

Phylogenetic and ecological inference of three *Halichoeres* (Perciformes: Labridae) species through geometric morphometrics

by

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ABSTRACT. - A study of geometric morphometrics was carried out based on 109 specimens of four Labridae species captured in north-eastern Brazil. The canonical variable analysis applied on the W Matrix discriminated the species, and the partial warps analysis located the morphological variations. According to analysis, the *Halichoeres* species constitute a monophyletic group, with *H. poeyi* as the sister-group of the clade *H. brasiliensis* + *H. dimidiatus*. The cladogram of these species was estimated using *Bodianus rufus* as outgroup. The *Halichoeres* species share shorter head lengths and deeper heads in relation to the outgroup. Within *Halichoeres*, the more basal taxon (*H. poeyi*) can be characterized by autapomorphies such as short snout and deeper head. In the clade *H. brasiliensis* + *H. dimidiatus*, the snout is longer and the caudal peduncle is deeper than in *H. poeyi*. The results obtained from the geometric morphometry are consistent with works of functional morphology and their applications for the testing of phylogenetic hypotheses are equally satisfactory. However, caution is necessary because the similarities in morphometric data can reflect non-homologous and convergent features due to ecological roles, without representing kinships.

RÉSUMÉ. - Inférence phylogénétique et écologique de trois *Halichoeres* (Perciformes : Labridae) par morphométrie géométrique.

Une étude de morphométrie géométrique a été conduite sur 109 spécimens de 4 espèces de Labridae capturés dans le nord-est du Brésil. L'analyse variable canonique appliquée sur la matrice W a discriminé les espèces et les analyses des flexions partielles ont mis en évidence les variations morphologiques. D'après les analyses, les espèces d'*Halichoeres* forment un groupe monophylétique, *H. poeyi* étant le groupe sœur du clade *H. brasiliensis* + *H. dimidiatus*. Le cladogramme de ces espèces a été construit en utilisant *Bodianus rufus* comme groupe externe. Les espèces d'*Halichoeres* se différencient par des têtes à la fois plus courtes et plus hautes par rapport au groupe externe. Au sein des *Halichoeres*, le taxon le plus basal (*H. poeyi*) peut être (grossièrement) défini par des autapomorphies telles un museau court et une tête plus haute. Dans le clade (*H. brasiliensis* et *H. dimidiatus*) le museau est plus long et le pédoncule caudal est plus haut que chez *H. poeyi*. Les résultats obtenus à partir de l'analyse de morphométrie géométrique sont en accord avec des travaux sur la morphologie fonctionnelle, et leurs applications pour la création d'hypothèses phylogénétiques sont tout autant satisfaisantes. Cependant, il est nécessaire d'être prudent car les similarités observées dans les données morphométriques peuvent refléter des traits convergents et non homologues liés à leurs rôles écologiques sans représenter pour autant des relations de parenté.

Key words. - Labridae - *Halichoeres* - Geometric morphometrics - Phylogeny - Ecology.

Fourteen Labridae species divided into six genera, namely *Bodianus*, *Clepticus*, *Doratonotus*, *Halichoeres*, *Thalassoma* and *Xyrichtys* (Floeter *et al.*, 2003), occur in Brazil, with *Bodianus* comprising three species and *Halichoeres* six species (Moura *et al.*, 2003). *Halichoeres* is the most species-rich genus in the family Labridae, with nearly 75 species (Parenti and Randall, 2000). Although usually considered as polyphyletic (Gomon, 1997; Westneat and Alfaro, 2005; Barber and Bellwood, 2005), this genus comprises lineages found in the Caribbean, South America and East Pacific that form monophyletic groups (Westneat and Alfaro, 2005; Barber and Bellwood, 2005).

The use of genetic tools associated with ecological and/or biomechanical information has increased the knowledge

of relationships into the family (Rocha, 2004; Westneat *et al.*, 2005). Furthermore, ecological investigations concerning behavioural patterns may be used as a source of important information for the establishment of the phylogenetic relationships of fish, as is the case for studies performed with the wrasse tribe Labrini involving parental care analysis (Hanel *et al.*, 2002) and with the colour pattern in cleaning behaviour (Arnal *et al.*, 2006).

