MULTIVARIATE MORPHOMETRICS AND EVOLUTIONARY PATTERNS IN SOME SPECIES OF THE GENUS *UCA* LEACH, 1814 (CRUSTACEA: BRACHYURA: OCYPODIDAE)

José Alexandre F. Diniz Filho

ABSTRACT

Twelve quantitative morphological characters were measured in 35 individuals belonging to six species of the genus *Uca* Leach 1814 (Crustacea: Brachyura: Ocypodidae). A multivariate statistical analysis (PCA) was performed to search for multidimensional allometric patterns and for consensus with some phylogenetic schemes proposed by Albrecht and Von Hagen (*Comp. Biochem. Physiol.* 70: 393-399, 1981). The first principal component (PCI), usually interpreted as a general size factor, accounted for 84.3% of the total variability of the sample. The second component (PCII), usually interpreted as a shape component, accounted for 8.9% of the variability. Regressions of PCII on PCI, per group, allowed the analysis of the allometric patterns of each species. The morphometric similarity in PCI and PCII, and also the allometric patterns, were compared with cladistic schemes, producing a clear view of the evolutionary lines of the group. The interspecific allometric variation permits concluding that the old genus *Minuca* is composed of species in which shape variation can be explained by size variation, without the need for another adaptive hypothesis to explain this interspecific shape variation.

INTRODUCTION

The genus *Uca* is composed of sixty-two species, living in mangrove swamps and coastal zones all around the world. The diversity of the "fiddler crabs", as they are usually called, has been studied in several ways, including ecological, physiological,

Departamento de Biologia, Instituto de Biociências - UNESP, Caixa Postal 178, 13500 Rio Claro, SP, Brasil.

morphological, behavioral and biochemical aspects. A major synthesis was made by Crane (1975). According to traditional classification, the genus is divided into two subgenera, comprising the "narrow-front" (*Uca*) and the "broad-front" (*Minuca*) species (Rathbun, 1918; Bott, 1954; Holthuis, 1959; Chace and Hobbs, 1969). Bott (1954) gave these groups a generic status, but Peters (1955), working on ecological and behavioral aspects of the same material, reduced *Minuca* and *Uca* to subgeneric rank (Crane, 1957). Nevertheless, in the work of Crane (1975), the genus was divided into nine formal subgenera.

More recently, the diversity of the genus *Uca* began to be analysed in detail in an evolutionary way. Since Crane's review, which included a section named "Toward an evolutionary synthesis", some authors have tried to find the "correct phylogeny" for the species of the genus, as Crane's phylogenetic inferences seemed to be very unsatisfactory (Von Hagen, 1976). Thus, Albrecht and Von Hagen (1981) established, based upon morphological, biochemical and behavioral data, cladograms for some species of the genus. The congruity between the cladograms based upon electrophoretic and upon morphological and behavioral data permitted arranging this genus into a satisfactory scheme. However, Albrecht and Von Hagen (1981) described relationship patterns with a different weighting of electrophoretic data, "single bands of protein patterns are discussed individually, under the heading ancestral-derived", which represents a cladistic viewpoint, in the sense of Henning (1965, 1966) and Farris (1986). Thus, the multidimensional similarity patterns were not considered to establish the relationships among the species or to test the congruity between evolutionary lineages (in a cladistic sense) and size-shape differences among species.

This paper has two objectives: 1) to show that the multivariate morphometric relationships among the species of *Uca* under study can be interpreted in a cladistic sense; 2) to establish how change in size can be an important factor to explain the interspecific shape variation through the evolution of the old subgenus *Minuca*.

MATERIAL AND METHODS

The material analysed came from the Federal University of Sergipe Benthos laboratory collection, mainly collected for the work of Souza (1988).

Twelve quantitative morphological characters (Table I) were measured in thirty-five adult males of the genus *Uca*, including *Uca* (*Uca*) *maracoani* Latreille, 1802-1803 (5), *Uca* (*Minuca*) *rapax* Smith, 1870 (10), *Uca* (*Minuca*) *vocator* Herbst 1804 (3), *Uca* (*Boboruca*) *thayeri* Rathbun, 1900 (8), *Uca* (*Celuca*) *cumulanta* Crane, 1943 (4) and *Uca* (*Celuca*) *leptodactyla* Rathbun 1898 (5). The numbers in parentheses

indicate the number of individuals analysed for each species. The subgenera are in accordance with the classification of Crane (1975). In the traditional classification scheme, only *Uca maracoani* was classified in the subgenus *Uca*, and all of the others in the subgenus *Minuca*.

