

## Landmark-based Morphometric Analysis in Selected Species of Serranid Fishes (Perciformes: Teleostei)

Mauro José Cavalcanti<sup>1</sup>, Leandro Rabello Monteiro<sup>2</sup> and Paulo Roberto Duarte Lopes<sup>3,\*</sup>

<sup>1</sup>Departamento de Biologia Geral, Universidade Santa Úrsula, Rua Fernando Ferrari, 75, 22231-040, Rio de Janeiro, RJ, Brazil

<sup>2</sup>Departamento de Zoologia, Universidade Estadual Paulista, Caixa Postal 199, 13506-900, Rio Claro, SP, Brazil

<sup>3</sup>Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Campus Universitário, Km 3, BR-116, 44031-460, Feira de Santana, BA, Brazil

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**Mauro José Cavalcanti, Leandro Rabello Monteiro and Paulo Roberto Duarte Lopes (1999)** Landmark-based morphometric analysis in selected species of serranid fishes (Perciformes: Teleostei). *Zoological Studies* 38(3): 287-294. Morphological differences among 6 species of marine fishes belonging to 2 subfamilies of the family Serranidae (Serraninae: *Dules auriga*, *Diplectrum formosum*, and *D. radiale*; Epinephelinae: *Epinephelus marginatus*, *Mycteroperca acutirostris*, and *M. bonaci*) were studied by the geometric morphometric method of thin-plate splines and multivariate analysis of partial-warp scores. The decomposition of shape variation into uniform and nonaffine components of shape change indicate that major differences among species are related to both components of shape variation. Significant differences were found among species with respect to the uniform components, but there is no clear separation of taxonomic groups related to these components, and species are instead separated on the basis of body height and caudal peduncle length. Non-uniform changes in body shape, in turn, clearly differentiate the species of Serraninae and Epinephelinae. These shape changes are probably related to differences in habitat and feeding habits among the species.

**Key words:** Serranidae, Truss networks, Geometric morphometrics, Partial-warp scores, Multivariate analysis.

The Serranidae is one of the least specialized families of the order Perciformes, and is generally considered to be close to the original stock from which other percoid fishes have evolved (Gosline 1966). Most serranids are large, piscivorous fishes associated with coral reefs or rocky bottoms and other inshore environments of tropical seas, with some representatives in inshore temperate areas and in freshwater (Heemstra and Randall 1993). The family is divided into 5 subfamilies (Heemstra and Randall 1993, Nelson 1994), of which Serraninae and Epinephelinae are included in the present study. On the southeastern Brazilian coast, serranid fishes can be grouped into 2 broad categories, according to the kinds of environments in which they occur: a group of species lives sheltered in crevices on rocky bottoms, whereas the other group is composed of free swimmers in sandy bottoms (Figueiredo and Menezes 1980). These

groups correspond, respectively, to the subfamilies Epinephelinae and Serraninae.

No study so far has examined the relation of body form and feeding habit in serranid fishes using the methods of geometric morphometrics for the analysis of landmark data as done by Carpenter (1996) in lethrinid fishes, and Walker (1996 1997) in threespine sticklebacks. Using multivariate analysis of distance measurements, Cavalcanti and Lopes (1993) found significant morphological differentiation in serranid fishes belonging to the above-mentioned groups. However, the shape variation documented by this type of analysis is restricted to the directions sampled by the measurement scheme (Bookstein 1991). The new landmark-based techniques of geometric morphometrics, on the other hand, pose no restriction on the directions of variation and localization of shape changes, and are much more effective in capturing information about the shape of an

\*To whom correspondence and reprint requests should be addressed.

organism. When combined with multivariate statistical procedures, they offer the most powerful tool for testing and graphically displaying differences in shape (Loy et al. 1993, Rohlf and Marcus 1993, Rohlf et al. 1996). The purpose of this paper is to reexamine the data analyzed by Cavalcanti and Lopes (1993), using a larger sample and geometric morphometric methods that should provide new insights into features of shape change which cannot be documented by the analysis of conventional distance measurements.