In the same way, information generated by morphometric studies may be used in the elaboration of phylogenetic hypotheses (Rohlf, 1990; Peres-Neto, 1995) through the interpretation of ecological aspects of the organisms and their characteristics concerning feeding biology, habitat use, selective pressure and competition (Peres-Neto, 1995).

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Many devices have been created from computational increments and the raise of mathematical applications in biological studies (molecular biology, embryology and phylogeny) (Rohlf and Marcus, 1993; Monteiro and Reis, 1999), spreading the use of morphometric data. Geometric morphometry consists of a descriptive tool that reveals with greater detail and precision the changes and variations in body shape based on homologous anatomical markings, generally used in evolutionary and ontogenetic development studies (Strauss and Bookstein, 1982; Cavalcanti *et al.*, 1999; Monteiro and Reis, 1999; Roth and Mercer, 2000).

Opinions among researchers are divided concerning the validity of application of data resultant from morphometric techniques in phylogenetical studies. Those that believe in the validity of this application defend the use of the Thin-Plate Splines (TPS) method, which possesses mechanisms that allow the definition of anatomical markings as homologous characters. Even admitting that the greatest challenge would be the codification of the quantitative data, Fink and Zelditch (1995) and Swiderski *et al.* (1998, 2000) consider that the TPS method can overcome this difficulty. The party contrary to the use of geometric morphometric techniques in phylogenetical issues presents the theoretical problems in mathematical bases as the greatest impediment (Adams and Rosenberg, 1998; Rohlf, 1998a), besides the real problem of the tridimensionality of the animals (Monteiro, 2000). Recently, Acero *et al.* (2005) applied the geometric morphometric techniques using the TPS method to infer the phylogenetic relationships of Siluriformes from both American coasts; the morphometric data sustained the phylogenetic relationships between the four *Bagre* species.

Therefore, the present work studies three species morphologically, namely *Halichoeres brasiliensis* (Bloch, 1791), *H. dimidiatus* (Agassiz, in Spix and Agassiz, 1831) and *H. poeyi* (Steindachner, 1867), using geometric morphometric techniques, and analyses the use of these techniques in the inference of phylogenetic relationships and in the ecology of these species, using *Bodianus rufus* (Linnaeus, 1758) as extra group.

MATERIAL AND METHODS

The studied specimens were collected in the beaches and coastal reefs of Itamaracá, Serrambi and Tamandaré, all municipalities of the State of Pernambuco, Brazil. A total of 109 individuals belonging to family Labridae were measured. The number of individuals (*n*) and variation in standard length for each collected species were: *Bodianus rufus*, *n* = 27, 174.3-257.8 mm; *Halichoeres brasiliensis*, *n* = 22, 120.0-222.8 mm; *Halichoeres dimidiatus*, *n* = 32, 190.7-232.4 mm; *Halichoeres poeyi*, *n* = 28, 54.0-106.0 mm. The examined specimens were selected according to size in

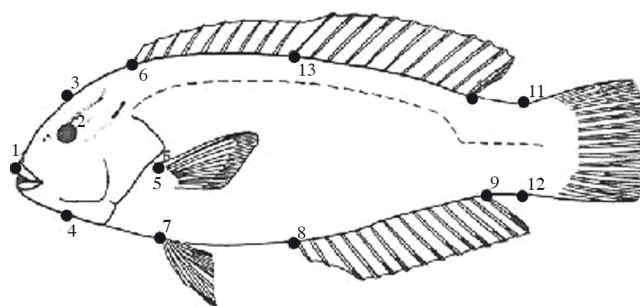


Figure 1. - Scheme of the 13 anatomical landmarks projected in homologous regions of the left lateral surface of a Labridae. [Schéma des 13 marques anatomiques projetées dans les régions homologues sur la surface latérale gauche d'un Labridae.]

order to avoid problems with ontogenetic dimorphisms, and were deposited in the Necton Collection of the Oceanography Department of the Federal University of Pernambuco.

