Morphometric variability in populations of *Palaemonetes* spp. (Crustacea, Decapoda, Palaemonidae) from the Peruvian and Brazilian Amazon Basin

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ABSTRACT. Morphometric variability among shrimp populations of the genus *Palaemonetes* Heller, 1869 from seven lakes (Huanayo and Urcococha, in Peru; Amanã, Mamirauá, Camaleão, Cristalino e Iruçanga, in Brasil) in the Amazon Basin, presumably belonging to *Palaemonetes carteri* Gordon, 1935 and *Palaemonetes ivonicus* Holthuis, 1950, were studied. The morphometric studies were carried out from the ratios obtained from the morphometric characters. Multivariated analysis (Principal Components Analysis-PCA, Discriminant Function Analysis and Cluster Analysis) were applied over the ratios. Intra- and interpopulation variations of the rostrum teeth, and the number of spines in the male appendix, were analyzed through descriptive statistics and bivariate analysis (Spearman Rank Correlation test). Results indicated a wide plasticity and overlapping in the studied ratios between populations. The Principal Components Analysis was not able to separate different populations, revealing a large intrapopulation plasticity and strong interpopulation similarity in the studied ratios. Although the Discriminant Functions Analysis was not able to fully discriminate populations, they could be allocated in three subgroups: 1) Cristalino and Iruçanga; 2) Huanayo, Urcococha and Camaleão and 3) Mamirauá and Amanã. The first two groups were morphometrically separated from each other, whereas the third one presented a strong overlap with the former two. The Cluster Analysis confirmed the first two subgroups separation, and indicated that the first and third groups were closely related. Rostrum teeth and number of spines in the *appendix masculina* showed a large intrapopulation variation and a strong overlapping among the studied populations, regardless of the species.

KEYWORDS. *Palaemonetes*, morphometry, Amazon Basin, sibling species, freshwater shrimp.

RESUMO. Variabilidade morfométrica em populações de *Palaemonetes* spp. (Crustacea, Decapoda, Palaemonidae) da Amazônia peruana e brasileira. Foram estudadas as variações morfométricas entre sete populações de camarões do gênero *Palaemonetes* Heller, 1869 da bacia Amazonica (lago Huanayo e lago Urcococha, no Peru; lago Amanã, lago Mamirauá, lago Camaleão, lago Cristalino e lago Iruçanga, no Brasil), presumivelmente das espécies *Palaemonetes carteri* Gordon, 1935 e *Palaemonetes ivonicus* Holthuis, 1950. Os estudos morfométricos foram realizados a partir das razões obtidas dos caracteres morfométricos. Análise multivariada (análise de componentes principais, análise de função discriminante e análise de agrupamento hierárquico) foram aplicadas unicamente sobre as razões. Variações intra- e interpopulacionais do número de dentes de rostro, assim como do número de espinhos no apêndice masculino, foram analisadas mediante estatística descritiva e análise bivariada (teste de Spearman). Os resultados indicaram uma grande plasticidade e sobreposição nos caracteres diagnósticos entre as populações. A análise de componentes principais não conseguiu separar as diferentes populações, revelando uma grande plasticidade intrapopulacional e forte semelhança interpopulacional nas razões estudadas. Embora a análise de funções discriminantes não tenha logrado discriminar completamente as populações, estas ficaram alocadas em três subgrupos: 1) Cristalino e Iruçanga; 2) Huanayo, Urcococha e Camaleão e 3) Mamirauá e Amanã. Os primeiros dois grupos ficaram morfologicamente separados entre si, enquanto que o terceiro apresentou uma forte sobreposição com os dois anteriores. A análise de agrupamento hierárquico confirmou a separação dos primeiros dois subgrupos, e indicou que o primeiro e o terceiro grupos se encontram mais estreitamente relacionados. O número de dentes de rostro e o número de espinhos do apêndice masculino apresentaram uma grande variação intrapopulacional e uma forte sobreposição entre as populações estudadas, independentemente da espécie.

PALAVRAS-CHAVE. *Palaemonetes*, morfometria, bacia amazônica, espécies-irmãs, camarões de água doce.