## MATERIALS AND METHODS

Choice of species for inclusion in this study was determined by the availability of an adequate size range and number of specimens. A total of 52 individuals from 6 species of Serranidae that are among the most common along the southeast coast of Brazil (Figueiredo and Menezes 1980, Heemstra and Randall 1993) were measured. Sample sizes and body size range for each species are as follows: *Dules auriga* Cuvier, 1829:  $n = 13$ , 44-101 mm in standard length (SL); *Diplectrum radiale* (Quoy and Gaimard, 1824):  $n = 11$ , 20-152 mm SL; *Diplectrum formosum* (Linnaeus, 1766):  $n = 4$ , 62-148 mm SL; *Epinephelus marginatus* (Lowe, 1834):  $n = 5$ , 68-190 mm SL; *Mycteroperca acutirostris* (Valenciennes, 1828):  $n = 5$ , 56-131 mm SL; and *Mycteroperca bonaci* (Poey, 1860):  $n = 4$ , 41-147 mm SL. The specimens examined are housed in the Departamento de Zoologia, Universidade Federal do Rio de Janeiro (DZ/UFRJ), Departamento de Biologia Animal e Vegetal, Universidade do Estado do Rio de Janeiro (DBAV/UERJ), and Laboratório de Ictiologia, Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana (LIUEFS).

Measurements were based on a truss network protocol (Strauss and Bookstein 1982, Bookstein et al. 1985), anchored at 10 homologous anatomical landmarks (Fig. 1). Landmarks refer to: (1) anterior tip of the snout on the upper jaw; (2) the most posterior aspect of the neurocranium (beginning of scaled nape); (3) origin of pelvic fin; (4) origin of spinous dorsal fin; (5) origin of anal fin; (6) origin of soft dorsal fin; (7) insertion of anal fin; (8) insertion of 2nd dorsal fin; (9) insertion of 1st ventral caudal fin ray; and (10) insertion of 1st dorsal caudal fin ray. Landmark 1 can be classified as type 1 and landmarks 2 to 10 as type 2, following the classification of Bookstein (1991). All measurements were taken with Vernier calipers to the nearest 0.05 mm.

The 21 inter-landmark distances obtained from

the truss network were converted to Cartesian coordinates by means of a simplified multidimensional scaling algorithm (Carpenter et al. 1996), using the UNFOLD program written by H.J.S. Sommer (unpubl.).

The raw coordinates of all specimens were aligned (i.e., translated, rotated, and scaled to match one another) using the Procrustes generalized orthogonal least-squares (GLS) superimposition method, which fits 1 configuration over another by minimizing the sum of squared distances between homologous landmarks (Rohlf 1990, Rohlf and Slice 1990). The average configuration of landmarks resulting from this procedure served as the "reference" or tangent configuration (defining the point of tangency between the non-linear shape space and the approximating tangent space, see Rohlf 1996) in subsequent computations.

For each specimen, centroid size and the  $x$  and  $y$  uniform components were also computed. Centroid size is an overall size measure and was calculated as the square root of the summed squared distances of each landmark to the centroid of the configuration. The uniform components express information on global scale (uniform, affine) shape variation (Bookstein 1991). The 1st uniform component accounts for the stretching along the  $x$ -axis of the configuration, whereas the 2nd uniform component indicates dilations or compressions along the  $y$ -axis. In the present study, the  $x$ -axis corresponds to the antero-posterior axis, and the  $y$ -axis corresponds to the dorso-ventral axis of the fish bodies. The uniform components were estimated by the linearized Procrustes method of Bookstein (1996b). Correlation and regression analysis (Sokal and Rohlf 1995) was performed between centroid size and the  $x$  and  $y$  uniform components. Centroid size was tested for differences among species by single classification analysis of variance (ANOVA: Sokal and Rohlf 1995). The uniform components were tested for sig-

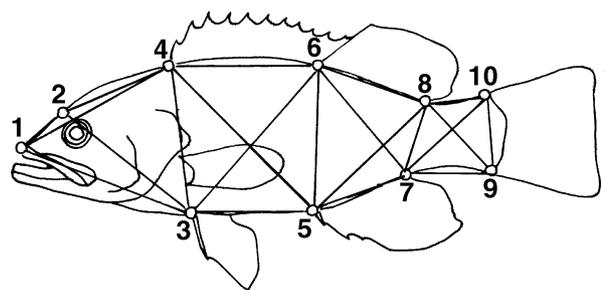


Fig. 1. Outline drawing of *Mycteroperca acutirostris*, showing the locations of the 10 anatomical landmarks (numbered points) and morphometric distance measures recorded on each individual.

nificant differences among species by multivariate analysis of variance (MANOVA: Neff and Marcus 1980). All specimens were scaled to unit centroid size before alignment by the GLS superimposition procedure.

