

Systematics of the genus *Bagre* (Siluriformes: Ariidae): A morphometric approach

by

Arturo ACERO P. (1), José Julián TAVERA (2) & Javier REYES (3)

ABSTRACT. - A preliminary morphometric study based on 17 landmarks was carried out, using 104 specimens of six species of sea catfishes from both South American coasts, the four accepted species of the genus *Bagre* and two reference species (*Ariopsis seemanni* and *Arius platypogon*). The landmarks were mainly located on the head and at the origin and end of fins. The partial warps weighted matrix was used to perform the discriminant analysis and the species pair-wise comparisons in order to establish if there were differences between the species. Thereafter, a partial-warps weighted matrix was generated with the average species consensus. Using PHYLIP maximum likelihood routine (CONTML), an additive tree was obtained. Shape changes were described over the tree using TPS tree (square change parsimony). *Bagre marinus* (western Atlantic) seems to be the most basal species of the genus. The species showing the larger shape changes are *B. pinnimaculatus* (eastern Pacific) and *B. bagre* (western Atlantic). Those two species are apparently more closely related to each other than to the other two species of *Bagre*.

RÉSUMÉ. - Étude systématique du genre *Bagre* (Siluriformes : Ariidae). Approche morphométrique.

Une étude morphométrique préliminaire, basée sur 17 repères, est réalisée sur 104 spécimens appartenant à six espèces de poissons-chats marins des deux côtes sud-américaines : les quatre espèces acceptées du genre *Bagre* et deux espèces de référence (*Ariopsis seemanni* et *Arius platypogon*). Les repères sont principalement localisés sur la tête ainsi qu'à l'origine et à l'extrémité postérieure des nageoires. Afin de mettre en évidence les différences interspécifiques, une analyse discriminante et des comparaisons interspécifiques deux à deux ont été réalisées sur la matrice des flexions partielles. Ensuite, une matrice des flexions partielles a été construite à partir du consensus obtenu sur les poissons moyens par espèce. Un arbre par addition a été obtenu en utilisant la routine du maximum de vraisemblance du progiciel PHYLIP (CONTML). Les changements de conformation ont été décrits d'après l'arbre par utilisation de TPS Tree (parcimonie sur les moindres carrés). *Bagre marinus* (Atlantique ouest) semble être l'espèce la plus plésiomorphe du genre. Les espèces montrant les plus importants changements morphologiques sont *B. pinnimaculatus* (Pacifique est) et *B. bagre* (Atlantique ouest). Ces deux espèces sont apparemment plus étroitement apparentées l'une à l'autre que les deux autres espèces de *Bagre*.

Key words. - Ariidae - *Bagre* - Sea catfishes - ASE - ASW - Phylogenetic - Morphometrics.

The family Ariidae (order Siluriformes), commonly known as sea catfishes, is widely distributed around the world in all the tropical and subtropical continental shelves, but the intrafamilial phylogenetic relationships are poorly known (Kailola and Bussing, 1995; Acero, 2002). Ariidae includes between 130 (Acero and Betancur, 2002) and 200 species (Acero, 2003) that inhabit mainly in estuaries and turbid coastal waters, but some species occur below 100 m depth and others dwell basically in freshwater. However, the number of valid genera is unclear as well as their distribution. Betancur *et al.* (2003) made a preliminary analysis of the systematic of the family in both coasts of northern South America, taking into account some osteologic and external characters. The resulting phylogenetic hypothesis is a cladogram where they show that there are many inconsistencies in the generic and suprageneric systematic of the family.

Simple morphometric procedures have been established and applied in systematic and taxonomic studies for more than a century, being employed with greater frequency since the decade of 1970, due to the development of more elaborated methods (Chapman *et al.*, 1997). Shape analysis, morphometrics, and statistics are available tools for researchers in order to increase the foundations of their results (Chapman, 1990). Morphometric techniques have been used to establish limits between species, populations, and stocks (Stracahan and Kell, 1995; Cadrin and Friedland, 1999; Littman *et al.*, 2000), as well as to describe biogeographic patterns and infer the phylogeny of a group (Loy and Corti, 1996).

Rohlf (1990) defined morphometrics as the quantitative description, analysis and interpretation of shapes and their variation in biology. He determined that description and comparison of structures' shapes are necessary in any sys-

(1) Universidad Nacional de Colombia (Instituto de Ciencias Naturales), Apartado 1016, Cerro de Punta Betín (INVEMAR), Santa Marta, COLOMBIA. [aacero@invemar.org.co]

(2) CICIMAR-IPN, Centro Interdisciplinario de Ciencias marinas, La Paz, Baja California Sur, MEXICO. [surfjota@ipn.mx]

(3) Instituto de Investigaciones Marinas y Costeras, Apartado 1016, Santa Marta, COLOMBIA.

tematic study that is based on organisms morphology. Several studies have shown that the recently developed techniques of geometric morphometrics are extremely powerful descriptive tools (Swiderski *et al.*, 2000).

