionary time. They expected most measures of dissimilarity to be correlated to the extent that these measures do not reflect biological factors such as habitat or body size. According to this point of view, common ancestry is a factor in the sense of a common linear cause of observed variables (see Bookstein et al., 1985:206).

Conventional morphometric methods were not tailored for phylogenetic studies. This fact alone does not automatically disqualify them from being used for such purposes because they might still be useful for discovering characters. However, they cannot be used for phylogenetic analyses for three reasons, all of which are related to application of the test of similarity: (1) comparisons are based on linear combinations that optimize discrimination or variance of scores rather than on homology of parts; (2) differences among organisms cannot be localized to parts of the organisms (except under very restrictive conditions); and (3) manipulation of variables chosen in advance of analysis limits the possibility of assessing detailed similarity.

Our first argument concerns the basis for comparisons. Conventional methods extract features of the covariance matrix, i.e., linear combinations of measured variables that optimize some quantity, such as between-group relative to within-group variation (CVA) or variance of the scores (PCA). In effect, these linear combinations are the characters found by these methods, but no principles of phylogenetic analysis justify such optimality criteria. There is no necessary relationship between what these methods optimize and phylogenetic informativeness. As a consequence of this emphasis on whatever varies most, addition of a distinctive taxon to the analysis modifies what is compared. Of course added taxa may often add information, in the sense of providing new characters, and the results obtained from the addition of new taxa could suggest that some characters have been misinterpreted. However, addition of a distinctive form phenetically "distant" from the average for a group should not by itself modify what is deemed comparable. Only revised interpretations of the homology of the parts should alter judgements of comparability. Furthermore, scores on CV1 or PC1 from different studies are not comparable because the components are different combinations of the original variables. Each CVA or PCA is conducted in a different morphospace, even though each begins with lengths and widths of the same structures. Although the practical problem might seem easily surmounted by including all taxa in a single study, the conceptual problem remains: comparisons are based on what varies most within the sample, not on homology of the parts.

The second serious problem is that conventional morphometric methods cannot say where shape differences are located on the organism. Even though these methods begin with measurements whose endpoints are corresponding points on comparable structures, they cannot extend this comparability to parts of the organism, i.e.,

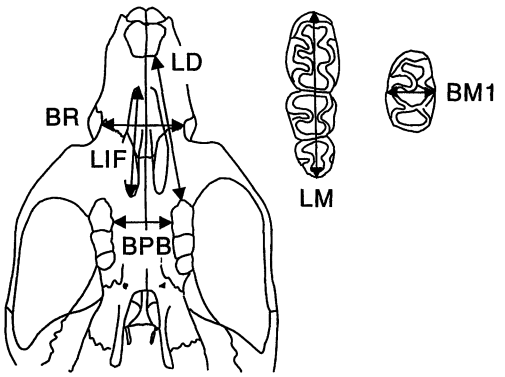

FIGURE 2. Measurements of dentition and skull of *Zygodontomys* in ventral view. The coefficients for the depicted subset of variables on sheared PCII are LM = 0.403, BM1 = 0.596, BPB = −0.521, BR = 0.061, LD = −0.042, and LIF = −0.013. [After Voss et al., 1990.]