The coordinates of all aligned specimens were used for the thin-plate splines relative warp analysis (Bookstein 1991, Rohlf 1993), in order to analyze and display the direction of shape differences among species. The thin-plate splines technique (Bookstein 1989) consists of fitting an interpolating function to the landmark coordinates of each specimen against the reference configuration so that all homologous landmarks coincide. The bending energy matrix resulting from the thin-plate spline function fitted to the reference configuration is then decomposed into orthogonal axes, the principal warps, that describe shape deformations of the reference configuration at different spatial scales. The projection of the superimposed specimens onto the principal warps produces the partial-warp scores, that describe their deviations from the reference configuration and that can be used as variables in subsequent multivariate statistical analyses (Rohlf 1995 1996, Rohlf et al. 1996). The relative warps are the principal components of the variation among specimens in this space (for computational details see Bookstein 1989 1991, Rohlf 1993). The average configuration of landmarks was used as the reference configuration in the relative warp analysis, and the reference was aligned to its principal axes. The relative warps were computed with the scaling option  $\alpha = 0$ , that weights all landmarks equally and is considered to be more appropriate for systematic studies (Loy et al. 1993, Rohlf 1993, Rohlf et al. 1996). The relative warps were computed in the full shape space (i.e., including both the uniform component and the non-uniform components), as recommended by Bookstein (1996a) for exploratory studies such as the present one. This usually provides effective low-dimensional ordinations, without requiring potentially unwarranted assumptions about the precise spatial scale of the shape changes (Bookstein 1996a). Furthermore, as pointed out by Walker (1996), relative warp analyses that separate the affine and non-affine components can make interpretation of the shape variation ambiguous if these components are correlated. Deformation grids using thin-plate splines were used to graphically portray the patterns of shape variation among the landmarks.

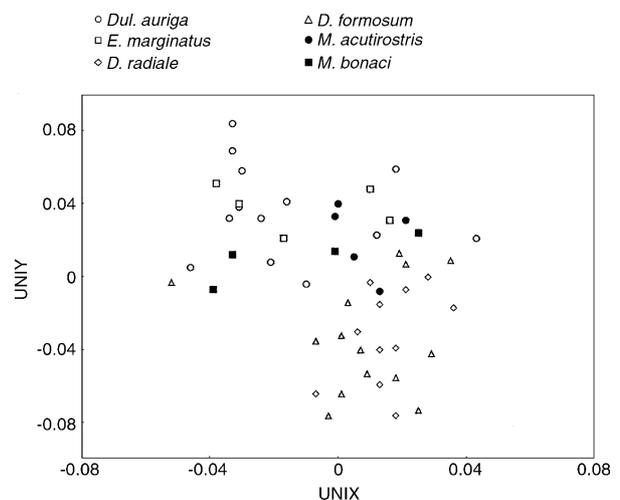
Patterns of among-species variation in total shape space (affine + nonaffine) were examined by canonical variates analysis (CVA: Neff and Marcus 1980) of the partial-warp scores matrix with the uni-

form components appended. Shape changes associated with the canonical variate axes were depicted as deformation grids generated by regressing the partial-warp scores onto each canonical axis (Rohlf et al. 1996). A cluster analysis using the unweighted-pair group average method (UPGMA: Sneath and Sokal 1973) was performed on the matrix of Mahalanobis distances produced by the CVA procedure, in order to depict hierarchically the shape differences among species.

The relative warps analysis and computation of partial-warp scores were done using F.J. Rohlf's TPSRelw program, version 1.16. Regressions between the partial warps and canonical variates were computed with the TPSRegrw program, version 1.13. Canonical variates analysis and clustering were performed with the STATISTICA package, version 4.3 (StatSoft 1993). All computations were performed on an IBM-compatible microcomputer. Most of the programs used in this study are available over the Internet by FTP from the "morphmet" directory at life.bio.sunysb.edu or via the WWW at <http://life.bio.sunysb.edu/morph/>.