The morphometric data were obtained from 13 anatomical markings fixed upon the left side of the animals, based on homologous points (Strauss and Bookstein, 1982; Cavalcanti *et al.*, 1999; Piorski and Nunes, 2001). The adopted anatomical markings correspond to the following structures: 1) snout tip; 2) left orbit; 3) superior portion of skull vertically aligned with the orbit; 4) inferior portion of the skull vertically aligned with the orbit; 5) origin of the pectoral fin; 6) origin of the dorsal fin; 7) base of pelvic fin; 8) base of the first ray of the anal fin; 9) posterior base of the anal fin; 10) posterior base of the dorsal fin; 11) base of the first ray of the superior lobe of the caudal fin; 12) inferior portion of the caudal peduncle vertically aligned with marking 11; 13) point in the base of the dorsal fin vertically aligned with the point in the base of the dorsal fin, vertically aligned with the origin of the anal fin (Fig. 1).

The specimens were photographed individually using a Sony Cyber-shot DSC-S40 digital camera, and the photographs were stored in Jpeg format with the same 1.0 Megapixel resolution and resized to 640X480 in the program Adobe Photoshop. Each anatomical marking was transformed into Cartesian coordinates using the program TPSdigit v.2.04, in order to establish a numerical matrix (Rohlf, 1998b, 2005; Piorski and Nunes, 2001).

The study of the geometric morphometrics of Labridae began with the alignment of all anatomical landmarks in order to produce a reference configuration (Rohlf *et al.*, 1996), which represents the average of the coordinates from these landmarks (Piorski and Nunes, 2001; Moraes, 2003). From this point on, the IMP (Integrated Morphometrics Package) software was used for the warp analyses, since it is a program that gathers all the TPS warp analyses (Sheets, 2002). Next, a matrix was constructed with all the distances between the original coordinates and those generated by the reference configuration (Monteiro and Reis, 1999; Moraes, 2003). A Principal Warp Analysis (PWA) was applied on this

matrix, where autovectors resultant from the matrix decomposition represent the main axes of a determined configuration of the anatomical landmarks (Monteiro and Reis, 1999; Moraes, 2003). The scores from the projection of each individual in the Principal Warps are named Partial Warps and were organized in a matrix named weight matrix or W matrix (Reis *et al.*, 1998). This matrix was used as a new data set and submitted to a Canonical Variable Analysis that considers group definition *a priori* and maximizes the differences between them (Bookstein, 1991; Zar, 1999).

The cladogram was constructed from data generated by the program IMP through the cladistic routine of program PAST v.1.37 (Palaeontological Statistics Software Package) developed by Hammer *et al.* (2001).

RESULTS

Geometric morphometrics

Analysis of the canonical variables applied upon the W matrix indicated differences between the groups (Wilks' $\lambda_{\text{axis1}} = 0.0008$; Wilks' $\lambda_{\text{axis2}} = 0.0220$; $p < 0.00001$), and the first three canonical axes accumulated 38.1% of variation between species. 25.9% of variation was obtained in the first axis, discriminating *B. rufus* from the three *Halichoeres* species (ANOVA, $F = 906.1$; $d.f. 3$; $p < 0.00001$) (Fig. 2). The anatomical modifications associated with the first canonical axis indicate that *B. rufus* is differentiated from the other species by variations in the skull and caudal regions (Fig. 3). The orbit and inferior portion of the skull are dislodged in the opposite direction of the movement of the snout tip and superior portion of the skull, indicating a larger space in the pre-orbital region and a lower head. In the caudal portion of the body, the anatomical landmarks of the superior and inferior portions of the peduncle average point presented the same sense and inverted directions.