However, the use of the morphometric techniques is still under debate. Swiderski *et al.* (1998, 2000) and Zelditch *et al.* (1998) consider that the homology principle may be applied to the relative deformation warps, which are used as characters to infer phylogenetic hypothesis. Adams and Rosenberg (1998), Rohlf (1998b), Monteiro (2000), and Roth and Mercer (2000), on the other hand, opine that the mathematical properties of the warps lack biological meaning; therefore, the use of those data as cladistic characters may lead to erroneous interpretations in the reconstruction of the evolutionary history of a group. Nevertheless, the group of warps coming from a selection of anatomical landmarks may be useful to infer a phylogenetic, non cladistic, hypothesis based on a technique such as square change parsimony and maximum likelihood because those procedures are invariant to the rotations inherent to the shape space (Rohlf, 2002).

The purpose of this study is to demonstrate how shape has changed from one species to another and that morphometric techniques could be used to infer phylogenetic relationships as well as congruent hypothesis of classification. The systematics of the genus *Bagre*, a sea catfish group endemic to the Neotropics and represented by four species, two from the Caribbean (*B. bagre* and *B. marinus*) and two from the eastern Pacific (*B. panamensis* and *B. pinnimaculatus*), are herewith analyzed.

MATERIAL AND METHODS

A total of 104 specimens representing six species were studied. Additionally to the four species of *Bagre*, two species from the eastern Pacific were chosen as the 'outgroups' for shape analysis. They were *Arius platypogon*, considered by Betancur *et al.* (2003) as the sister species to the genus *Bagre* as a whole, and *Ariopsis seemanni*, selected because it is included in the same suprageneric group as *Bagre* (Betancur *et al.*, 2003). The Caribbean specimens were collected in the Guajira peninsula (Colombia) (11° 25'N, 73° 5'W) and in Margarita Island (Venezuela) (11°N, 64° 01'W); the Pacific species were all collected in Buenaventura, Colombia (3° 55'N, 77° 05'W).

The specimens were preserved in formaline for two to five days, in order to avoid bending and possible errors caused by differences in the position of selected landmarks. The digital images were obtained using a flat bed scanner (Epson ES1200 C). The images, taken only on the right side of the fishes, were carefully taken to not mask important

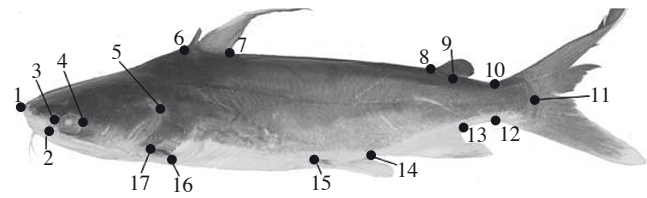


Figure 1. - Location of the 17 selected landmarks (black dots) over one image of *Bagre marinus* species. [Localisation des 17 repères sélectionnés (points noirs) sur *Bagre marinus*.]

structures, and were edited in the program Adobe Photoshop v.3.0. Finally, 17 landmarks were digitalized employing the TPSdig v.1.39 application developed by Rohlf (2003) (Fig. 1).

The shape variation was analyzed using TPSrelw v1.23 application (Rohlf, 1998c). The technique consists in the superimposition and alignment of all the specimens to a consensus, showing the changes in function of the averaged Procrustes distance in Kendall's shape space among the consensus and the entire sample of data, using generalized orthogonal least-squares (GLS) (Rohlf and Slice, 1990). The alignment is then projected to a tangent shape space (Rohlf 1999b, 2000) in which a principal components arrangement known as relative warps is performed using a partial warp matrix (Bookstein, 1989, 1991, 1996; Rohlf, 1996, 2000). Relative warps are just principal components vectors in the space used to describe the major trends of the shape variations between the specimens as deformations to a reference (Rohlf, 1999a). TPSsmall (*ibid.*) application was used to check if the tangent projection is close to the original Kendall's shape space defined by the whole data.

The weighted matrix of the partial warps that is obtained in TPSrelw was introduced in the statistic software SYSTAT v.9.0 to perform a step by step discriminant analysis using jackknife procedure. Once it was established that there were significant statistic differences among the species, a centroid image from all the species was generated with TPSsuper (Rohlf, 1998a), as a value to estimate a matrix of the species and generate a weighted matrix of the partial warps to the averaged value of the landmarks configuration for each species with TPSrelw (Rohlf, 2000).