## RESULTS

There was a slight but significant correlation between the  $x$  and  $y$  uniform components ( $r = 0.366$ ,  $p < 0.007$ ), and these components also showed a highly significant difference among species (Wilks  $\Lambda = 0.2965$ ,  $F_{[10, 90]} = 7.5282$ ,  $p < 0.0001$ ). The uniform components depict large differences from the reference configuration, but there was no clear taxonomic

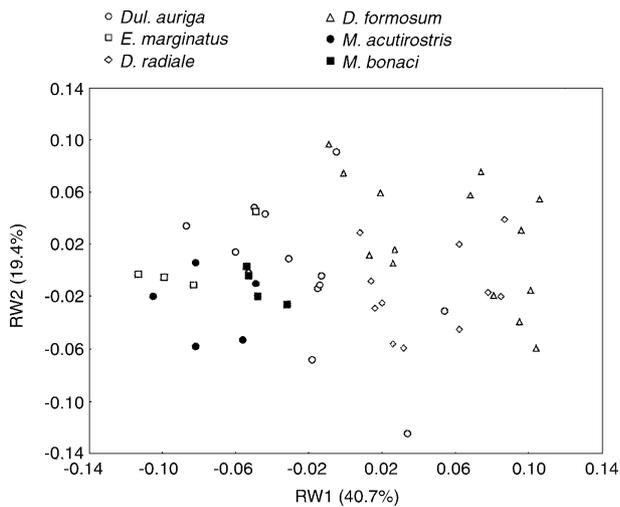


**Fig. 2.** Scatterplot for individual scores on the  $x$  and  $y$  uniform components (U1 and U2) of shape change.

pattern or grouping related to either uniform component, and the species of Serraninae and Epinephelinae overlap broadly (Fig. 2). The uniform components instead separate the higher-bodied species (*Dules* and *Epinephelus*) from the lower-bodied ones (*Diplectrum* and *Mycteroperca*). *Diplectrum* species have low somewhat elongate bodies, as shown by their high scores along *x* (antero-posterior shearing). *Mycteroperca* species approach the mean shape of the group, and *Dules auriga* and *Epinephelus marginatus* are high bodied species with high scores along *y* (dorsoventral dilation) and low scores along *x*. *Diplectrum radiale* has a lower and relatively more elongated body than *D. formosum*. *Dules* has the highest body among the species in the sample.

Centroid size was not significantly correlated with either *x* or *y* uniform components for all specimens pooled ( $r = 0.121$ ,  $p < 0.39$  for *x*;  $r = 0.217$ ,  $p < 0.12$  for *y*). Single classification ANOVA however showed a significant difference of centroid size ( $F_{[5, 46]} = 4.5654$ ,  $p < 0.01$ ) among species.

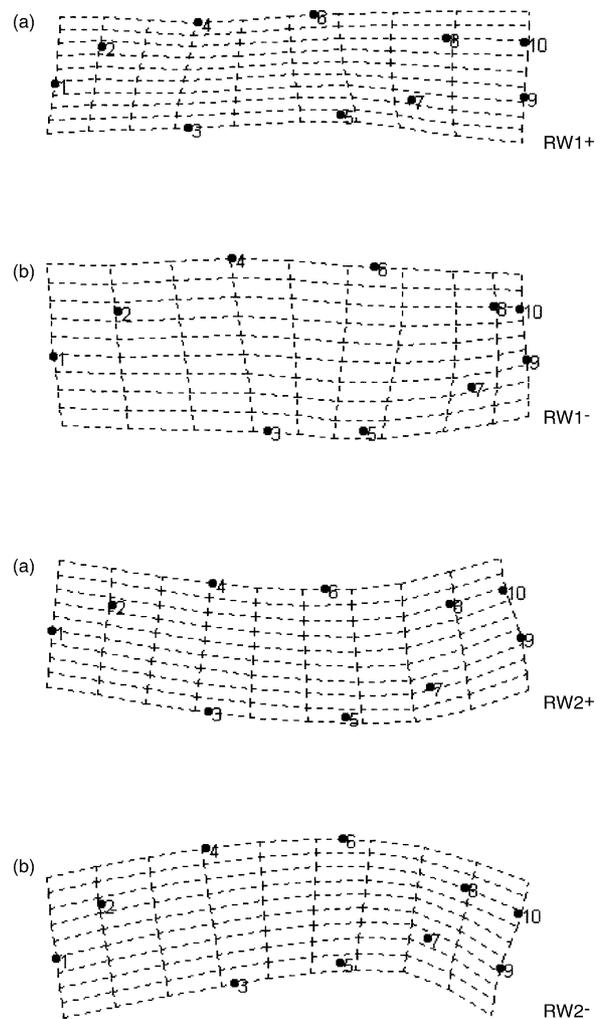
The 1st relative warp extracted from the matrix of the partial-warp scores accounted for about 40.7% of the total nonaffine shape variation, whereas the 2nd relative warp explained 19.4% of the total variation. The pattern of shape change on the first 2 relative warps is shown in figure 3. The 1st relative warp is characterized by shape changes along the *y*-axis, showing an upward displacement of the dorsal landmarks and the posterior stretching of ventral and caudal peduncle landmarks (Fig. 4a). The specimens with highest scores on the 1st relative warp are those belonging to the subfamily Epinephelinae (*M.*



