

Taxonomic congruence between external morphology and male and female genitalia characters of members of *Rasahus* Amyot & Serville (Heteroptera: Reduviidae: Peiratinae)

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Zool. Med. Leiden 68 (10), 15.vii.1994: 97-108, figs. 1-8, tables 1-4.— ISSN 0024-0672.

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Key words: Taxonomic congruence; external morphology; genitalia; Heteroptera; Reduviidae; Peiratinae; *Rasahus*.

The occurrence and degree of taxonomic congruence is analyzed between classifications based on the external morphology and male and female genitalia of the genus *Rasahus* Amyot & Serville, 1843 (Reduviidae) using multivariate analyses. The results demonstrate that a classification based on size differences, and a data set of ratios are incongruent with a classification of a set of characters of the male and the female genitalia. The last two classifications are congruent with each other at a species-group level, e.g., that of the *R. scutellaris* and *R. hamatus* group. The classifications are discussed and a generalized phenetic classification is given.

Introduction

One of the most significant problems for biological systematics is the fact that two or more classifications of the same group of taxa, but based on different sets of characters, are not always coincident. How, in a taxonomic sense, constant is the information sampled from the taxa? This problem gave rise to the concept of taxonomic congruence, which is the degree to which classifications of the same taxa postulate the same groupings (Mickey, 1978: 143; Crisci, 1984: 233). Identical classifications are said to be perfectly congruent.

Because there is a substantial amount of information known about the external morphology of the members of the genus *Rasahus* Amyot & Serville, 1843, this genus seems to be a good example to study the effect of different data sets on their classification. The genus consists of 26 species with a Nearctic and Neotropical distribution. Recently their taxonomy has been revised in detail (Coscarón, 1983: 75). A study of the phenetic relationships among the species has been performed using morphological characters of the body, and the male genitalia (Coscarón, 1989: 131).

Accordingly, the existence of two species groups was noticed, viz. the *R. scutellaris*- and *R. hamatus*-group (Coscarón, 1989: 140). To contribute to the understanding of the behaviour of taxonomic information by the analysis of the taxonomic congruence, data sets were collected from different parts of the body and composed of different character types. One of the main questions to be answered is whether, and to which amount both species groups can also be recognized in the various similarity matrices and classifications.

Material and methods

The genus *Rasahus* contains 26 species, 19 of which were studied here (table 1). Of each species the males and females are clearly distinguishable. This study has also been based on material provided by various institutions: American Museum of Natural History (New York, U.S.A.); British Museum (Natural History) (London, U.K.); California Academy of Sciences (California, U.S.A.); Canadian National Collections of Insects, Arachnids, and Nematodes (San Francisco, Canada); Fundación Miguel Lillo (Tucumán, Argentina); Instituto Entomológico San Miguel (San Miguel, Argentina); Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina); Museo de La Plata (La Plata, Argentina); Museo Goeldi (Belen, Brasil); Museum National d'Histoire Naturelle (Paris, France); Museo de Zoología de São Paulo (São Paulo, Brasil); Naturhistoriska Riksmuseet (Stockholm, Sweden); Nationaal Natuurhistorisch Museum (Leiden, The Netherlands); Snow Entomological Museum, University of Kansas (Kansas, U.S.A.); United States National Museum (Washington, U.S.A.); Universitetets Zoologiske Museum (Copenhagen, Denmark); Zoologisches Museum der Humboldt Universität zu Berlin (Berlin, G.F.R.); private collection of Mr. Martinez (Salta, Argentina).

Table 1. Name list of the species of *Rasahus* used in this study.