Finally, a tree was estimated using the maximum likelihood procedure developed by Felsenstein (2001) in the program PHYLIP v 3.6 using the routine CONT (continuous variables, no rotted tree, randomized order of the sample, and 100 replicates). This tree produces a phylogenetic hypothesis. After that the tree is introduced in the program TPStree (Rohlf, 1999a) to find how its topology can reflect the changes in form.

Table I. - Maximum, minimum and medium values of the Procrustes and tangent distances. [Valeurs maximales, minimales et moyennes des distances Procrustes et des distances tangentés.]

	Procrustes distances	Tangent distances
Minimum	0.022922	0.022908
Maximum	0.186963	0.186690
Medium	0.089733	0.089690

Table II. - Statisticals for the discriminant analysis. [Statistiques pour l'analyse discriminante.]

Statistical	Value	F Value	Probability
Wilks's lambda	0	42.140	0
Pillai's trace	4.19	24.436	0

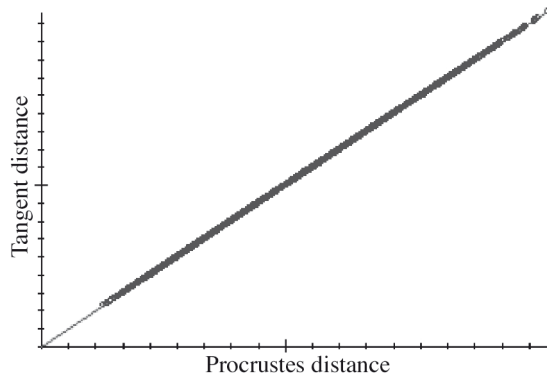


Figure 2. - Tangent against Procrustes distances regression for all analyzed specimens. [Régression entre distances dans l'espace tangent et distances Procrustes pour tous les spécimens analysés.]

RESULTS AND DISCUSSION

Tangent distances vs. Procrustes distances

Procrustes distance and tangent space distance of the shapes of the sea catfishes were compared. The relation of the regression between the shape spaces was almost lineal, with none of the studied specimens showing any significant deviation from the slope determining the relation between the shape spaces (Fig. 2). Table I includes the maximum, minimum, and mean values of the Procrustes and tangent distances, as well as the slope (0.999439) and correlation (1) values. Marcus *et al.* (2000), in their morphometric analysis of mammal skulls, show slope and correlation values of 0.9947 and 0.9997, respectively. Even though there are differences in the configuration of the spaces, the distortion of the multidimensional space projection (Procrustes distance) in the tangent space is small enough to allow the use of the traditional statistic methods to describe the variation in shape, as it was proposed by Rohlf (1999b).

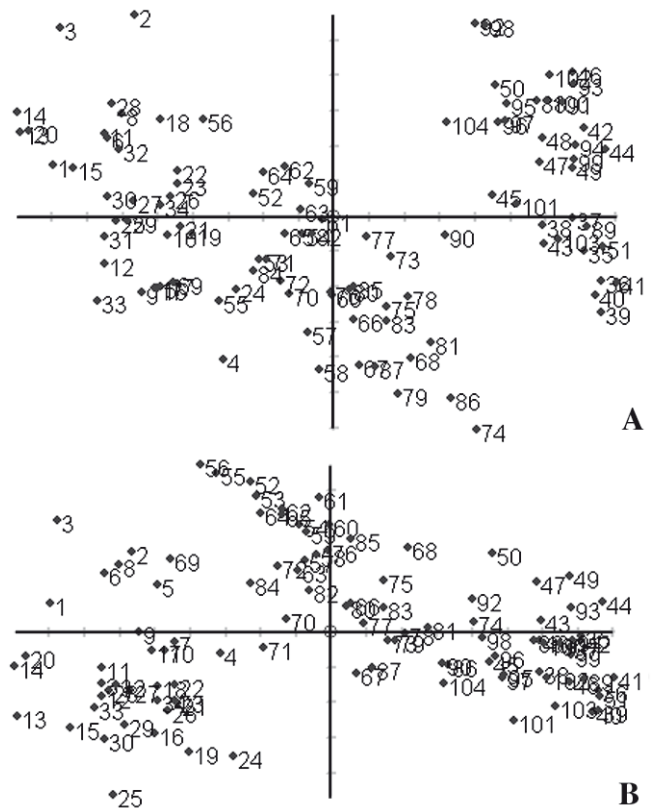


Figure 3. - PCA Ordination plot showing the 104 specimens over two first relative warps. **A:** Relative warp 1x vs 1y for 2D data; **B:** relative warp 1x vs 2x for 2D data. [Analyse en composantes principales montrant les 104 spécimens pour les deux premières flexions relatives. **A :** Flexion relative 1x en fonction de 1y ; **B :** Flexion relative 1x en fonction de 2x.]