**Fig. 3.** Scatterplot of individual scores from the relative warps analysis of all specimens, with the uniform component included and  $\alpha = 0$ .

*acutirostris*, *M. bonaci*, and *E. marginatus*), which are almost completely distinguished from the specimens belonging to the subfamily Serraninae along this warp (Fig. 3). The 2nd relative warp is in turn characterized by shape changes along the *x*-axis, not showing differences in body height, but clearly disclosing an upward and downward arching of the body (Fig. 4b).

Three statistically significant canonical vectors were extracted from the matrix resulting from the product of the among-group by the within-group covariance matrix ( $\chi^2$ -test,  $p < 0.0001$ ). These vectors together accounted for 93.9% of the among-group relative to within-group variation. The CVA indicated the existence of large and highly significant among-group differences (Wilks  $\Lambda = 0.0030468$ ,  $F_{[80, 153]} = 4.475838$ ,  $p < 0.0001$ ). The projection of the in-



**Fig. 4.** Non-affine shape changes along relative warps 1 (a) and 2 (b), expressed as deformations using thin-plate splines.

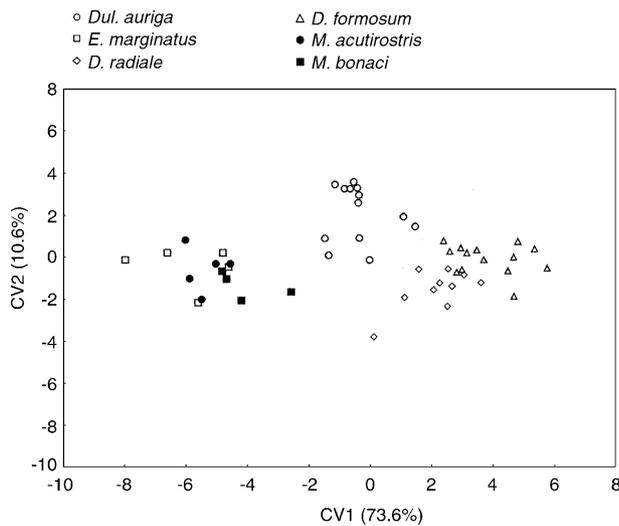
dividual scores onto the first 2 canonical variates (Fig. 5) shows a clear separation of the low-bodied species of the subfamily Serraninae from the high-bodied species of Epinephelinae, along the 1st canonical variate axis (Fig. 6a). The 2nd canonical variate axis discloses an interesting pattern, showing a separation of some species on the basis of a relative enlargement of the caudal peduncle (Fig. 6b).

As shown on the UPGMA phenogram based on the matrix of Mahalanobis distances computed from the partial-warp scores (Fig. 7), the species studied were assigned to 2 very distinct clusters, according to their respective subfamilies. Species within the same genus (*Diplectrum radiale* and *D. formosum*; *Mycteroperca acutirostris* and *M. bonaci*) were also grouped together in the phenogram.

**DISCUSSION**

Although no significant correlation was found between centroid size and the uniform components of shape change, there were significant differences in centroid size among species. This may be due simply to sampling effects, but the small size of the sample available for study within each species precluded an analysis of patterns of allometric growth. As pointed out by Carpenter (1996) in his geometric morphometric study of lethrinid fishes, the investigation of individual species is required for a more complete understanding of allometry patterns.