The genus *Palaemonetes* Heller, 1869 has three species in the Amazon Basin: *Palaemonetes carteri* Gordon, 1935, *P. ivonicus* Holthuis, 1950, and *P. mercedae* Pereira, 1986 (Melo, 2003). While the former is clearly characterized by its smaller size, morphology and ratios of the second pair of pereiopods, shape of telson (Pereira, 1986), and larval development (Magalhães, 1988), the latter two show a great morphological resemblance, which makes their taxonomic separation very difficult. In his revision of the genus, Holthuis (1952) used the position of the branchiostegal spine and the rostral shape and dentition to distinguish both species. Recent studies showed that these characters are quite variable, indicating that they are not useful as diagnostic characters for taxonomic differentiation (Odinetz-Collart & Enriconi, 1993; García-Dávila & Magalhães, 2003). In the Amazon Basin, the river systems are roughly classified in black, white and clear water (Sioli, 1968). The occurrence of these two species has been mostly related to their environmental distribution, with *P. carteri* being associated to environments of black and clear water river systems and *P. ivonicus*, to the white and mixed water river systems. Notwithstanding, García-Dávila & Magalhães (2003) showed the overlap of morphological characters in specimens from both types of environments.

The adult morphology is the main source of taxonomic characters, although keys and descriptions often use subjective features with little or no discussion of the character intraspecific variation or measurable differences in the shape between the species (McClure & Wicksten, 1997). In spite of the fact that morphological differences are useful in distinguishing species, it is not always possible to describe new species based on those differences (Pough *et al.*, 1993), as individuals within a species can present morphological variations related to sex, *i.e.* secondary sexual dimorphism related to behavior and external morphology (Vazzoler, 1971). This is emphasized in sibling species, in which different species can be grouped together under the same name, considering the differences between them as intraspecific variation, or, on the other hand, a single species can be treated as a separate species based on small morphological differences.

As organisms are essentially multidimensional, morphological studies should be mainly carried out using multivariate methods. Morphometric studies in decapod crustaceans based on multivariate analysis have been directed mainly to studies of growth patterns and determination of sexual maturity (Grandjean *et al.*, 1997; Sampedro *et al.*, 1999; Muiño *et al.*, 1999; Fernandez-Vergaz *et al.*, 2000). Morphometric studies of Amazonian shrimps are not currently available.

The present study aims to verify the intra- and interpopulational morphometric variability using multivariate analysis in populations of the presumptive species, *P. carteri* and *P. ivonicus*, in order to confirm if both constitute two separate taxonomic entities in the Amazon Basin.

MATERIAL AND METHODS

A total of 490 specimens (70 specimens/population: 35 males and 35 females) were studied, from seven localities in the Amazon Basin: lake Huanayo (Rio Pastaza basin) and lake Urcococha (Rio Amazonas), in the Peruvian Amazon; lake Amanã (Rio Japurá basin), lake Mamirauá (Rio Solimões basin), lake Cristalino (Rio Negro basin), lake Camaleão (Rio Solimões basin) and lake Iruçanga (Rio Tapajós basin), in the Brazilian Amazon (Fig. 1). The specimens were identified *a priori* according to water type (Sioli, 1968) from their locality of collection. Therefore, populations from lake Huanayo, lake Iruçanga (clear water), lake Amanã and lake Cristalino (black water) were assigned to *P. carteri*, while populations from lake Urcococha, lake Mamirauá and lake Camaleão (white water) were considered as *P. ivonicus*. Voucher specimens were deposited in the Collection of Crustacea, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil.

Morphometric studies were carried out with the ratios obtained from the morphometric characters and were abbreviated as follows: number of rostrum dorsal teeth (MS); number of rostrum ventral teeth (MI); cephalotorax length/rostral length (CL/R); rostral length/rostral height (R/AR); branchiostegal spine length/distance between base of branchiostegal spine and anterior margin of cephalotorax (B/BM); branchiostegal spine length/height of the insertion of the branchiostegal spine in the cephalotorax (B/AB); telson length/width of telson base (T/BT); dactyl length/palm length of second pereiopod (D/P); carpus length/palm length of second pereiopod (C/P); carpus length/merus length of second pereiopod (C/M); numbers 3, 4, 5 indicated the third, fourth and fifth pereiopod, respectively. Another abbreviation used was CV for coefficient of variability.

Data Analysis. To run the following analysis the raw ratios were log10 transformed and only those that proved to be normal (Kolmogorov-Smirnov test, $P<0.05$) were used (Sokal & Rohlf, 1995; Zar, 1996; Fowler *et*