The second canonical axis explained 8.4% of the variation between the studied groups, discriminating *H. poeyi* from a group formed by *H. brasiliensis* and *H. dimidiatus* (ANOVA, $F = 292.7$; $d.f. 3$; $p < 0.00001$) (Fig. 4). In this axis, *H. poeyi* is characterized by the dislocation in opposite directions of the orbit and the superior portion of the skull, indicating that the pre-orbital region is shorter and the skull is slightly more elevated than in the other *Halichoeres* species (Fig. 5).

Only 3.1% of data variation was accumulated in the third canonical axis, allowing the discrimination between *H. brasiliensis* and *H. dimidiatus* (ANOVA, $F = 134.7$; $d.f. 3$; $p < 0.00001$) (Fig. 4). According to morphological warps associated with this axis, *H. dimidiatus* differentiates from *H. brasiliensis* through variations in the upper skull and in the caudal peduncle region (Figs 5, 6). At the top of the head, the orbit tends to further itself from the snout while the supe-

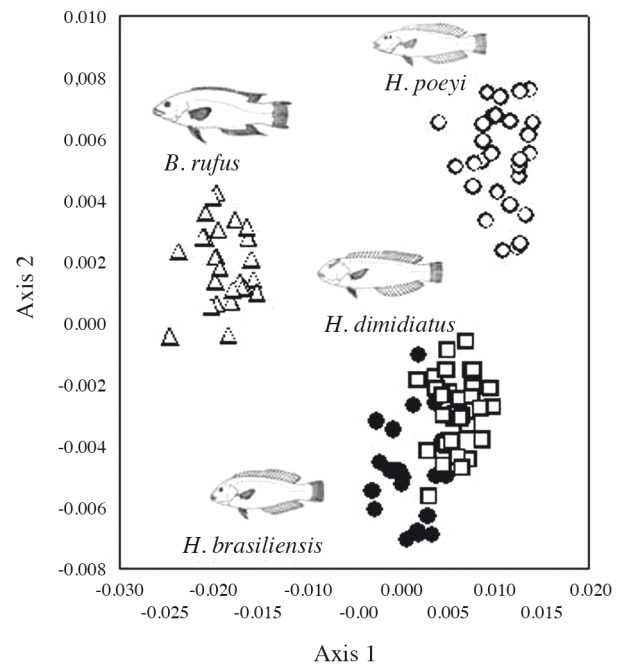


Figure 2. - Projection of the individual scores of Labridae in the space of the first and second canonical axes. [Projection des différents scores de Labridae dans l'espace du premier et du deuxième axes canoniques.]

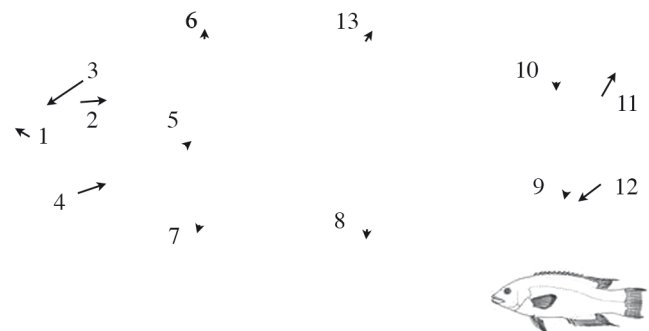


Figure 3. - Vector of the warps representing the alterations in the body of *B. rufus*. Variation upon the first canonical axis. [Vecteur des flexions représentant les changements du corps d'un *B. rufus*. Variation sur le premier axe canonique.]

rior portion of the head nears the anterior extremity of the head. In the caudal peduncle, the vertical dislocation of the posterior base of the dorsal fin indicates a raise in height for this region.