Relative deformation warps and discriminant analysis

After aligning and overlapping the group of landmarks for the 104 specimens, the first three deformation axes accumulate 80.5% of the information on the body form variation. The graphics of the relative deformation warps show that the species get organized in three groups in the ordination (Fig. 3A: 1x vs 1y; Fig. 3B: 1x vs 2x), which are relatively well separated. *Bagre bagre* (points 35 to 51 in the ordination) and *B. pinnimaculatus* (points 88 to 104) appear in the positive space of 1x warp. *Bagre marinus* (points 52 to 65) and *B. panamensis* (points 66 to 87) appear in the middle part of 1x warp. On the other hand, *Ariopsis seemanni* (points 7 to 34) and *A. platypogon* (points 1 to 6) appear in the negative space of 1x warp. Finally, *B. marinus* and *B. panamensis* as well as *A. platypogon* and *A. seemanni* are clearly separated on the 2x warp (Fig. 3B).

The results obtained with the discriminant analysis lead to know the existence of statistical differences between the studied species (Tab. II). With the Mahalanobis distance classification, 100% of the individuals are correctly assigned to their

Table III. - Classification matrix after Jackknife procedure in the discriminant SYSTAT routine. Rows correspond to species and columns correspond to specimens correctly assigned (%) to their original taxa. [Matrice de classification après procédé de Jackknife dans la routine discriminante SYSTAT. Les lignes correspondent à l'espèce et les colonnes correspondent aux spécimens correctement assignés (%) à leurs taxons originaux.]

Species	<i>A. platypogon</i>	<i>A. seemanni</i>	<i>B. bagre</i>	<i>B. marinus</i>	<i>B. panamensis</i>	<i>B. pinnimaculatus</i>	% assignment
<i>A. platypogon</i>	6	0	0	0	0	0	100
<i>A. seemanni</i>	0	28	0	0	0	0	100
<i>B. bagre</i>	0	0	17	0	0	0	100
<i>B. marinus</i>	0	0	0	14	0	0	100
<i>B. panamensis</i>	0	0	0	0	22	0	100
<i>B. pinnimaculatus</i>	0	0	1	0	0	16	94
Total	6	28	18	14	22	16	99

relative species; after the jackknife procedure the percentage diminish to 99% (Tab. III). With the canonic functions, the cumulative variation for the first and second factor is 85.66%. The ordination of the species using the first three canonic variables was similar to the one shown in figure 3; that is each one of the species pairs (*A. platypogon*-*A. seemanni*, *B. marinus*-*B. panamensis*, and *B. pinnimaculatus*-*B. bagre*) shows a shape relatively similar within the space (Fig. 4).

The way that the species are placed in the ordinations (Figs 3, 4) suggests that there is a direction in the change of the body shape that may be interpreted as a signal of the phylogeny of the group, due to the low diversity of shapes in the bulk of analyzed data. This differs clearly to what was found by Marcus *et al.* (2000) in their mammal skulls study. Zelditch *et al.* (1995), Marcus *et al.* (2000) and Swiderski *et al.* (2000) have clarified the objections about the homology principle (de Pinna, 1991) with this kind of data sets. Therefore, the features analyzed may be used to infer phylogenies without using

Figure 5. - Schematic shape changes over first relative warp. **A**: Positive 1x side; **B**: Negative 1x side. Dots shows consensus configuration, arrows shows direction and magnitude of the vectors of the shape change. [Changements schématiques de conformation en fonction de la première flexion relative. **A** : Coordonnées 1x positives ; **B** : Coordonnées 1x négatives. Les points représentent la conformation consensus, les flèches représentent la direction et la norme des vecteurs de déformation.]