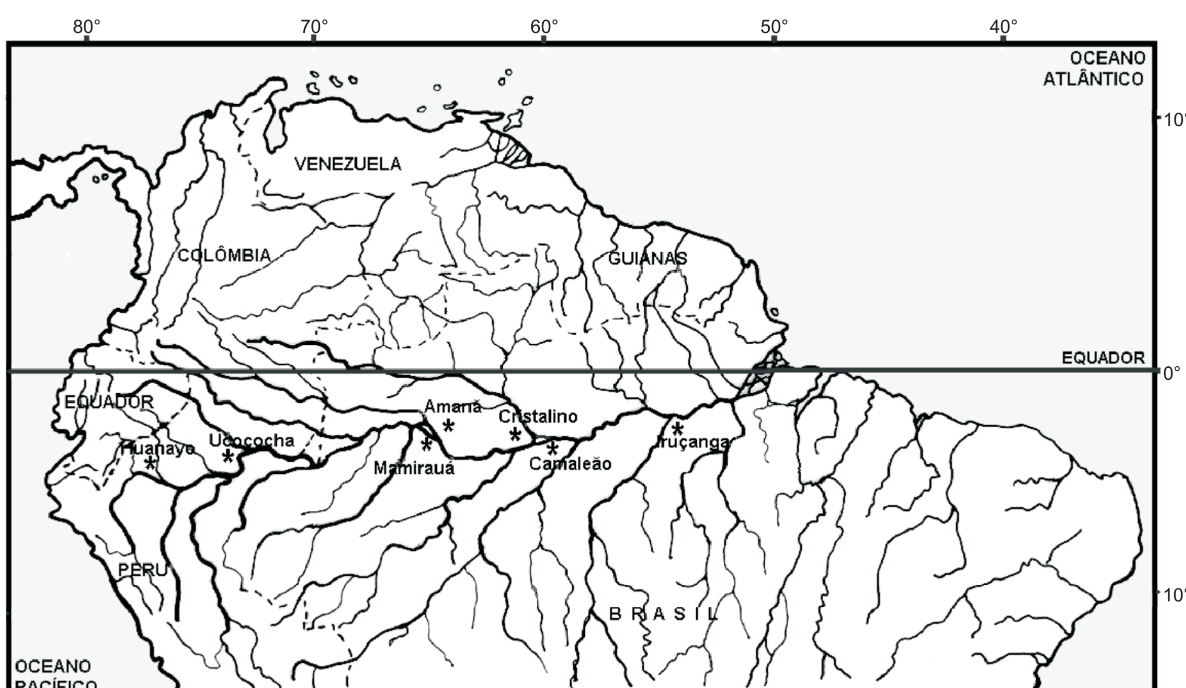

Fig. 1. Geographic localization of the seven lakes from the Peruvian and Brazilian Amazon Basin where populations of *Palaemonetes* spp. were collected.

al., 1998; TOWNEND, 2003; MANLY, 1994).

Bivariante analysis (Spearman Rank Correlation test) was used to test correlation between cephalotorax length and number of rostral teeth, and between cephalotorax length and position branchiostegal spine.

A Discriminant Function Analysis (DFA) was run to test the effectiveness of the selected ratios in predicting different group locations. The DFA calculates linear combinations of variables that maximize differences between groups which were classified *a priori*. The problem that is addressed with DFA is how distinct the separation of two or more groups of individuals or localities (MANLY, 1994; FOWLER *et al*., 1998).

A Principal Components Analysis (PCA) was conducted to compare variation within the shrimp populations. The object of a PCA is to take "p" variables $X_1, X_2, ..., X_p$ and to find combinations of these to produce indices $Z_1, Z_2, \ldots Z_p$ that are uncorrelated. The lack of correlation is a useful property because it means that the indices are measuring different 'dimensions' of the data. However, the indices are also ordered so that Z_1 displays the greatest amount of variation, Z_2 the second greatest amount of variation, and so on (MANLY, 1994; FOWLER *et al*., 1998).

An UPGMA Cluster Analysis on Euclidian Distance was undertaken to evaluate the similarity among shrimp population from different localities. Cluster analysis is a technique that classifies sampling units into a small number of homogenous clusters. In cluster analysis, the true number of clusters is not known and part of the analysis is to identify the number of clusters (MANLY, 1994; FOWLER *et al*., 1998).

RESULTS

Bivariate analysis of the rostral dentition (MS and MI) showed a strong overlap among populations and a high variability within them (Tab. I), regardless of the species. The variability within populations for rostral ventral teeth was low for lake Cristalino (CV = 11%) and high for lake Camaleão (CV = 24%) (Tab. I).

The position of the branchiostegal spine, given the seven populations as a whole, resulted in the following: tip of branchiostegal spine reaching (20%), overreaching (61%) or clearly failing to reach the anterior margin of carapace. This variation occurred independently of the species. The variability (CV) for B/BM was 18% - 28% and for B/AB was 16% - 26%, respectively.

The Principal Component Analysis indicated that the accumulated variance for the first four principal components (PC) represented 64% of the total (Tab. II). It seems that both PC1 and PC2 were closely associated to pereiopod segment variation. On the other hand, PC3 and PC4 were better discriminants for cephalotorax dimensions (Tab. II). The individual score projections of each population for the first and second principal components showed an overlap, which indicates that there is a great resemblance among them (Fig. 2).