number	name
1	<i>R. aeneus</i> (Walker, 1873)
2	<i>R. maculipennis</i> (Lepelletier & Serville, 1825)
3	<i>R. rufiventris</i> (Walker, 1873)
4	<i>R. bifurcatus</i> Champion, 1899
5	<i>R. guttatipennis</i> (Stål, 1862)
6	<i>R. arcuiger</i> (Stål, 1862)
7	<i>R. grandis</i> (Fallou, 1889)
8	<i>R. limai</i> Pinto, 1935
9	<i>R. thoracicus</i> Stål, 1872
10	<i>R. hamatus</i> (Fabricius, 1781)
11	<i>R. biguttatus</i> (Say, 1832)
12	<i>R. surinamensis</i> Coscarón, 1983
13	<i>R. albomaculatus</i> (Mayr, 1865)
14	<i>R. peruensis</i> Coscarón, 1983
15	<i>R. brasiliensis</i> Coscarón, 1983
16	<i>R. sulcicollis</i> (Serville, 1831)
17	<i>R. scutellaris</i> (Fabricius, 1787)
18	<i>R. castaneus</i> Coscarón, 1983
19	<i>R. angulatus</i> Coscarón, 1986

From the specimens 30 characters were measured of the external morphology of the body (head, thorax, abdomen), and the male and female genitalia (table 2). The methodology for extraction, dissection, inflation, and drawings of the male and female genitalia is given by Coscarón (1983: 76). The terminology of the characters is according to Lent & Jurberg (1966: 297), and Lent & Wygodzinsky (1979). The terminology of the male and female genitalia, is according to Dupuis (1955: 185), Davis

(1966: 912) and Coscarón (In press).

The characters include continuous measurements (characters 1 to 3), ratios (characters 4 to 9), and ranked qualitative characters. For each species the mean character values (centroids) were used, based on up to five males and females. The data sets of the body, and male and female genitalia are shown in table 4, data set A, B, and C, respectively. For more detailed descriptions one is referred to the literature cited above.

Cluster and other multivariate analyses were performed with BIOPAT, Program System for Bioinformatic Pattern Analysis (Hogeweg & Hesper, 1972), at the CRI, Leiden University. As a measure of overall dissimilarity the Euclidean Distance (D) was used. As it gives the highest cophenetic correlation ($CC_{sim/ult}$) between similarity and ultrametric matrices, the UPGMA was used as the method for cluster analysis.

Table 2. Description of the morphological characters.

Characters of the body:

- 1 length;
- 2 width pronotum;
- 3 width abdomen;
- 4 length head/width head at eye;
- 5 length head/length pronotum;
- 6 length anteocular region/length postocular region;
- 7 length rostral segment I/length rostral segment II;
- 8 length rostral segment I/length rostral segment III;
- 9 height head/eyes height;
- 10 body shape: 1 stout; 2 slender;
- 11 postocular region: 1 angulate; 2 rounded;
- 12 eyes position: 1 not surpassing under or upper surface of head; 2 surpassing;
- 13 scutellum: 1 not or very little acuminate; 2 acuminate;
- 14 femur coloration: 1 uniform; 2 more than one colour;
- 15 hemelytra with oval dot: 0 absence; 1 presence;
- 16 conexivum: 1 dorsally visible; 2 not dorsally visible;
- 17 conexivum: 1 homogeneous; 2 not homogeneous;
- 18 8th sternite pilosity: 0 absent; 1 present.

Male genitalia:

- 1 pygophore: 1 rounded; 1.5 subrectangular; 2 quadrangular;
- 2 inferior edge pygophore: 1 straight; 1.5 sinuose; 2 evaginated;
- 3 median distal region of medial process of the pygophore: 1 not curved; 2 curved;
- 4 medial process of the pygophore: length/width;
- 5 parameres: 1 subrectangular; 2 subtriangular.

Female genitalia:

- 1 gonocoxite IX: shape distal edge: 1 elongated; 2 straight;
 - 2 gonocoxite IX: internal edge hairs: 1 not reaching distal edge; 2 reaching distal edge;
 - 3 gonocoxite IX: sclerotization area: 1 unsclerotized internal; 1.5 sclerotized medial; 2 without unsclerotized internal nor sclerotized medial;
 - 4 gonocoxite IX: shape: 1 wider than long; 2 as wide as long;
 - 5 IX & X tergites: shape: 1 wider than long; 2 as wide as long;
 - 6 IX & X tergites: intersegmental line: 1 sclerotized and complete; 1.5 unsclerotized and complete; 2 unsclerotized and incomplete;
 - 7 X tergite: pilosity: 1 abundant; 2 scarce.
-

Results

The characters of the body cover various aspects of information, e.g., size and shape differences. From each aspect a UPGMA dendrogram was derived.