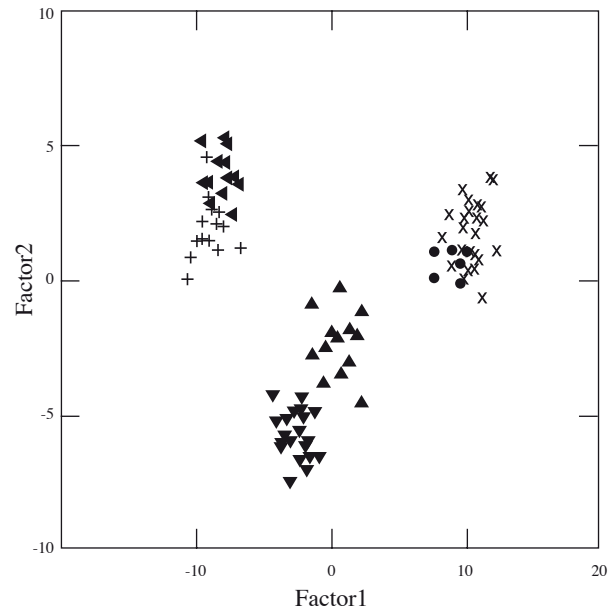
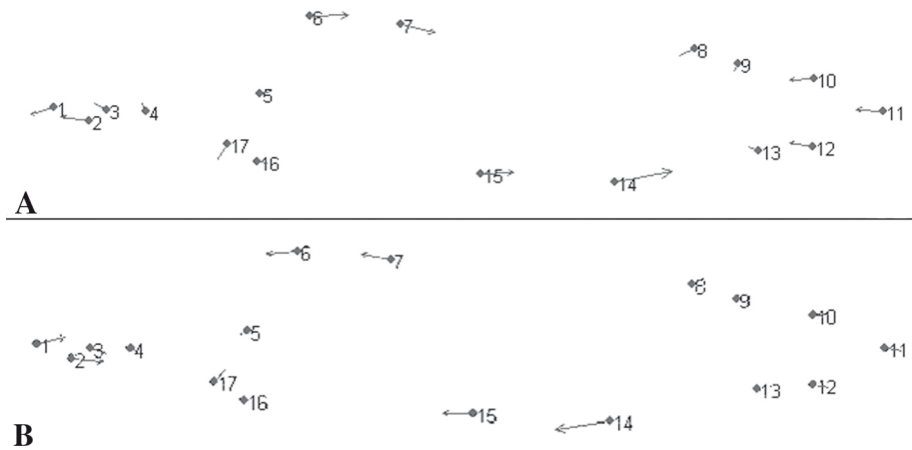


Figure 4. Plot of the first two canonical factors, after Jackknife SYSTAT routine, showing specimens clusters, using species as dummy group variant: (▲) *Bagre pinnimaculatus*, (+) *B. bagre*, (▲) *B. marinus* (▼) *B. panamensis*, (x) *Ariopsis seemanni*, and (●) *Occidentarius platypogon*. [Deux premiers facteurs canoniques, d'après la routine Jackknife SYSTAT, montrant les regroupements de spécimens, en utilisant les espèces comme groupes d'objets différents.]

cladistic methods because the codification of continuous variables is unjustified (Felsenstein, 1988).

Arius platypogon and *A. seemanni* are located in the ordinations in a position opposite to the species of *Bagre*, which may be in agreement with the outgroup principle. Those taxa (i.e., species, genera) that may be related but are not included in the target taxa may be considered part of the outgroup. Ideally the outgroup should be the sister group to the ingroup (Brooks *et al.*, 1984), which then may give an indication of the shape changes and infer evolutionary novelties. The species closer to the consensus are *B. marinus* and *B. panamen-*



Figure 6. - Schematic shape changes over second relative warp. **A**: Positive 1X side; **B**: Negative 1X side. Dots show consensus configuration, arrows show direction and magnitude of the vectors of the shape change. [Changements schématiques de conformation en fonction de la deuxième flexion relative. **A** : Coordonnées 1x positives ; **B** : Coordonnées 1x négatives. Les points représentent la conformation consensus, les flèches représentent la direction et la norme des vecteurs de déformation.]

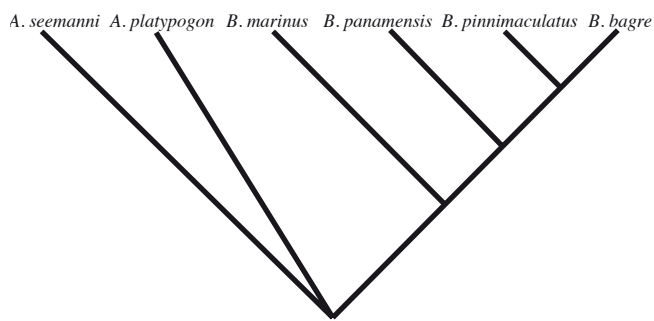


Figure 7. - Phylogenetic hypothesis tree (additive tree), using unwarped average species from TPSsuper procedures, as hypothetic taxonomic units for each species. Weighted matrix (TPSrelw) was generated with average specimens; tree was generated using Phylip CONT routine (maximum likelihood, random order samples, no rooted tree, 100 replicates). [Hypothèse phylogénétique (arbre additif), à partir des consensus moyens des espèces (TPSsuper) utilisés comme représentants hypothétiques pour chaque espèce. La matrice des flexions partielles a été créée à partir du consensus des spécimens et l'arbre est calculé avec la routine CONT de PHYLIP (maximum de vraisemblance, ordre aléatoire des échantillons, arbre non enraciné, 100 répliquats).]

sis, while *B. pinnimaculatus* and *B. bagre* are placed as the most distant to the consensus (Figs 3, 4).