The Discriminant Function Analysis resulted in six discriminant functions, which explained 100% of the accumulated population variance (Tab. III). The eigenvalues for the last five functions were less than 1, suggesting that the functions were not able to totally discriminate the studied groups. The coefficients (C/R,

Table I. Descriptive statistics and correlation for diagnostic characters of the seven populations of the freshwater shrimp *Palaemonetes* spp. from the Amazon Basin (taxa according to *a priori* identification; CV, coefficient of variability; *P*, probability value; r_s, Spearman correlation).

Presumptive Species	Lake	Median	Range	CV	Correlation r_s	*P*
			A. Upper mandible teeth			
P. carteri	Huanayo	8	6 - 12	13%	0.008	0.947
P. ivonicus	Urcococha	8	7 - 11	11%	-0.080	0.512
P. carteri	Amanã	8	5 - 12	14%	0.090	0.459
P. ivonicus	Mamirauá	8	6 - 11	12%	0.231	0.055
P. carteri	Cristalino	8	7 – 10	11%	-0.029	0.810
P. ivonicus	Camaleão	8	6 - 10	11%	0.131	0.280
P. carteri	Iruçanga	9	6 - 11	15%	0.281	0.019
			B. Lower mandible teeth			
P. carteri	Huanayo	3	2 – 4	23%	0.052	0.667
P. ivonicus	Urcococha	3	2 – 4	23%	0.077	0.528
P. carteri	Amanã	3	2 – 5	22%	-0.006	0.962
P. ivonicus	Mamirauá	3	2 – 5	20%	-0.025	0.840
P. carteri	Cristalino	4	3 – 5	11%	0.146	0.228
P. ivonicus	Camaleão	3	2 – 5	24%	0.153	0.207
P. carteri	Irunçaga	4	3 – 5	14%	0.311	0.009
			C. Distance from branchiostegal spine to mandible			
P. carteri	Huanayo	0.022	0.010-0.041	30%	0.632	<0.001
P. ivonicus	Urcococha	0.015	0.002-0.032	30%	0.374	<0.001
P. carteri	Amanã	0.019	0.007-0.036	35%	0.600	<0.001
P. ivonicus	Mamirauá	0.020	0.012-0.036	27%	0.339	<0.001
P. carteri	Cristalino	0.020	0.012-0.034	21%	0.542	<0.001
P. ivonicus	Camaleão	0.017	0.010-0.032	24%	0.359	<0.001
P. carteri	Irunçaga	0.021	0.015-0.036	21%	0.575	<0.001

T/BT, D5/P5, D4/P4) and (C4/P4, D3/P3, C3/P3, R/AR) contributed the most to the first and second discriminant function, respectively (Tab. IV). The projection of the first two-discriminant functions is shown in figure 3. The reclassification of individuals based on results of the analysis of discriminant functions showed that 79% of the total were reclassified correctly in their groups of origin (*a priori* groups) and 21% were reclassified in other groups (*a posteriori* groups) (Tab. V).

The dendrogram resulted from cluster analysis revealed two groups of populations. The larger group, including five populations, is divided into two subgroups: one formed by populations from lake Huanayo, lake Camaleão, and lake Urcocucha; and the other formed by populations from lake Amanã and lake Mamirauá. The smaller group includes populations from lake Cristalino and lake Iruçanga (Fig. 4).

Table II. Component loadings for the first four principal components based on the 14 ratios of the morphometric characters of the populations of the freshwater shrimp *Palaemonetes* spp. from seven lakes of the Peruvian and Brazilian Amazon Basin (B/AB, length of branchiostegal spine/height of the base of branchiostegal spine to branchiostegal groove; C, carpus; CL/R, cephalotorax/rostrum; D, dactylus; M, merus; PP, propodus; R/AR, rostrum/rostrum height; T/BT, length of telson/ width of telson base).

Ratios	PC1	PC2	PC3	PC4
CL/R	-0.102	-0.043	-0.873	0.100
R/AR	0.761	0.200	0.081	-0.003
B/AB	-0.032	-0.095	0.427	-0.694
T/BT	-0.066	-0.020	-0.466	0.018
C1/PP1	-0.062	-0.648	0.212	0.249
C2/PP2P	0.004	-0.281	0.463	0.270
D3/PP3	0.126	0.733	0.360	0.276
C3/PP3	0.490	0.220	0.243	0.558
D4/PP4	0.063	0.868	0.169	0.145
C4/PP4	0.668	0.147	0.156	0.505
C4/M4	0.602	-0.010	0.233	0.299
D5/PP5	0.027	0.853	-0.026	0.114
C5/PP5	0.844	0.103	-0.120	0.017
C5/M5	0.871	0.003	0.112	-0.130
Eingenvalues	3.794	2.209	1.994	1.020
Total variance	27.102	15.776	14.242	7.287
Cumulative variance	27.102	42.879	57.121	64.408