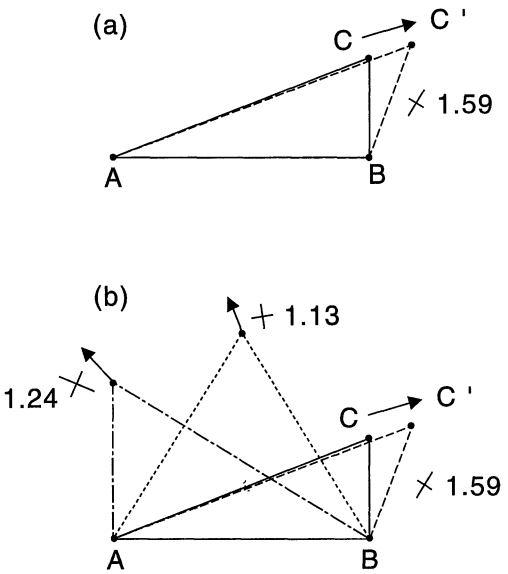

FIGURE 3. (a) Shape change of a triangle compared between two forms. When two points of the triangle (A, B) are fixed, the difference between the two forms lies in the displacement (arrow) of the third vertex (C to C'). The difference between the two forms is described by the principal axes (cross), indicating the directions of greatest and least relative change (anisotropy is the ratio of the lengths of these two arms; this value is printed next to the cross). (b) Two triangles are added to those in (a), sharing a common baseline (between points A and B). For each triangle, the displacements of the third vertex are depicted by the arrows (only the starting triangles are fully illustrated); principal axes and values of anisotropy for the change of each triangle separately are presented alongside each triangle.

they cannot specify the center and spatial extent of the regions that differ. An example of this problem is a particularly careful multivariate analysis of the shape differences between nominally conspecific populations of *Zygodontomys* (at constant size) by Voss and his colleagues (Voss et al., 1990; Voss and Marcus, 1992). They interpreted their coefficients as evidence that dimensions of the molars (Fig. 2, LM and BM) increased and that the palate narrowed. Yet, their methods cannot actually document narrowing of the palate. They could not show that the palate as a whole, instead of the diastema or the maxillary portion of the diastema, had narrowed. Even if the authors had more densely sampled the skull, they could not have made these distinctions. In short, these methods cannot specify the parts that differ in form. The shape coefficients can be drawn back onto the skull and visual inspection of this graphic can suggest insights into the regional pattern of shape variation, but there is no explicit basis for comparing features such as relative narrowing from region to region. Instead, what is compared is merely the list of coefficients. This lack of an explicit basis for localizing the characters is a fundamental defect of these methods.

Sometimes conventional methods are adequate for describing and locating what differs. In the comparison of triangles in Figure 3a, the small cross shows the directions of greatest and least rates of change (the principal axes), and the ratio of the arms of the cross is the shape variable most differing between forms (detailed protocols for computing these principal axes and their ratios were presented by Bookstein et al. [1985] and Bookstein [1992]). In this example, the ratio of the arms of the cross provides the description of what differs between the triangles, and this is the shape variable that would be subjected to tests of homology.

If we were concerned only with this triangle, the ratio would be an adequate description of what differs. Further, if we added more landmarks but were still able

to describe the difference between forms unambiguously and nonarbitrarily by a single pair of principal axes, then we would have no more to analyze than this one shape variable. This would be a uniform transformation. We could construct many ratios of measured line segments but would have but a single character because these ratios would be describing the same feature, that uniform change. As long as transformations are this simple, conventional morphometric methods are adequate.

Conventional methods fail when the problem is to dissect differences among forms in terms of changes spanning several regions (i.e., multiple triangles) and those specific to particular subregions. In other words, the problem of locating shape differences arises when transformations vary from region to region across the organism, i.e., when they are nonuniform. This nonuniform shape change is depicted in Figure 3b, in which two more triangles are added to the one in Figure 3a. The principal axes (small crosses) of these three triangles are oriented in different directions, and the ratios of the arms differ. We cannot describe the difference between two forms made up of these three triangles by a single variable or a global descriptor, such as increased skull width relative to skull length. We need a way to dissect the nonuniform changes by region. In our empirical studies (body form ontogeny of piranhas, shapes of adult piranhas, skull form ontogeny of cotton rats, and scapular shape in squirrels; see also examples presented by Bookstein et al. [1985]), we have not yet found a single case of an entirely uniform transformation, so we expect that localization of differences is likely to be a frequent concern.

The third problem is reliance on measurements chosen in advance of the study. Quite possibly none of them are aligned with the principal axes of the transformation, yet these measurements provide the only terms for comparing shapes by these methods. As a result, we may overstate evidence of similarities whenever differences lie in directions oblique to the measured lengths and widths. Use of a truss protocol (Strauss and Bookstein, 1982; Bookstein et al., 1985) can alleviate this problem because more directions are sampled, but the analysis remains confined to the variables chosen a priori.