Description of the changes in shape in relative deformation warps

The most evident changes in shape on the first warp appear in:

A. Head, mainly in the region anterior to the snout (landmarks one to three) (Fig. 5). Landmark 1 may elongate, causing the forward displacement of the insertion of maxillary barbel (landmark 2) and the anterior border of eye (landmark 3). The movement of landmark 3 corresponds to the increase in eye diameter.

B. Dorsal fin (landmarks six and seven); dorsal fin base length remains unchanged, however predorsal fin length changes (Fig. 5).

C. Anal fin (landmarks 13 and 14); the length of the fin base changes, however its end remains invariant. Due the movement of the anterior extreme, the fin moves forward and, as a consequence, the pelvic fin position changes as well.

D. Insertion and orientation of pectoral fin (landmarks 16 and 17); the insertion angle varies causing that the complex moves ventrally to end up parallel to the longitudinal body axis (Fig. 5).

In the second relative deformation warp the body shape changes are associated to a dorso-ventral displacement of the landmarks. Therefore, when the shape space gets depressed, anal fin base length and adipose fin base length increase. If the body gets deeper, the base lengths of the two fins decrease (Fig. 6A, B).

Additive trees and shape changes

Figure 7 shows the additive tree obtained using PHYLIP, on which the variation of the landmarks position in the shape space on each one of the tree nodes was studied. When the distance scale is analyzed, it can be seen that *B. pinnimaculatus* and *B. bagre* are widely separated from the other two species of the genus. Furthermore, it is clear that the landmark configuration in *B. marinus* is the most plesiomorphic of the genus, making it the most adequate for shape comparisons.

Phylogenetic hypothesis

The final result, the tree showing the relationships existing between the species of *Bagre* and the outgroup species, is presented in figure 7. Basally the tree is a trichotomy, with the relationships between *A. platypogon*, *A. seemanni*, and *Bagre* unresolved. Therefore, the evidence provided by the morphometric characters was not sufficient to determine which of the two outgroup configurations is closer to *Bagre*. The tree shows the relationships between the species of *Bagre* in the same way as the ordinations (Fig. 7).

Table IV. - Anal fin rays range in the genera and selected species of neotropical sea catfishes. It is indicated whether the taxon occurs in the western Atlantic (A) or in the eastern Pacific (P) and the number of species in each ocean. *Cathorops* n.sp. is in description process (Betancur and Acero, in press). [Nombre de rayons de la nageoire anale chez les genres et les espèces sélectionnés de poissons-chats des mers tropicales. Il est indiqué si le taxon apparaît dans l'Atlantique occidentale (A) ou dans le Pacifique oriental (P) et le nombre d'espèces pour chaque océan. *Cathorops* n. sp. est en cours de description (Betancur et Acero, sous presse).]

Genera or species	Anal fin rays	A	P
<i>Ariopsis</i>	17-20	3	2
<i>Arius</i>	17-23	6	4
<i>A. lentiginosus</i>	23-28	-	1
<i>A. platypogon</i>	18-20	-	1
<i>Bagre bagre</i>	29-37	1	-
<i>B. marinus</i>	22-28	1	-
<i>B. panamensis</i>	25-30	-	1
<i>B. pinnimaculatus</i>	27-32	-	1
<i>Cathorops</i>	19-25	9	4
<i>C. multiradiatus</i>	24-28	-	1
<i>Cathorops</i> n. sp.	21-25	1	-
<i>Galeichthys</i>	15-18	-	1
<i>Selenaspis</i>	17-21	3	1

For the phylogeny of the genus *Bagre*, all the available recurrent evidence produced by geometric morphometry (relative deformation warps, discriminant analysis, and additive trees) points towards the strong similarity between *B. bagre* and *B. pinnimaculatus*. They are also placed as the most derived species within the genus, which tends to back the systematic hypothesis of their close relationship. On the other hand, it seems that *B. marinus* and *B. panamensis* are the most generalized species, with *B. marinus* being the most plesiomorphic and, therefore, hypothetically the oldest living species of the genus.