Phylogenetic hypothesis

Since we analysed only three species of this diverse genus, caution should be used when interpreting phylogenetic results. However, some general patterns can be drawn from our analysis. The cladogram generated by PAST from data obtained through geometric morphometrics indicated that the studied *Halichoeres* species form a monophyletic

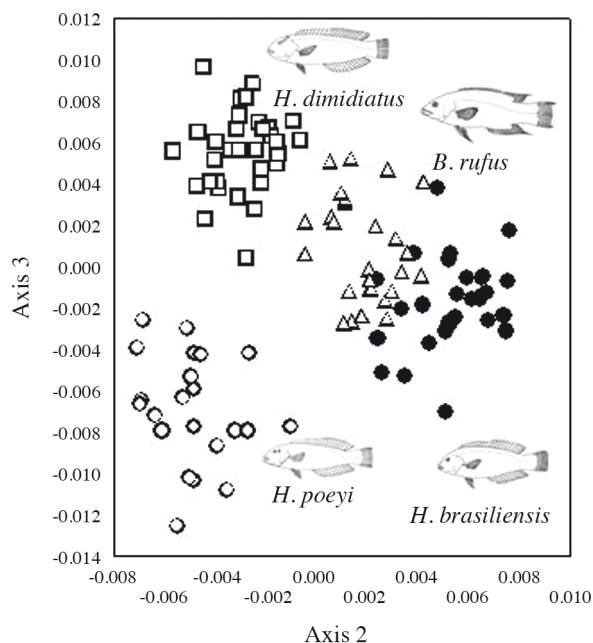


Figure 4. - Projection of the individual scores of Labridae in the space of the second and third canonical axes. [Projection des scores individuels de Labridae dans l'espace du deuxième et du troisième axes canoniques.]

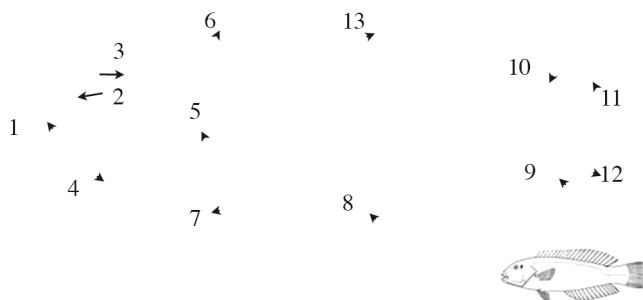


Figure 5. - Vectors of the warps representing the alterations in the body of *H. poeyi*. Variation upon the second canonical axis. [Vecteurs des flexions représentant les changements du corps d'un *H. poeyi*. Variation sur le deuxième axe canonique.]

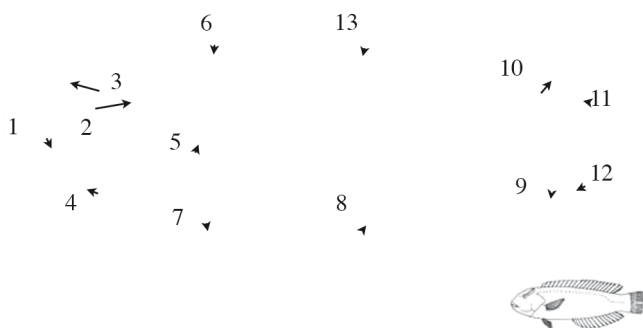


Figure 6. - Vectors of the warps representing the alterations in the body of *H. dimidiatus*. Variation upon the second canonical axis. [Vecteurs des flexions représentant les changements du corps d'un *H. dimidiatus*. Variation sur le deuxième axe canonique.]

group, with *Bodianus rufus* as an outgroup and *H. poeyi* as a sister group of the clade *H. brasiliensis* + *H. dimidiatus* (Fig. 7). Analysis of the comparative alterations found between the states of the characters resulted in synapomorphies and a series of transformations from different morphological variations found.

Synapomorphies. - The heads of the three *Halichoeres* species have smaller lengths (22% of SL) and are deeper than those of the outgroup; the pre-orbital distances were smaller (32% of SL) and the caudal peduncles were lower (18.5% of SL) than the measurements found for *B. rufus*. Within *Halichoeres*, the most basal taxon (*H. poeyi*) may be defined by the autapomorphy of the slightly shorter snout ($\leq 7.8\%$ of SL) and more elevated head (20% of SL). The clade *H. brasiliensis* + *H. dimidiatus* shares a longer snout ($>7.8\%$ of SL) than *H. poeyi* and a larger height of the caudal peduncle ($> 14\%$ of SL).