Table I - Characters analysed and their coordinates (loads) in the first three principal components.

Variables	PCI	PCII	PCIII
Carapace length	0.991	-0.025	0.040
Carapace width	0.990	-0.063	0.050
Front width	0.229	0.956	-0.176
Interorbital width	0.987	-0.067	0.061
Abdominal carapace width	0.978	-0.166	-0.054
Position of carap. max. width	0.676	0.236	0.693
Dist. between the coxa chela	0.978	0.060	-0.068
Chelipode length	0.980	-0.022	-0.142
Chelipode hight	0.994	0.020	-0.050
Palm length	0.980	0.129	-0.096
Dactylus length	0.966	-0.092	-0.154
Dactylus hight	0.957	-0.166	-0.028

The multivariate similarity patterns were studied with a Principal Component Analysis (PCA) (Sneath and Sokal, 1973). This analysis is applied to the study of shape and size relationships among species, when these patterns are not defined as measured variables, but as general factors, linear combinations most parsimoniously accounting for the association among the distance measures (Bookstein *et al.*, 1985). In this study, the eigen values and the factor load matrix were extracted from a correlation matrix among the twelve characters, after transformation to base ten logarithms (Jolicoeur, 1963).

Regression analyses with the individual scores, per group, of principal component II (PCII) on principal component I (PCI) were performed to establish the dependence of variation in shape (PCII) in relation to size (PCI), and, in this way, to compare the allometric patterns of each species.

The statistical analysis was done with a microcomputer, using the program ACOMP, written by J.L. Valentin.

RESULTS

Table I shows the loads of each variable for the first three principal components. The PCI, with an eigen value of 84.3%, is usually interpreted as a general size factor, and PCII, with an eigen value of 8.9%, represents the shape variability of the analysed sample. The slopes of the regression equations of the PCII scores on PCI scores, per group, showed a similar tendency in all groups, and the values also indicated a dependence of shape in relation to size, for each group (Table II).

Table II - Results of regression analyses of PCII on PCI, for each group.

Species	n	r	Intercept	Slope
U. maracoani	5	0.838	-0.933	0.277
U. rapax	10	0.968	0.183	0.257
U. thayeri	8	0.949	0.022	0.249
U. vocator	3	0.999	0.188	0.474
U. leptodactyla	5	0.915	0.440	0.485
U. cumulanta	4	0.966	0.355	0.305

By projecting the scores in the orthogonal space of PCI and PCII (Figure 1), it is possible to see that the species are almost perfectly discriminated. The only partial cluster is seen between *U. rapax* and *U. vocator*, although they have different slopes (Table II). A cluster analysis (UPGMA), performed with the results of the regression analyses (using as variables the slope and the intercept shown in Table II) indicates the most similar species in terms of allometric patterns. The phenogram of this classification can be seen in Figure 2. It is clear that *U. maracoani* is a distinct species. *U. vocator* has an intermediate position between the group formed by *U. rapax/U. thayeri* and the one formed by *U. cumulanta/U. leptodactyla*, although it is more closely related to the latter.