In summary, standard morphometric methods may be adequate when transformations are entirely uniform and measured distances are aligned with principal axes of the transformation. Under those conditions, conventional methods might adequately describe shape differences among taxa. Even then, we find it hard to justify using eigenanalysis of a variance–covariance matrix to find characters. Under what we expect to be more common conditions, when changes are at least partly nonuniform and in directions not sampled by the measured distances, these methods cannot serve even the most basic of descriptive purposes: describing how comparable parts of organisms differ in form.

Geometric Methods

The method of thin-plate spline decomposed by its partial warps (TPS) is an alternative approach to multivariate morphometrics that has arisen from a concern for localization (Bookstein, 1989, 1992; Zelditch et al., 1992, 1993; Swiderski, 1993). This approach can be thought of as a way to obtain shape variables that have a location on the form and to ensure that the homology of anatomical parts provides the common basis for comparisons.

TPS is the one method capable of discovering characters suitable for cladistic analysis. Shape change is modelled as a deformation that is decomposed into geometrically independent components. First, it is decomposed into uniform and nonuniform components, and the nonuniform component is then further decomposed into geometrically independent, progressively more localized components, each one describing change on a smaller spatial scale.

Before discussing results of a comparative study of body form in a teleost fish group, the piranhas, we present an example to clarify the notions of localization