DISCUSSION

The existence of sibling species among decapod crustaceans is widely reported in the literature (KNOWLTON, 1986; PALUMBI & BENZIE, 1991; FELDER & STATON, 1994; CUESTA & SCHUBART, 1998; GRANDJEAN *et al.*, 1998; KING & HANNER, 1998; SCHUBART *et al.*, 2000; STANTON *et al.*, 2000). These investigators showed that closely related species are often hardly distinguished using morphologic characters, mainly due to their intraspecific variability. Little knowledge of the degree of intraspecific variability can compromise the differentiation of closely related species, making the process of identification and validation of their taxonomic status very problematic (CUESTA & SCHUBART, 1998).

Taxonomic delimitation of *Palaemonetes carteri* and *P. ivonicus*, based on the adult morphology, was established by HOLTHUIS (1952). The current taxonomic status of these two species is questioned by the apparent

Table III. Statistical analysis of first six discriminant functions for the ratios of the populations of *Palaemonetes* spp. from seven lakes of the Peruvian and Brazilian Amazon Basin (DF, degrees of freedom; *p*, probability value).

Function	Value	Variance(%)	Cumulative variance(%)	ChiSquare	DF	*p*
1	3.676	63.9	63.9	1514.326	84	< 0.001
2	0.738	12.8	76.7	776.293	65	< 0.001
3	0.710	12.3	89.0	511.804	48	< 0.001
4	0.498	8.7	97.7	254.965	33	< 0.001
5	0.084	1.4	99.1	61.730	20	< 0.001
6	0.049	0.9	100	23.039	9	0.006

Table IV. Discriminant functions and coefficients for the ratios of the populations of *Palaemonetes* spp. from seven lakes of the Peruvian and Brazilian Amazon Basin (B/AB, length of branchiostegal spine/height of the base of branchiostegal spine to branchiostegal groove; C, carpus; CL/R, cephalotorax/rostrum; D, dactylus; M, merus; PP, propodus; R/AR, rostrum/rostrum height; T/BT, length of telson/width of telson base).

Ratios	Discriminant functions and coefficients					
	1	2	3	4	5	6
CL/R	1.001	0.010	0.697	0.267	0.003	0.077
R/AR	0.048	0.496	0.888	0.626	0.132	0.178
B/AB	-0.274	0.309	0.092	-0.123	0.266	-0.095
T/BT	0.437	0.272	-0.254	0.009	0.415	-0.240
C1/PP1	-0.218	-0.347	0.400	-0.597	-0.051	0.453
C2/PP2	-0.174	-0.129	0.420	0.155	0.010	-0.326
D3/PP3	0.035	-0.403	-0.103	-0.304	-0.488	0.066
C3/PP3	-0.034	-0.423	-0.012	0.003	0.944	-0.212
D4/PP4	0.138	0.375	0.000	-0.467	-0.518	-0.710
C4/PP4	0.086	-0.607	0.184	0.500	-0.048	-0.388
C4/M4	-0.079	0.334	0.050	-0.295	-0.130	0.617
D5/PP5	0.231	0.119	0.677	-0.345	0.656	0.362
C5/PP5	0.048	0.296	-0.131	0.390	-0.635	0.560
C5/M5	-0.108	-0.294	0.121	-0.048	0.055	-0.636