Figures 3 and 4 show the relationships between morphometric and cladistic patterns, as defined by Albrecht and Von Hagen (1981). These relationships are made clear in the two graphs in which the Y axis represented the centroid values of PCI and PCII for each species, and the X axis indicates the order of cladistic linkages. By considering the centroid coordinates of the size component (Figure 3) it is possible to see that the morphometric groups have no great incongruity with those constructed
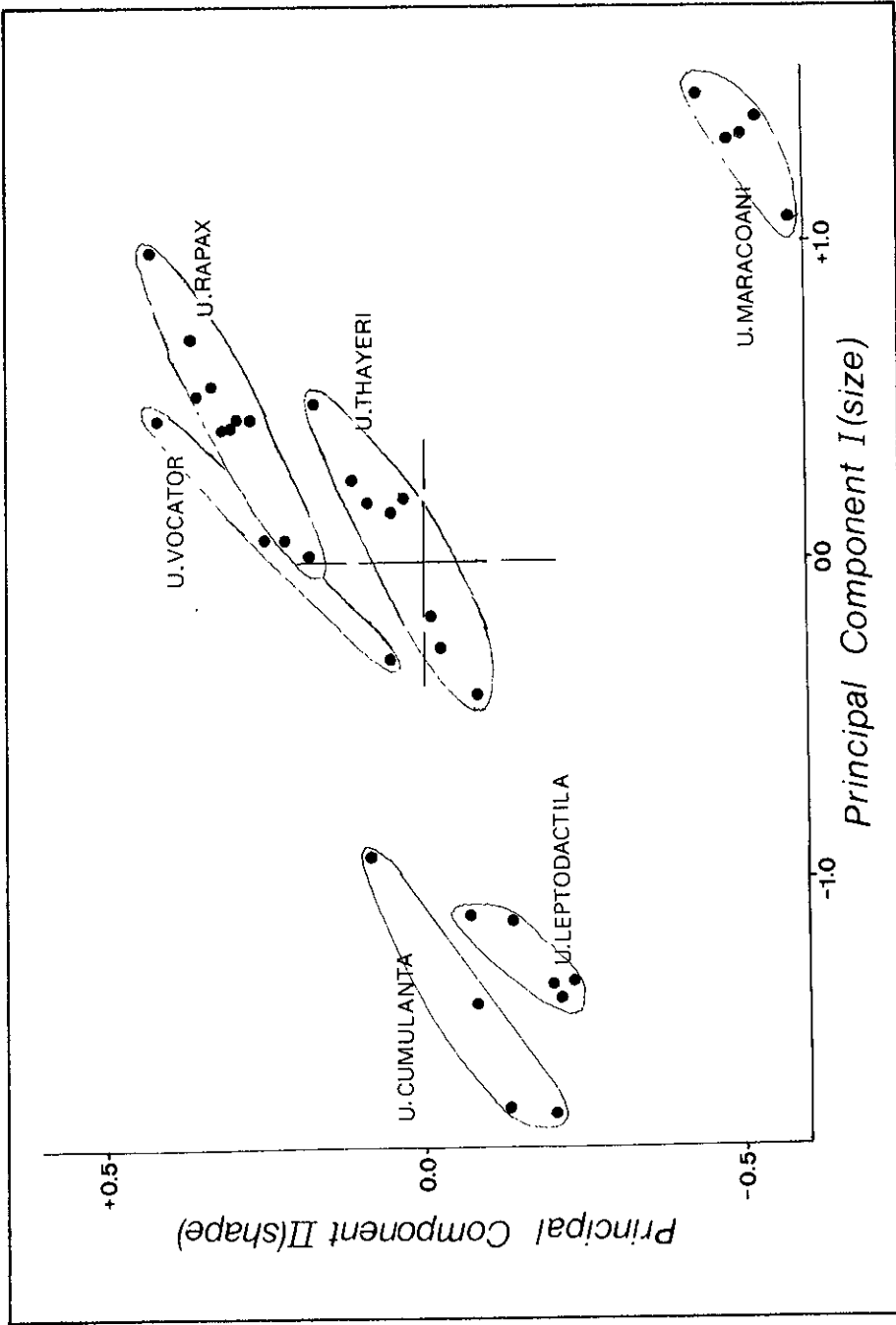
Figure 1 - Individual score dispersion in PCI and PCII for six species of the genus *Uca*.
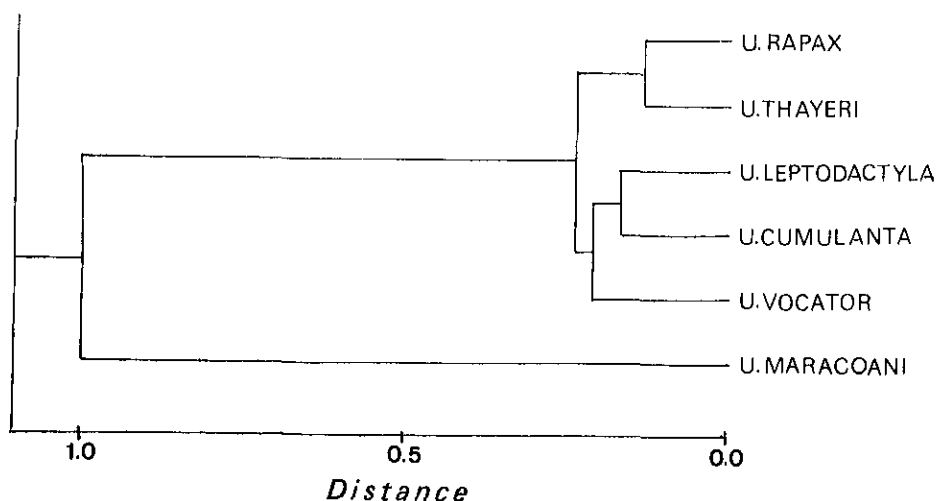
Figure 2 - Dendrogram for six species of the genus *Uca*, considering its allometric patterns (intercept and slopes of Table II).