Another feature that seems to support the proposed hypothesis is the evolution of the number of anal-fin elements. If our hypothesis is correct, the number of anal-fin elements has been increasing in the same direction than the evolution within the genus *Bagre*. Hence, *B. marinus*, considered the most basal species, has 22-28 anal-fin rays, *B. panamensis* has 25-30, *B. pinnimaculatus* has 27-32, and *B. bagre* has 29-37. The other species of sea catfishes in the western Atlantic and the eastern Pacific have 15-25 anal-fin elements (except *Arius lentiginosus*, 23-28, and two *Cathorops* species, 24-28) (Cervigón, 1991; Kailola and Bussing, 1995; Marceniuk, 1997; Acero, 2002; Acero and Betancur, 2002; Betancur and Acero, in press) (Tab. IV). Therefore, it seems that the speciation processes linked to the evolution of *Bagre* have been accompanied by an increase in the number of anal-fin elements. The species of

Bagre have more anal-fin rays than any catfish of the clade *Ariopsis* - *A. platypogon* - *Bagre* - *Selenaspis*, which has been considered monophyletic (Betancur *et al.*, in press). Since no species of this clade, other than the members of *Bagre*, has more than 21 rays, it seems that the origin and evolution of the genus has been linked to an increase in the number of anal-fin elements.

Acknowledgments. - COLCIENCIAS and the Universidad Nacional de Colombia funded this study through proposals 1101-09-138-98, 210509-11248, and DIB 803708. This is contribution 240 of the Centro de Estudios en Ciencias del Mar, Cecimar, of the Universidad Nacional de Colombia, and 847 of the Instituto de Investigaciones Marinas y Costeras, Invemar.

REFERENCES

- ACERO P.A., 2002. - Family Ariidae. *In: The living marine Resources of the western central Atlantic* (Carpenter K.E., ed.), pp. 831-852. Rome: FAO.
- ACERO P.A., 2003. - Siluriformes (catfishes). *In: Grzimek's Animal Life Encyclopedia*, 2nd edit. (Hutchins M., Thoney D.A., Loiselle P.V. & N. Schlager, eds), Vol. 4-5, Fishes I-II, pp. 351-367. Farmington Hills, USA: Gale Group.
- ACERO P.A. & R. BETANCUR-R., 2002. - *Arius cookei*, a new species of ariid catfish from the tropical American Pacific. *Aqua J. Ichtyol. Aquat. Biol.*, 5: 133-138.
- ADAMS D.C. & M.S. ROSENBERG, 1998. - Partial warps, phylogeny, and ontogeny: A comment on Fink and Zelditch (1995). *Syst. Biol.*, 47: 168-173.
- BETANCUR-R. R. & A. ACERO P., in press. - Description of *Cathorops mapale*, a new species of ariid catfish (Pisces: Siluriformes) from the Colombian Caribbean, based on morphological and mitochondrial evidence. *Zootaxa*.
- BETANCUR-R. R., ACERO P. A. & L.M. MEJÍA-LADINO, 2003. - Sistemática filogenética preliminar de algunos bagres marinos (Siluriformes: Ariidae) neotropicales. *Mem. Fund. La Salle Cienc. Nat.*, 158: 68-81.
- BOOKSTEIN F.L., 1989. - Principal warps: Thin-plate splines and the decomposition of deformations. *IEEE Trans. Pat. Anal. Mach. Intell.*, 11: 567- 585.
- BOOKSTEIN F.L., 1991. - *Morphometric Tools for Landmark Data: Geometry and Biology*. 435 p. Cambridge: Cambridge Univ. Press.
- BOOKSTEIN F.L., 1996. - Combining the tools of geometric morphometrics. *In: Advances in Morphometrics* (Marcus L.F., Corti M., Loy A., Naylor G.J.P. & D. Slice, eds), pp. 131-151. New York: Plenum Press.
- BROOKS D.R., CAIRA J.N., PLATT T.R. & M.R. PRITCHARD, 1984. - Principles and methods of phylogenetic systematics: A cladistics workbook. *Univ. Kansas, Mus. Nat. Hist. Spec. Publ.*, 12: 1-92.
- CADRIN S.X. & K.D. FRIEDLAND, 1999. - The utility of image processing techniques for morphometric analysis and stock identification. *Fish. Res.*, 43: 129-139.
- CERVIGÓN F., 1991. - *Los Peces marinos de Venezuela*. Vol I. 423 p. Caracas: Seg. Ed. Fundación Científica Los Roques.