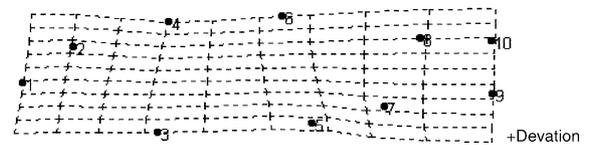
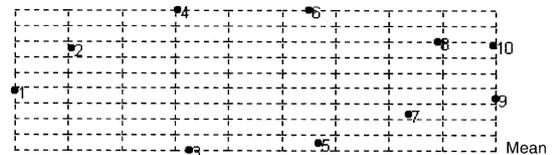
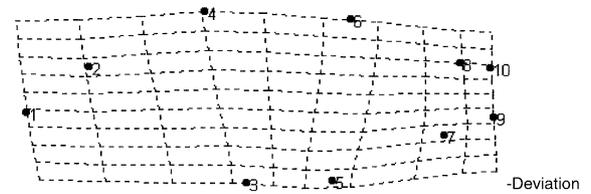
The analysis of the uniform components alone



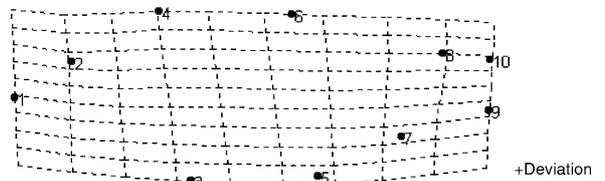
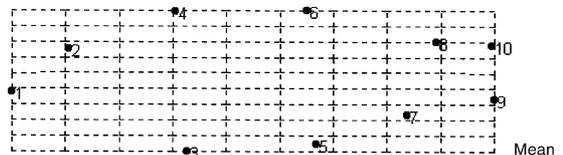
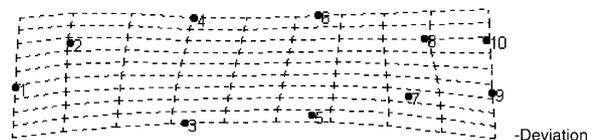
**Fig. 5.** Scatterplot of individual scores from the canonical variates analysis of all specimens, with the uniform component included.

was overall less informative (regarding species systematic relationships) than the analysis using only the nonaffine components. The uniform components indicate that at large spatial scales, body shape is similar in functional groups, mainly separating the high-bodied species associated with hard bottoms and more sedentary habits, from the low-bodied ones associated with soft bottoms and more vagile habits. At small scales, in turn, nonaffine

(a) Canonical variate 1



(b) Canonical variate 2



**Fig. 6.** Results of regression of the partial-warp scores onto the 1st (a) and 2nd (b) canonical vectors with the uniform component included, depicted as deformations using thin-plate splines.

shape differences depicted by the partial warps ordinated species mainly according to their systematic relationships. This agrees with the findings of Loy et al. (1993) and Rohlf et al. (1996), and suggests that the nonaffine shape components may contain more taxonomic information (possibly reflecting the phylogenetic relationships among these species) than do the uniform components of shape variation.

We can also determine the relative importance of localized and global morphological changes in the shape differentiation of the species. Shape modifications seem to occur in large and small spatial scales. The most important global differences in body shape are related to body elongation or shortening; this leads to large differences in body height and caudal peduncle length among the species. *Dules* and *Epinephelus* are different from the other species in this aspect of form, having considerably higher bodies and shorter caudal peduncles. The primary non-uniform component of shape change is related to an up-and-down arching in the body of the specimens, as clearly depicted by the 2nd relative warp (Fig. 4b). Carpenter (1996) suggested that such an "arching effect" of fish bodies in his relative warp analysis of lethriniid fishes might either be a measurement artifact, resulting from problems in the preservation of the specimens, or instead have a functional explanation. Since our sample also consists of preserved specimens, the arching observed in this study could also be attributed to a similar effect of preservation.

Some of the shape changes herein analyzed can, however, be given a functional interpretation, being conceivably related to differences in habitat

and feeding ecology of each species. *Mycteroperca* and *Epinephelus* have higher bodies and larger heads, and live mostly in rocky crevices close to the shore. They feed mainly on fishes, crustaceans, and cephalopods, and behave as ambush predators, hiding in holes and caves and catching prey with a sudden rush and snap of the jaws (Heemstra and Randall 1993). The elongate *Diplectrum* species, with smaller heads and longer caudal peduncles, are better swimmers and are found mostly on sandy bottoms, feeding actively on benthic crustaceans and fishes (Darcy 1985). *Dules auriga*, in turn, is intermediate in shape between species of the subfamily Epinephelinae and those of genus *Diplectrum*, with a feeding ecology and habitat preferences more similar to the latter (Cussac and Molero 1987). The results of the relative warp analysis as depicted by the thin-plate splines deformation grids (Fig. 4a) are consistent with this interpretation. This pattern of shape variation seems to be the opposite of that observed in freshwater fish communities, where in general piscivorous species tend to be more elongate than deeper-bodied benthic foragers (Winemiller 1991), and deserves further investigation.