with cladistic relationships. *U. maracoani* is the most distant species, while the group formed by the five other species is divided into two subgroups: one including *U. leptodactyla* and *U. cumulanta* and the other, *U. rapax, U. thayeri* and *U. vocator*. The incongruity between the two kinds of relationship is below this level, since *U. thayeri*, although seeming to be more similar to *U. rapax* in the cladistic scheme, does not fit in this position when morphometrics are taken into account. Thus, the cladistic lineages of *U. thayeri* and *U. vocator* cross each other. According to the centroid coordinates of PCII (Figure 4), there is a perfect congruity between morphometric and cladistic patterns, with no cladistic lineages crossing.

DISCUSSION

It is possible to conclude, from the present results, that there is good agreement between cladistic and morphometric schemes in the species under study.

The results show that there are two principle evolutionary lineages, one represented by *U. maracoani*, or the "narrow-front" species, and the other represented by the "broad-front" species. This division is in agreement not only with the accepted cladistic scheme, but also with an old division, defined by Rathbun (1918) and Bott (1954), at least for the species under study. In this analysis, these two groups can be seen in Figure 1 and in Table II, or in the cluster scheme (Figure 2).
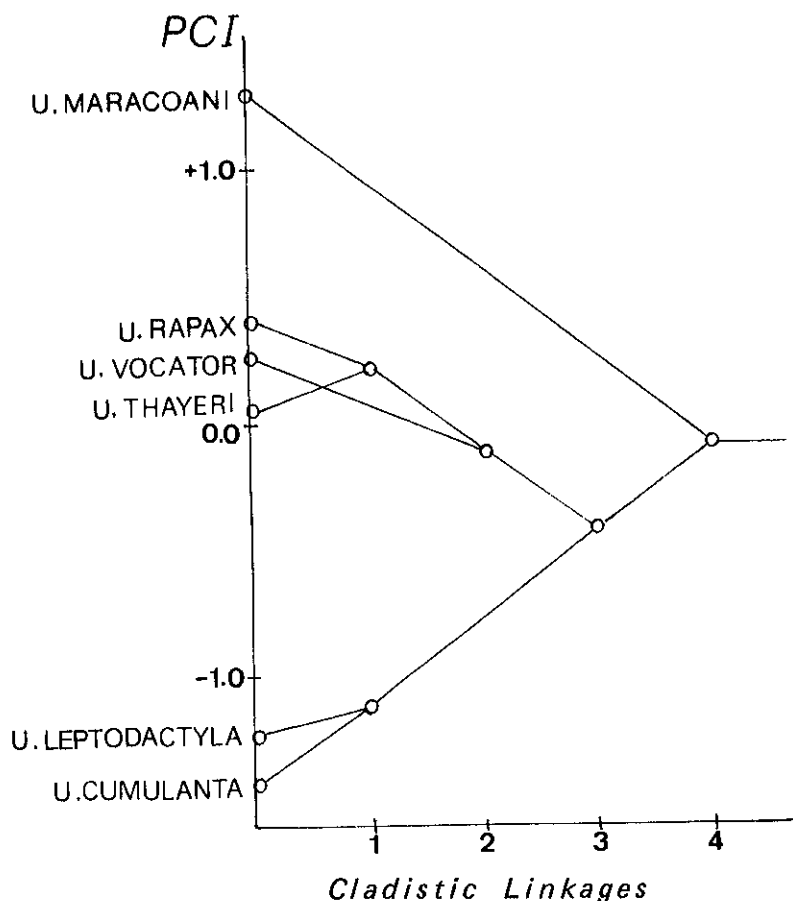
Figure 3 - Relationship between morphometric pattern (PCI) and Albrecht and Von Hagen's cladistic scheme.