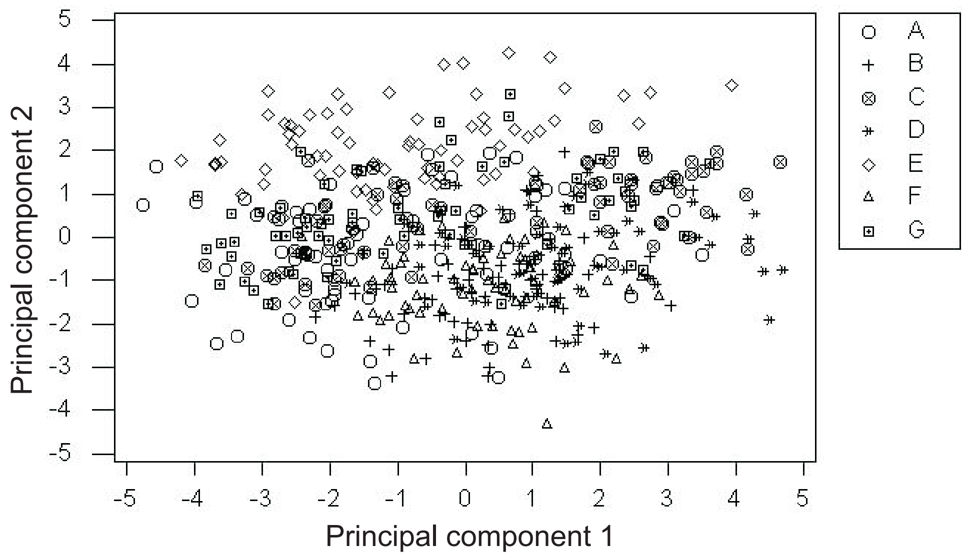

Fig. 2. Projection scores of first and second principal components for populations of *Palaemonetes* spp. from seven lakes of the Peruvian and Brazilian Amazon Basin (A, lake Iruçanga; B, lake Camaleão; C, lake Cristalino; D, lake Mamirauá; E, lake Amanã; F, lake Urcococha; G, lake Huanayo).

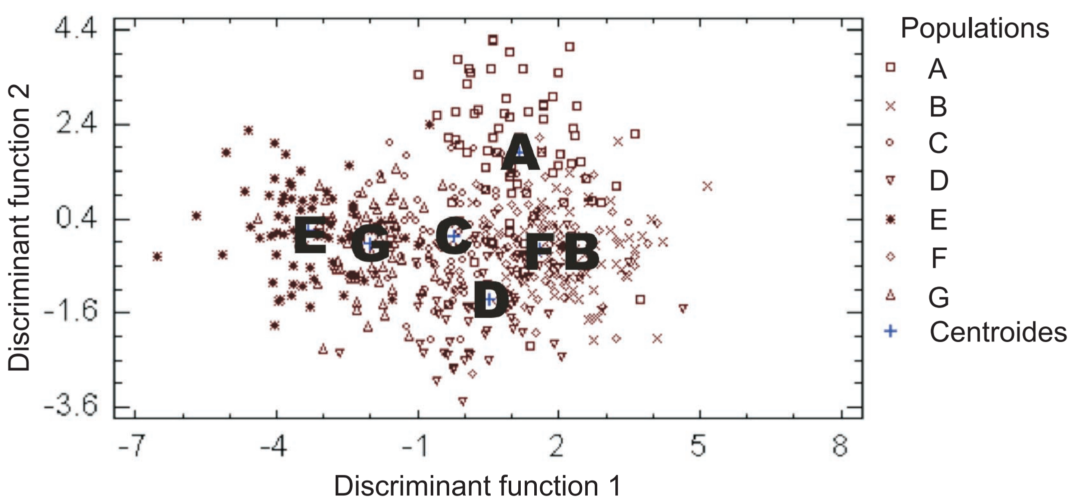

Fig. 3. Projection scores of first and second discriminant function for populations of *Palaemonetes* spp. from seven lakes of the Peruvian and Brazilian Amazon Basin (A, lake Huanayo; B, lake Urcococha; C, lake Amanã; D, lake Mamirauá; E, lake Cristalino; F, lake Camaleão; G, lake Iruçanga).

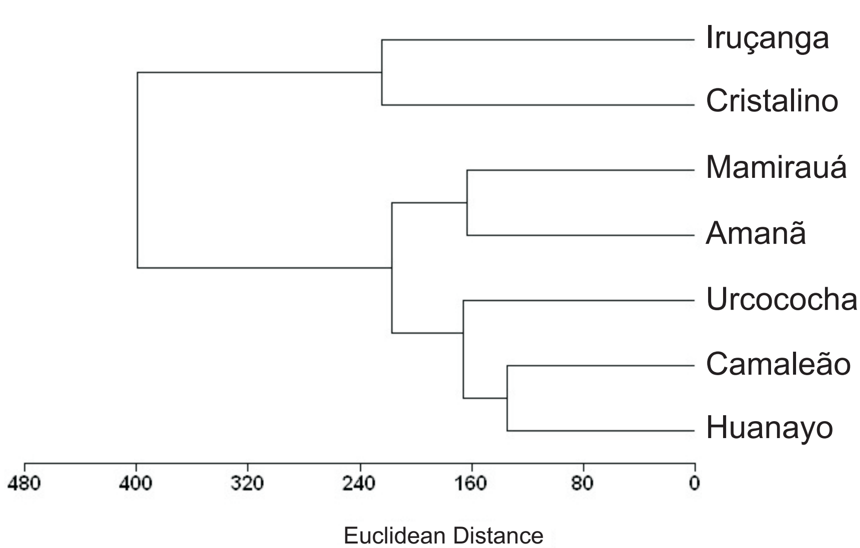

Fig. 4. Dendrogram grouping for populations of *Palaemonetes* spp. from seven lakes of Peruvian and Brazilian Amazon Basin.