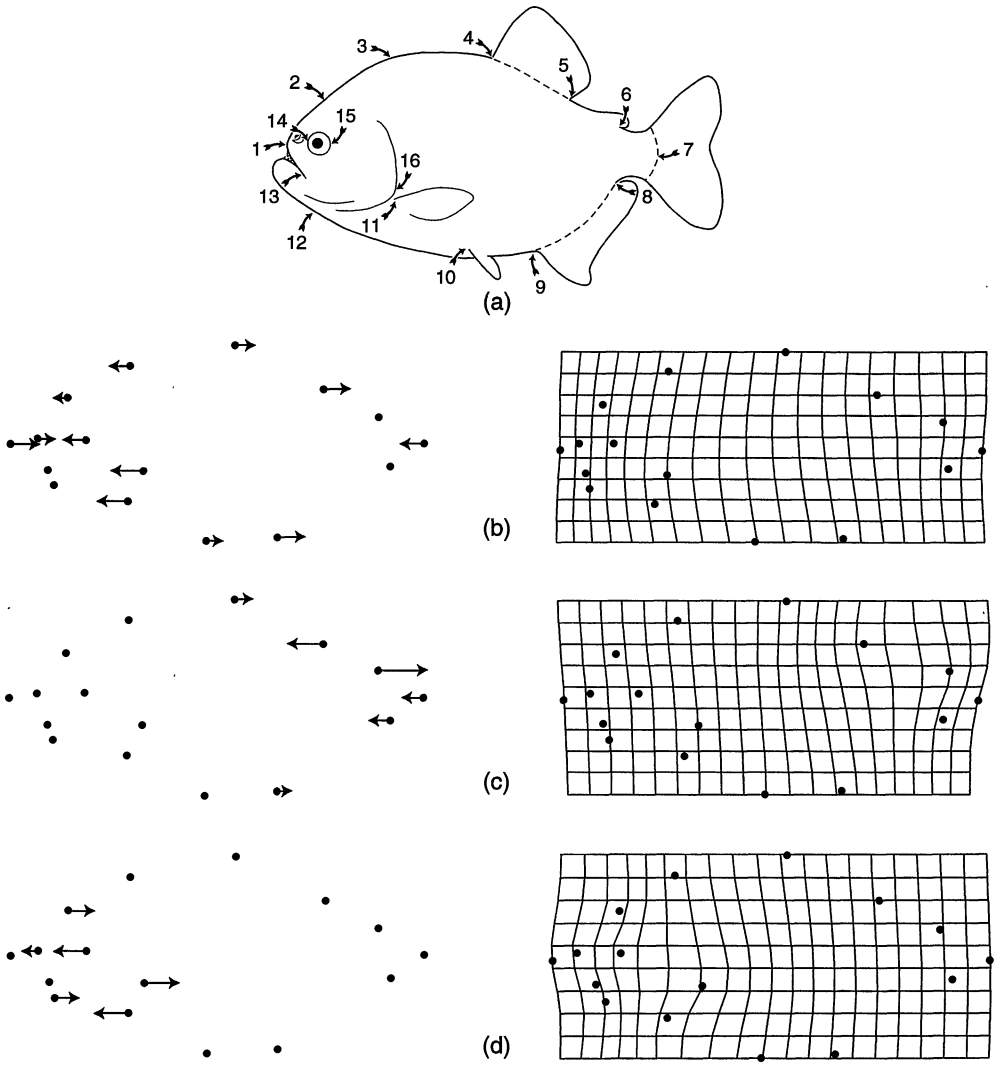

FIGURE 4. Three components of shape change for the landmarks (a) from large (b) to intermediate (c) to small (d) spatial scale. Each change is shown as vectors depicting relative landmark displacements and as a Cartesian transformation.

and spatial scale. We then show how we have discerned a character in the shape difference at one of these scales. We present examples of three nonuniform components, the *principal warps*. These principal warps are eigenvectors of the bending-energy matrix, which is a function of the location and spacing of the landmarks of the starting form (landmarks depicted on a *Pygocentrus*, Fig. 4a). The starting form is the form to which all other forms are compared. In this example, we use an averaged juvenile of our outgroup, *Pygopristis denticulata*, as the starting form. (We computed the average of shape coordinates constructed to the baseline points 1 and 7, see Fig. 4a. For more details see Fink and Zelditch, 1995; for an alternative strategy in choice of starting form, see Swiderski, 1993.) As long as we

use the same starting form for all our comparisons, we obtain the same components. The principal warps have no direction or magnitude, so for the moment we draw them arbitrarily as oriented in the x-direction (aligned with the anteroposterior body axis of the fish).

One feature at high spatial scale (Fig. 4b) describes a contrast between points within the midbody region and those in the anterior and posterior ends of the body. As drawn here, oriented along the anteroposterior body axis, this feature describes relative elongation of the midbody. A feature at intermediate spatial scale (Fig. 4c) describes a contrast between points at the posterior dorsal fin base, base of the caudal fin, and posterior termination of the anal fin. As oriented here, this feature describes shortening of the caudal peduncle relative to the region of the back between the dorsal fin and adipose fin. A quite localized feature in the head region (Fig. 4d) describes a contrast between points on the nape, lower jaw, and border of the operculum with the posterior eye orbit and pectoral fin. As drawn here, this feature describes elongation of the postorbital region of the head relative to the eye and snout.

Because the principal warps are determined by the starting form, the biological signal does not lie in their number nor in where they are localized. Rather, the signal lies in the two-dimensional scores, the vectors multiplying these components. These vectors (the *partial warps*) express the contribution each principal warp makes to the realized shape difference between two forms. Like the more familiar principal component scores, the partial warps are computed by multiplying eigenvectors (the principal warps) by an individual's data (here the landmark locations for the final form). Principal warps can be thought of as the geometric terms in which morphological differences can be described, whereas the partial warps describe realized changes in those geometric terms.

The principal warps depicted in Figure 4 were oriented arbitrarily; the differences in forms were aligned with the anteroposterior body form. Now we consider an empirical analysis. The scatter plot in Figure 5 depicts the partial warp scores for the feature at intermediate spatial scale (Fig. 4c). Each point in the plot represents the comparison of each individual specimen to the starting form. *Pygopristis denticulata* and *Serrasalmus gouldingi*, the two outgroups, are designated by d and g on the plot. Specimens of *Pygocentrus cariba*, *P. nattereri*, and *P. piraya* are designated c, n, and p, respectively. Members of the genus *Pygocentrus* have lower scores on the y-axis (aligned with the dorsoventral body axis). Compared with the outgroups, this represents a less steeply inclined posterior body profile (posterior to the dorsal fin) and deeper caudal peduncle relative to the depth of the region between the adipose and dorsal fins (Fig. 6). This is the picture shown in Figure 4c but with all the arrows now oriented vertically. The individuals of each species of *Pygocentrus* overlap in the scatter plot to such a degree that we judge these three species indistinguishable; together they are distinguished from the out-