The main difference between morphometric and cladistic patterns appears when considering the position of *U. vocator*. In terms of general morphometric relationships, this species is more closely related to *U. rapax*, since the two are almost fused in Figure 1. However, it is interesting to note that this relationship is a function of size similarity, not of shape (and, in some sense, evolutionary) similarity. This aspect can be confirmed by an evaluation of Figure 3 (size relationships) and Figure 4 (shape relationships). In the first, *U. vocator* is close to *U. rapax*, when considering their similar size, but, in the second, they are not necessarily clustered together, which removes the incongruity of cladistic and morphometric patterns. The comparison of
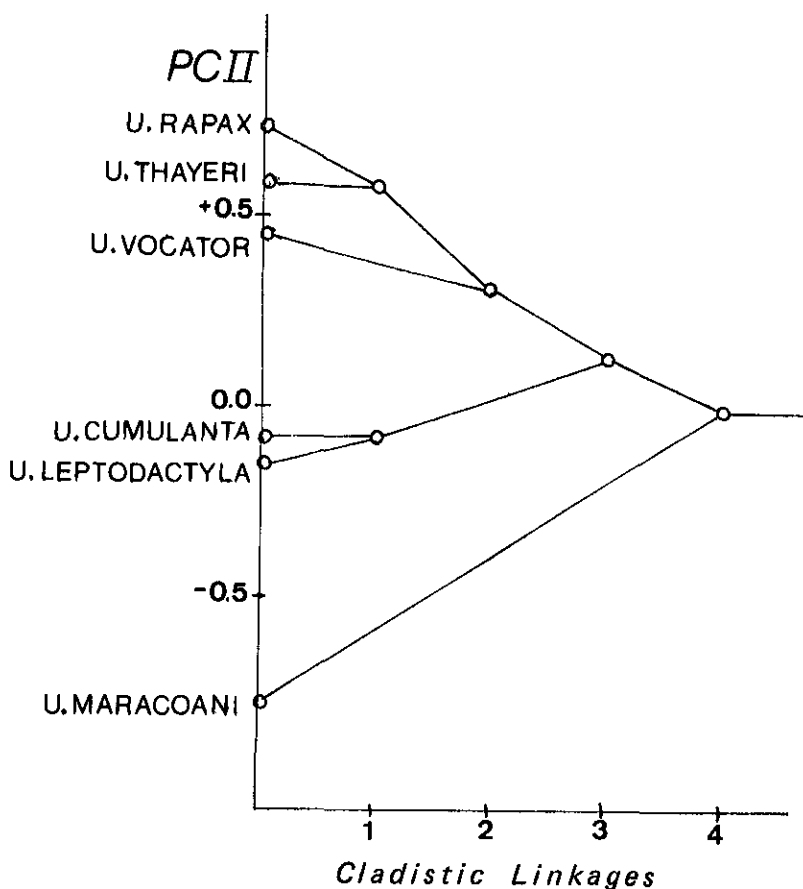
Figure 4 - Relationship between morphometric pattern (PCII) and Albrecht and Von Hagen's cladistic scheme.

allometric interespecific variation, graphically represented in Figure 2, also indicates that morphometric similarity of *U. vocator* and *U. rapax* must be a function of a parallelism in size increase. The phenogram in Figure 2 shows *U. vocator* as a transitional type between *U. rapax/U. thayeri* and *U. leptodactyla/U. cumulanta*, although closely related to this last group, in agreement with the cladistic scheme of Albrecht and von Hagen (1981). The interspecific allometric variation also shows that the old subgenus *Minuca* is composed of species in which variation in shape can be explained by size variation, without the need for another adaptative hypothesis to explain this interspecific shape variation.

ACKNOWLEDGMENTS

RESUMO

Trinta e cinco indivíduos pertencentes a seis espécies do gênero *Uca* Leach 1814 (Crustacea: Brachyura: Ocypodidae) foram mensurados por doze caracteres quantitativos, que foram transformados em logarítmos decimais e submetidos a uma Análise em Componentes Principais. O primeiro componente, interpretado como um fator de tamanho generalizado, apresentou um eigen value de 84,3%, e o segundo componente, interpretado como um fator de forma, apresentou um eigen value de 8,9%. Todas as espécies analisadas foram discriminadas no espaço ortogonal dos dois primeiros componentes, à exceção de um grupo *U. rapax/U. vocator*. Uma análise de regressão dos escores do componente II sobre o componente I, por espécie, permitiu analisar os padrões de alometria inter e intraespecífica. Todos esses padrões foram comparados com aqueles obtidos em estudos cladísticos, a partir de dados bioquímicos, morfológicos e etológicos, indicando uma grande congruência nos resultados. Além disso, os padrões de alometria no subgênero *Minuca* possibilitam a utilização da variação alométrica em substituição a hipóteses adaptativas mais tradicionais, a fim de explicar as diferenças morfométricas nas espécies estudadas desse subgênero.

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