Table V. *A posteriori* classification matrix of the members of populations of *Palaemonetes* spp. from seven lakes of the Peruvian and Brazilian Amazon Basin (values in parenthesis represent the percentage of reclassification within each group).

Lakes	Classification matrix							
	Huanayo	Urcococha	Amanã	Mamirauá	Cristalino	Camaleão	Iruçanga	Total
Huanayo	49 (70.0)	4 (5.7)	2 (2.9)	4 (5.7)	-	10 (14.3)	1 (1.4)	70/(100)
Urcococha	1 (1.4)	59 (84.3)	-	1 (1.4)	-	9 (12.9)	-	70/(100)
Amanã	2 (2.9)	2 (2.9)	61 (87.1)	3 (4.3)	1 (1.4)	1 (1.4)	-	70/(100)
Mamirauá	-	5 (7.1)	4 (5.7)	48 (68.6)	-	11 (15.7)	2 (2.9)	70/(100)
Cristalino	-	-	1 (1.4)	-	63 (90.0)	-	6 (8.6)	70/(100)
Camaleão	7 (10.0)	7 (10.0)	1 (1.4)	8 (11.4)	-	47 (67.2)	-	70/(100)
Iruçanga	-	-	1 (1.4)	-	7 (10.0)	-	62 (88.6)	70/(100)

high morphologic plasticity of the two main diagnostic characters (number of rostral teeth and position of the branchiostegal spine) used for their separation. In spite of not being a morphometric character, the number of rostral teeth was considered in the present study because of its current use in separating both species.

Historically, rostral dentition was considered a good character for identification of some palaemonid shrimps. There have been taxa established solely on the basis of rostral characteristics (De Grave, 1999a), a situation that was attributed to the fact that many authors were unaware of the variability shown by this structure (De Grave, 1999b). Variation in the number of rostral teeth has already been studied in other species of *Palaemonetes* (De Grave, 1999a).

Sixteen specimens of *P. carteri* described by Gordon (1935) had five to eight dorsal and three to seven ventral rostral teeth, while Holthuis (1950) counted six to ten dorsal and three ventral rostral teeth in just two type specimens of *P. ivonicus*. Later, Odinetz-Collart & Enriconi (1993), studying a population of *P. carteri* from the lower Rio Negro, found similar variability with this characteristic (five to nine dorsal teeth; two to six ventral teeth) as reported by Holthuis (1952). However, Odinetz-Collart & Enriconi (1993) pointed out that most of their specimens (94.8%) had six to eight dorsal, and two to five ventral rostral teeth. The present data also show great variation in this character: the number of dorsal teeth varied from five to twelve. Such variation suggests a great plasticity for this character, although the variation is quite similar among all the populations studied (most of the specimens had seven to nine dorsal, and two to four ventral rostral teeth), regardless of the species (Tab. I). On the other hand, such variation is not related to the size of the individual because the rostral dentition did not show any relationship with the carapace length. Due to this plasticity, the rostral dentition is not a good characteristic for separating both species of *Palaemonetes*. Similar findings were verified in *Palaemonetes varians* by De Grave (1999a), who reported a high variability in this characteristic, although it showed some relationship with latitude. However, in *Palaemon concinnus* the variation in the number of rostral teeth was relatively constant within the populations studied (De Grave, 1999b).

Variability in the position of the branchiostegal spine in these species was reported by Odinetz-Collart & Enriconi (1993) and García-Dávila & Magalhães (2003). In the present study, this character showed a great intrapopulational variability (BM: CV 21-35%; CB/BM: CV 18-28%; CB/AV: CV 16-26%). The plasticity of this characteristic was verified with the Student Newman-Keuls *a posteriori* test, which revealed that BM was one of the two characteristics (the other was D3) that did not show significance among the populations under study.

Holthuis (1950) described *P. ivonicus*, but the number of specimens was so small that it did not allow a verification of the difference in the diagnostic characteristics used to separate *P. ivonicus* from *P. carteri*. This lack of clarity in the patterns of morphological variation, as already mentioned by Odinetz-Collart & Enriconi (1993) and García-Dávila & Magalhães (2003), demand the necessity of more precise tools to measure in what proportions such morphological variability could compromise, in both species, the recognition of their real taxonomic status. Fleming (1969) also questioned the taxonomic character used by Holthuis (1952) to distinguish some species of this genus due to the overlap, variability and indistinctiveness of some of these traits.