Head. - The vector of anatomical landmark 3, located at the top of the head, is oriented in a posterior sense, reducing the length of the snout ($< 7.8\%$ of SL) of *H. poeyi*, while in the individuals from the *H. brasiliensis* + *H. dimidiatus* clade this vector is inclined towards the dorsum, leading to a higher snout.

Eyes. - Considering the relative positions of the eyes between the species, it is noted that anatomical landmark 2 directs itself towards the frontal portion, shortening the distance between the eyes (26% of SL) and the anterior margin

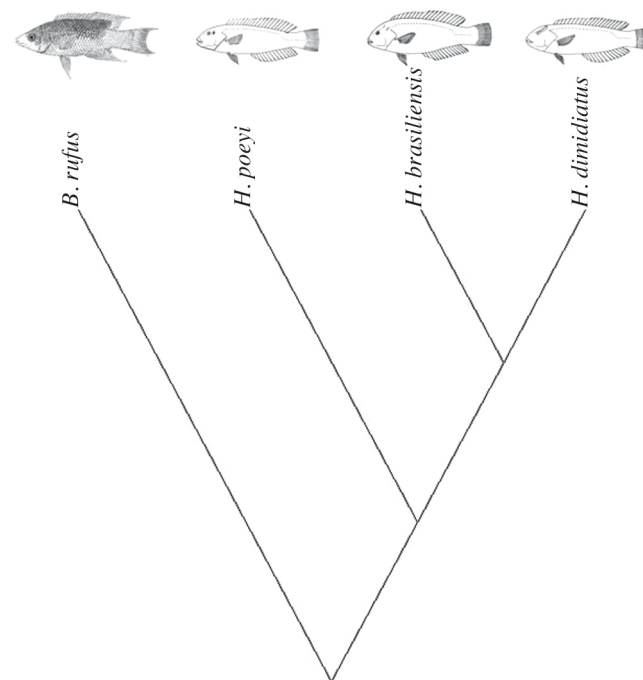


Figure 7. - Phylogenetical hypothesis of three *Halichoeres* species generated by routine cladistics in the program PAST. [Hypothèse phylogénétique de trois espèces de *Halichoeres* produites par routine cladistique dans le programme PAST.]

of the head in *H. poeyi*. The position of the eyes in the *H. brasiliensis* + *H. dimidiatus* clade, however, is located more posteriorly, reverting to the plesiomorphic state of this character, found in *B. rufus*.

Caudal peduncle. - The height of the caudal peduncle in *H. poeyi* maintained an orientation similar to the outgroup. However, in the clade formed by the congeneric species, a raise (of more than 14% of SL) is verified in the region located between the final insertion of the dorsal fin in the caudal peduncle, indicated by the vector of anatomical landmark 10.

DISCUSSION

Morphometric analyses of these labrid species showed that the main morphological variations are located in the head and caudal peduncle. In the comparison between *Bodianus rufus* and *Halichoeres*, analyses discriminated the long and slender snout and deeper caudal peduncle of the first species. Morphological modifications were more evident in the cranial region, where *H. poeyi* is differentiated from *H. brasiliensis* and *H. dimidiatus* for the smaller pre-orbital distance and especially for its more elevated skull. On the other hand, *H. brasiliensis* moves further from *H. dimidiatus* due to variations in the skull ceiling and greater height of the caudal peduncle.

Morphological knowledge is essential for the interpretation of many biological components such as functional morphology, physiology, systematics and evolutionary patterns (Lowe-McConnell, 1999). Thus, the variation in functional morphology observed in different feeding mechanisms allows the coexistence of sympatric species, minimizing or avoiding interspecific competition (Labropoulou and Eleftheriou, 1997), supported by adaptations for the capture of potential prey and by manoeuvrability (Romer and Parson, 1985; Lowe-McConnell, 1999).