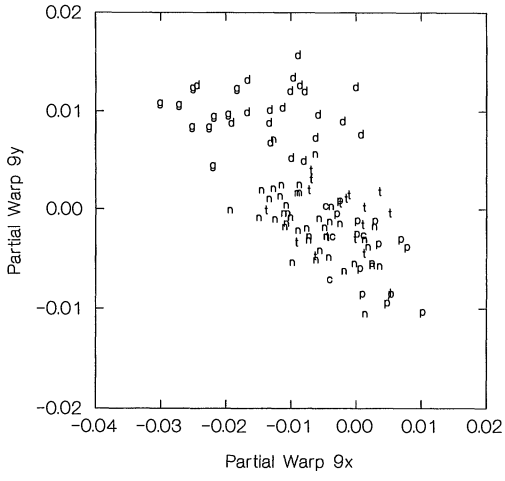

FIGURE 5. Scatter plot of the shape variable at intermediate spatial scale (Partial Warp 9) depicted in Figure 4c. The x-axis represents variation of this feature aligned with the anteroposterior body axis; the y-axis is variation aligned with the dorsoventral body axis. d = *Pygopristis denticulata*; g = *Serrasalmus gouldingi*; c = *Pygocentrus cariba*; n = *P. nattereri*; p = *P. piraya*. The point (0, 0) represents the average juvenile *Pygopristis denticulata*.

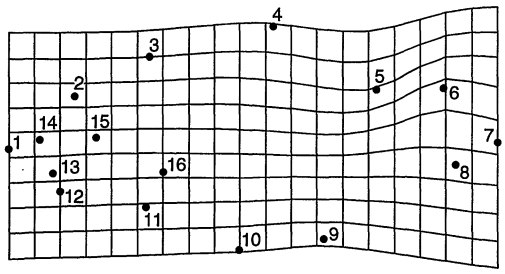

FIGURE 6. A Cartesian transformation depicting a shape variable (Partial Warp 9y) diagnosing *Pygocentrus* (see Fig. 5). Differences from the outgroup scores along the *x*-axis represent changes at this scale oriented along the anteroposterior body axis; the *y*-axis represents change oriented dorsoventrally on the body.

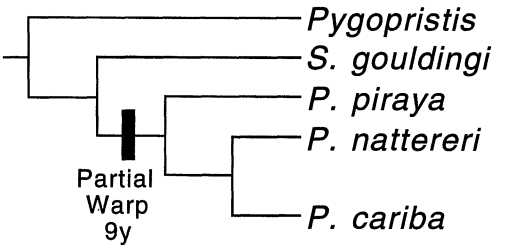

FIGURE 7. Congruence of the morphometric character (Partial Warp 9y) with the cladogram for the piranhas, based on a data matrix consisting of osteological, meristic, and myological features (Fink and Zelditch, 1995).

groups by their lower scores in the *y*-direction. That difference suggests that there is a character at this spatial scale, the partial warp oriented in the negative *y*-direction (aligned with the dorsoventral body axis).

This feature passes both aspects of the test of similarity: comparability and detailed similarity (conjunction is applicable but not particularly useful for these characters). It passes the test of comparability because, having used a common starting form for each comparison, the principal warps are constant. Each comparison examines change in terms of the same pattern of relative landmark displacements. This character passes the test of similarity because, based on the scatter plots, there is no evidence of any discrete differences among species of *Pygocentrus*. This feature also passes the test of congruence with other characters diagnosing *Pygocentrus*, as depicted on the cladogram based on all available information (Fig. 7). Thus, we consider this aspect of shape a homologous feature of *Pygocentrus*.