The relationship between morphology and ecology in fishes has long been known, and a few studies have applied multivariate morphometric methods to investigate ecomorphological patterns in multi-species fish communities (see Douglas and Matthews 1992, and references therein). The decomposition of shape variation into uniform and non-uniform (partial warps) components through geometrical analysis of landmark data takes into account the configuration of the sample data points, and can thus describe and locate differences of form in organisms

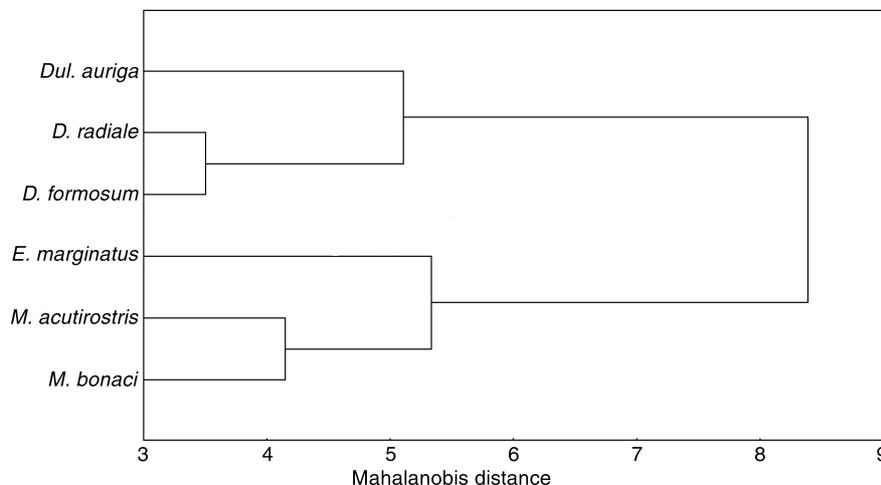


Fig. 7. UPGMA phenogram constructed from Mahalanobis distances computed on all partial warps.

more efficiently than can multivariate analyses of traditional distance measurements, even when the set of measurements corresponds to a truss system (Bookstein 1991). This approach has been shown to yield the most rewarding information in fish ecomorphological studies (see Walker 1996 1997), and is expected to find increasing applications in the near future.

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## 幾種鯔魚（真骨魚類：鱸形目）地標點基礎之形態測量分析

Mauro José Cavalcanti<sup>1</sup> Leandro Rabello Monteiro<sup>2</sup> Paulo Roberto Duarte Lopes<sup>3</sup>

鯔科魚類中，隸屬於鯔亞科 (Serraninae) 的 *Dulus auriga*, *Diplectrum formosum*, *D. radiale* 及石斑亞科 (Epinephelinae) 的 *Epinephelus marginatus*, *Mycteroperca acutirostris*, *M. bonaci* 等六種海生魚類，以薄板曲線幾何分析法與部份扭曲多變量分析法研究其種間之形態差異。將形狀變異解構為形狀改變的均勻性和非仿射性成分，顯示出在種間的主要差異是與此兩個成分相關。均勻性成分在種間有顯著差異，但這些成分無法清楚的將分類群做區分，而體高及尾柄長則可將種分離。體型非均勻性的改變可以清楚的區分出鯔亞科與石斑亞科。這些形態的改變可能與種間棲地與攝食習慣的差異相關。

**關鍵詞：**鯔科，網狀架構，幾何形態，部份扭曲分數，多變量分析。

<sup>1</sup>Departamento de Biologia Geral, Universidade Santa Úrsula, Rua Fernando Ferrari, 75, 22231-040, Rio de Janeiro, RJ, Brazil

<sup>2</sup>Departamento de Zoologia, Universidade Estadual Paulista, Caixa Postal 199, 13506-900, Rio Claro, SP, Brazil

<sup>3</sup>Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Campus Universitário, Km 3, BR-116, 44031-460, Feira de Santana, BA, Brazil