- CHAPMAN R.E., 1990. - Shape analysis in the study of dinosaur morphology. *In: Dinosaur Systematics: Perspectives and Approaches* (Carpenter K. & P.J. Currie, eds), pp. 21-42. Cambridge: Cambridge Univ. Press.
- CHAPMAN R.E., WEISHAMPEL D.B., HUNT G. & D. RASSKIN-GUTMAN, 1997. - On using the shapes of dinosaurs. *Dinofest Int. Proc.*, 3: 31-37.
- FELSENSTEIN J., 1988. - Phylogenetics and quantitative characters. *Ann. Rev. Ecol. Syst.*, 19: 445-471.
- FELSENSTEIN J., 2001. - PHYLIP v.3.6, Phylogeny Inference Package. Washington Univ. 1999-2001.
- KAILOLA P.J. & W.A. BUSSING, 1995. - Ariidae, bagres marinos. *In: Guía FAO para la Identificación de Especies para los Fines de la Pesca. Pacífico centro-oriental. Vol. II. Vertebrados. Parte 1* (Fischer W., Krupp F., Schneider W., Sommer C., Carpenter K.E. & V.H. Niem, eds), pp. 860-886. Rome: FAO.
- LITTMANN M.W., BROOKS M.B. & P. NASS, 2000. - *Sorubium cuspidus*, a new long-whiskered catfish from northwestern South America (Siluriformes: Pimelodidae). *Proc. Biol. Soc. Wash.*, 113: 900-917.
- LOY A. & M. CORTI, 1996. - Distribution of *Talpa europea* (Mammalia, Insectivora, Talpidae) in Europe: A biogeographic hypothesis based on morphometric data. *Ital. J. Zool.*, 63: 277-284.
- MARCENIUK A.P., 1997. - Revisão sistemática do gênero *Cathorops* (Osteichthyes; Siluriformes, Ariidae). M. Sc. Thesis, 315 p. Univ. São Paulo, Brasil.
- MARCUS L.F., HINGST-ZAHER E. & H. ZAHER, 2000. - Application of landmark morphometrics to skulls representing the orders of living mammals. *Hystrix*, 11: 27-47.
- MONTEIRO R.L., 2000. - Why morphometrics is special: The problem with using partial warps as characters for phylogenetic inference. *Syst. Biol.*, 49: 796-800.
- PINNA DE M., 1991. - Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7: 367-394.
- ROHLF F.J., 1990. - Morphometrics. *Ann. Rev. Ecol. Syst.*, 21: 299-316.
- ROHLF F.J., 1996. - Morphometrics spaces, shape components and the effects of linear transformations. *In: Advances in Morphometrics* (Marcus L.F., Corti M., Loy A., Naylor G.J.P. & D. Slice, eds), pp. 131-151. New York: Plenum Press.
- ROHLF F.J., 1998a. - TPSsuper. Department of Ecology and Evolution, State Univ. New York: Stony Brook.
- ROHLF F.J., 1998b. - On applications of geometric morphometrics to studies of ontogeny and phylogeny. *Syst. Biol.*, 47: 147-158.
- ROHLF F.J., 1998c. - TPSrelw. Department of Ecology and Evolution, State Univ. New York: Stony Brook.
- ROHLF F.J., 1999a. - TPStree. Department of Ecology and Evolution, State Univ. New York: Stony Brook.
- ROHLF F.J., 1999b. - Shape statistics: Procrustes superimpositions and tangent spaces. *J. Classif.*, 16: 197-223.
- ROHLF F.J., 2000. - Statistical power comparisons among alternative morphometric methods. *Am. J. Phys. Anthr.*, 111: 463-478.
- ROHLF F.J., 2002. - Geometric morphometrics in systematics. *In: Morphology, Shape and Phylogenetics* (Macleod N. & P. Forey, eds), pp. 175-193. London: Taylor & Francis.
- ROHLF F.J., 2003. - TPSdig v.1.39. Department of Ecology and Evolution, State Univ. New York: Stony Brook.
- ROHLF F.J. & D. SLICE, 1990. - Extensions of the Procrustes method for the optimal superimposition of landmarks. *Syst. Zool.*, 39: 40-59.
- ROTH V.L. & J.M. MERCER, 2000. - Morphometrics in development and evolution. *Am. Zool.*, 40: 801-810.
- STRACAHAN N.J. & L. KELL, 1995. - A potential method for the differentiation between haddock fish stocks by computer vision using canonical discriminant analysis. *ICES J. Mar. Sci.*, 5: 146-150.
- SWIDERSKI D.L., ZELDITCH M.L. & W.L. FINK, 1998. - Why morphometrics is not special: Coding quantitative data for phylogenetic analysis. *Syst. Biol.*, 47: 508-519.
- SWIDERSKI D.L., ZELDITCH M.L. & W.L. FINK, 2000. - Phylogenetic analysis of skull shape evolution in marmotine squirrels using landmarks and thin-plate splines. *Hystrix*, 11: 49-75.
- ZELDTICH M.L., FINK W.L. & D.L. SWIDERSKI, 1995. - Morphometrics, homology and phylogenetics: Quantified characters as synapomorphies. *Syst. Biol.*, 44: 179-189.
- ZELDITCH M.L., FINK W.L., SWIDERSKI D.L. & B.L. LUNDRIGAN, 1998. - On applications of geometric morphometrics to studies of ontogeny and phylogeny: A reply to Rohlf. *Syst. Biol.*, 47: 159-167.

Reçu le 9 décembre 2003.

Accepté pour publication le 5 juin 2004.