Two aspects of this method are distinctive. First, this method is inherently comparative. Instead of describing each form in isolation and then comparing the descriptors, the descriptors are the features that differ among forms. When used in the context of outgroup comparisons, the vector multipliers provide a description of how each taxon differs from the outgroup. Second, the components of the deformation are constants; as long as the same starting form is used in all analyses all will have a common basis. This common basis is determined by the location of the landmarks sampling homologous anatomical parts.

There are four ways in which this method could be considered arbitrary. First, the places where change can be localized (the principal warps) are a function of the location and spacing of landmarks on the starting form. Thus, we would obtain different descriptions of the ways in which shape differs with different starting forms (e.g., different outgroups used as starting forms). Second, because these principal warps are a function of the landmark configuration, we would obtain different descriptors with different selections of landmarks. But there are nonarbitrary biological decisions that come into play when choosing landmarks and starting forms, such as choice between a juvenile, adult, or mean form of an outgroup species to study ontogeny. Third, there are many other ways of analyzing the information in shape changes, such as finite-element descriptions, Procrustes superpositions, etc.; however, because of the way decomposition by partial warps localizes shape change at progressively smaller spatial scales, we prefer it on biological grounds (Zelditch et al., 1992). Fourth, unlike some other multivariate methods, this method does not optimize sample variance or co-

variance, and for this reason, it might also be considered arbitrary; however, we do not regard that as a defect because our systematic analyses should not be designed to optimize such parameters.

The TPS method generates geometrically independent features of shape change. We cannot presume, however, that descriptions at different spatial scales are either developmentally or historically independent. In this particular analysis, we analyzed the partial warps separately and found an example of a character at a single spatial scale. We cannot generalize from this one example because a single character might be described by partial warps at several scales. A single developmental process, for example, might have spatially complex effects. As in any other analysis, we would examine character independence by the phylogenetic distribution of the shape features. In addition, we might look to ontogeny to see if these several characters were all ontogenetically associated.

CONCLUSIONS

Despite the perception that morphometric characters are unsuitable for phylogenetic analyses, no previous critique has shown that most of these characters are inherently flawed because of the way they are discovered. We examined several methods used to discover morphometric characters and asked whether or not they can be subjected to the same tests of homology routinely applied to all other characters. The characters found by most morphometric procedures are indeed unsuitable for cladistic analysis under most conditions. However, the method of the thin-plate spline decomposed by its partial warps can yield shape characters suitable for cladistic analysis.

We emphasize the test of similarity because it is the test of homology most difficult to apply to features discovered by most morphometric methods. In particular, the test of comparability may often be inapplicable to morphometric characters. Yet we cannot judge shapes of anatomical parts to be homologous without having some assurance that comparisons were restricted to comparable anatomical parts. Currently available outline-based methods make no attempt to ensure comparability and should therefore be avoided by systematists. Conventional multivariate methods can find characters suitable for cladistic analysis under highly restrictive conditions (the distances are measured between corresponding landmarks, the measured distances are aligned with the principal axes of the transformation, the transformations are uniform, and the comparisons are all performed in a common morphospace). In most cases, these methods will fail. Even when they meet these restrictive conditions, it may still be problematic to consider linear combinations of measured variables optimizing some quantity such as variance of the scores to be characters. However, TPS can find characters suitable for cladistic analysis. The method ensures that there is a basis determined by what was judged homologous by previous analyses and that these eigenvectors localize the shape characters on the organism.

Although morphometricians may judge methods by other criteria, such as their ability to describe shape differences with full statistical efficiency, we have judged these methods according to their ability to find characters that can be viewed as homologies in a phylogenetic sense. Bookstein (1994) argued that it is not possible to assess the homology of biometrical shape. However, he did so in the context of a view of cladistics that we do not agree with. We regard homology as a general principle to be applied in all aspects of comparative biology—morphometric, biomechanical, osteological, molecular, behavioral, etc. Quantified shape features can meet the same standards that we apply to characters from other sources of data.

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