Although PCA failed to separate the populations, it revealed that pereiopod ratios (C4/P4, C4/M4, C5/P5, C5/M5, C1/P1, D3/P3, D4/P4, D5/P5) and R/AR ratio showed the greatest differences among populations in the first two components, which represented, both, 43% of the total variation. According to these results, the few distinctive characters among the populations were those of the pereiopods and rostrum, and not the position of the branchiostegal spine, which ratio was responsible for very little of the variation in these two components (-0.032 and -0.095, respectively). The great similarity of the populations is also corroborated by the fact that the four principal components found in this study explained 64% of the total variation among the species. The first two components were responsible for over 80% of total variation in other studies about sibling species in Crustacea (McClure & Wicksten, 1997; Scapini *et al.*, 1999).

In spite of the fact that the Discriminant Function Analysis - DFA was not able to clearly separate the populations studied (due to the overlapping range among groups), it contributed to clarify the relationship among them. Therefore, three groups could be identified: a close related group formed by the lake Cristalino and lake Iruçanga populations; a group including the populations of lake Huanayo, lake Urcococha and lake Camaleão; and a third group, with the populations of lake Amanã and lake Mamirauá (Fig. 3). The former two groups were slightly separated, showing a small morphometric difference between them, while the latter was morphometrically in between the other two groups.

On the other hand, the fact that in the reclassification *a posteriori* all populations showed individuals in one or other population confirming that the great intrapopulational plasticity in the two nominal species determines the overlapping of characteristics that interferes in their taxonomic separation. However, some relationships could be inferred on the basis of such reclassification: (a) populations from lake Huanayo, lake Urcococha and lake Mamirauá showed a high degree of reclassification in the population from lake Camaleão, and vice-versa; (b) populations from lake Cristalino and lake Iruçanga, besides presenting a percentage of reclassification very close to each other, showed a slight degree of reclassification with that of the lake Amanã (1.4%); and (c) populations from lake Amanã and lake Mamirauá had individuals reclassified in almost all other populations. These relationships would indicate that the first relationship was established among populations from white water environments or situated near them and the second relationship was established among populations from black and clear water environments.

Collectively, the type of environment could help in the taxonomic separation of the two species in the Amazon Basin, being *P. ivonicus* related to white and mixed water environments, and *P. carteri* related to black and clear water river systems. However, the plasticity shown by the populations from lake Amanã (black water) and lake Mamirauá (white water) that presented a percentage of individuals reclassified in opposite environments seems to contradict such trend in the reclassification. Morphometric differences and variability in morphologic characteristics as possible adaptive responses to the environment have been reported in the literature for other populations of crustaceans (Amat *et al.*, 1995; Cuesta & Schubart, 1998; Daniels *et al.*, 1998; Grandjean *et al.*, 1998; Sarda *et al.*, 1998; Scapini *et al.*, 1999).

The fact that the Cluster Analysis grouped together the populations from lake Cristalino and lake Iruçanga (Fig. 4) reaffirms the idea that the morphological similarity could be related to the type of environment, which would be reflecting the geological history of the basin. These lakes are black and clear water bodies belonging to hydrographic basins (Rio Negro and Rio Tapajós, respectively) whose origins are in Archean shields of Guiana and Central Brazil, respectively. In addition, these rivers run mostly through ancient areas of leached soils, having only their lower course on more recent (Tertiary) zones. Such waters are usually transparent or darkened by dissolved humic acids, with small quantities of inorganic sediments (Sioli, 1968). The other group includes populations from lakes Urcococha, Mamirauá and Camaleão, typical of the Amazon River floodplain system, a large sedimentary area from tertiary and quaternary sediments eroded from Andean and pre-Andean regions. Such waters are called “white waters” due to their heavy load of suspended inorganic material, giving them a muddy appearance, or “mixed waters”, when decanted or mixed with clear water from the adjacent terra firme areas (Sioli, 1968).

Although the populations of lake Huanayo and lake Amanã have been *a priori* classified as *P. carteri* due to the clear or dark appearance of their water, the morphometric results (*a posteriori*) indicate that these populations are more closely related to the group that was considered as *P. ivonicus*. Although visually classified as clear/black water environments, the geological history of both areas is similar to that of the above mentioned lakes of the Amazon River floodplain (Lundberg *et al.*, 1998). Lake Huanayo belongs to the Rio Pastaza basin, which originates in the Ecuadorian Andes and drains an area of volcanic origin in the Holocene (Quaternary); this gives a relatively dark color to the water (Räsänen, 1993), whereas lake Amanã has a strong yearly influence from the white water floodplain system of Rio Japurá and Rio Solimões.

However, a clear taxonomic separation of these two species should not rely on environmental characteristics, as definition of the watercolor could be influenced by seasonal factors, water quality and the subjectiveness of the observer (Kalliola & Puhakka, 1993). Considering that a clear separation of both taxa on the basis of morphological characteristics is compromised by a high degree of intra- and interpopulational variability, other characteristics, such as those provided by molecular analysis, should be taken into account for a more comprehensive interpretation of their taxonomic status.

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