In the study of the functional morphology of labrid skulls presented by Wainwright *et al.* (2004), different patterns between *Bodianus* and *Halichoeres* species were obtained. Their analyses discriminated patterns from the function of mandible kinetics; mouth size and larger adductor muscle in *Bodianus* and suggested that they could potentially prey upon elusive animals with large sizes. However, the *Halichoeres* species present a more diversified pattern in its functional morphology and ecology, being considered as generalists regarding exploration of food items (Wainwright, 1988; Ferry-Graham *et al.*, 2002; Wainwright *et al.*, 2004).

Phylogenetic analyses performed through geometric morphometry highlight the measurable relations among the morphological characteristics that emphasize body shape. Elaborating phylogenies from measurements, as is proposed in the current study, may generate approximations of groups

based on morphological similarities, leading to a representation of homoplasies within the group (Amorim, 2002). In this way, the relationships obtained between the species may suffer a distortion in their phylogenetic that translate into ecological similarity, as obtained in the Mahalanobis distance phenogram performed by Cavalcanti *et al.* (1999) while studying geometric morphometry in Serranidae.

Even though the current phylogenetic proposal was built upon a small group composed of three *Halichoeres* species out of the six occurring in Brazil and an outgroup, the importance of this research as a phylogenetic assay of the use of geometric morphometrics data (and also the state of these characters) is recognized through the series of transformations proposed. Studies performed with molecular methods and applied to phylogeny demonstrate that *Halichoeres* needs a taxonomical review since it is notably polyphyletic (Westneat and Alfaro, 2005; Barber and Bellwood, 2005). The non-definition of phylogenetic relationships in *Halichoeres* is related to unresolved taxonomy, where the problem can be seen in the large quantity of synonymies (Randall and Böhlke, 1965; Böhlke and Chaplin, 1993; Parenti and Randall, 2000). According to Froese and Pauly (2007), there are close to 23 synonymies among the *Halichoeres* species occurring in the Brazilian provinces, which can be divided between the following species: *H. brasiliensis* (3 synonymies), *H. bivittatus* (7), *H. dimidiatus* (1), *H. penrosei* (2), *H. poeyi* (1) and *H. radiatus* (9).

The 75 species of this genus form at least four clades with distinct evolutionary histories. Nevertheless, the New World species form a monophyletic group. The groupings of *Halichoeres* are polyphyletic for species in the Indo-Pacific and Eastern Pacific regions, and monophyletic for the Western Atlantic (Westneat and Alfaro, 2005; Barber and Bellwood, 2005). These authors evidenced that this phylogenetic situation follows the pattern of most reef fish, considering that the Indo-Pacific region would be the centre of origin for these groups, and the Caribbean the locality most recently occupied by this fauna. The barrier formed by the Amazon and Orinoco rivers caused speciation of a few western Atlantic species resulting in Brazilian endemics (Rocha, 2003; Rocha *et al.*, 2005). The Caribbean *H. radiatus* (Linnaeus, 1758), *H. cyanocephalus* (Bloch, 1791) and *H. maculipinna* (Muller and Troschel, 1848), are considered sister-species of *H. brasiliensis*, *H. dimidiatus* and *H. penrosei* Starks, 1913, (Rocha and Rosa, 2001; Rocha, 2004). However, it is worthy to point out that the inclusion of *H. maculipinna* and its sister *H. penrosei* in *Halichoeres* is probably incorrect (Barber and Bellwood, 2005; Westneat and Alfaro, 2005).

The results obtained from geometric morphometrics show consistency when compared with works of functional morphology (Wainwright, 1988; Wainwright *et al.*, 2004) because they indicate that the variations seen in the labrids occur mainly in the area of the skull. Despite the rejection

related to the use of data generated by geometric morphometrics for phylogenetic purposes (Fink and Zelditch, 1995; Swiderski *et al.*, 1998, 2000; Acero *et al.*, 2005), the results are satisfactory in this and other previous studies. However, caution is suggested in inferring phylogenetic relationships, since the results of morphometric similarities may be reflecting non-homologous and convergent characters due to ecological roles, without representing kinships.

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