The general size of the body was estimated by means of a Principal Component Analysis (PCA) of the first three characters of data set A. The elements of the eigenvector of the first main axis, explaining 94% of the variation, were all positive and of the same magnitude (loadings ranging between .99 and .95), thus were considered to explain a general size factor. A UPGMA dendrogram ($CC_{sim/ult} = 0.81$) based on D between the coordinates of the OTUs according to this first main axis revealed two main clusters with a reasonable gap in between, containing the smaller and larger OTUs (fig. 1). The *scutellaris*-group members are equally distributed over the two clusters, of which *aeneus* is the smallest and *albomaculatus* is the largest (table 4). Four large members of the *hamatus*-group members are clustered with two of medial length.

Because the three characters used above showed to contain almost no information on shape difference, only the ratios between two individual characters were used as an estimate of shape. To consider these as a generalized estimate of shape differences between the OTUs, e.g., by the use of D, the OTUs should match a model in which they are on equal distance to the centre of A-space. As the majority of the OTUs, using characters 4-9 (table 2), had a D between 0.42 and 0.5, whereas two had a D of 0.39 and three between 0.55 and 0.64, they were considered to fit the model. A UPGMA dendrogram ($CC_{sim/ult} = 0.82$) showed that the members of both species groups were heterogeneously distributed over several clusters (fig. 2).

A UPGMA dendrogram of D of the nine characters of the body ($CC_{sim/ult} = 0.87$) shows two main clusters (fig. 3). One of these clusters contains all the members of the *scutellaris*-group (of which *aeneus*, *maculipennis* and *castaneus*, and *guttatipennis* and *scutellaris* are identical), and three *hamatus*-group members, viz. *arcuiger*, *rufiventris*, and *hamatus*, whereas the other cluster contains the remaining five *hamatus*-group members.

The subdivision is mainly caused by characters 10-12, and 15 (table 2, 4). It means that the *hamatus*-group has a more slender body, rounded postocular region, an eye position which is surpassing the surface of the head, and an oval dot on the hemelytra.

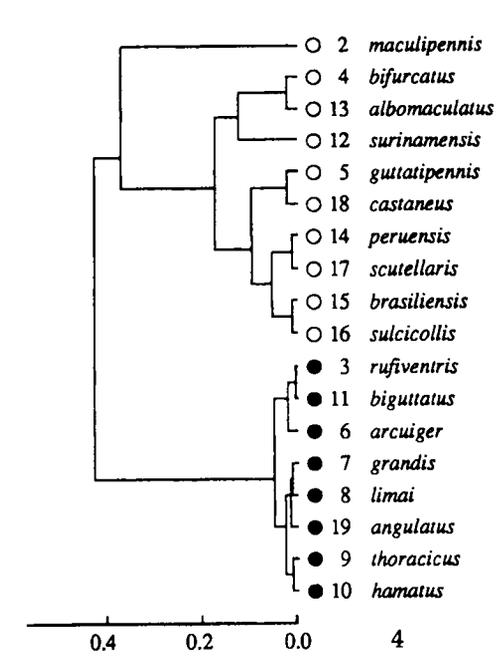
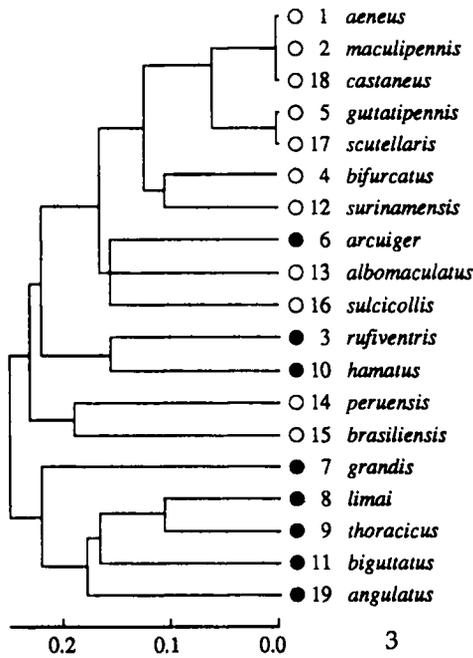
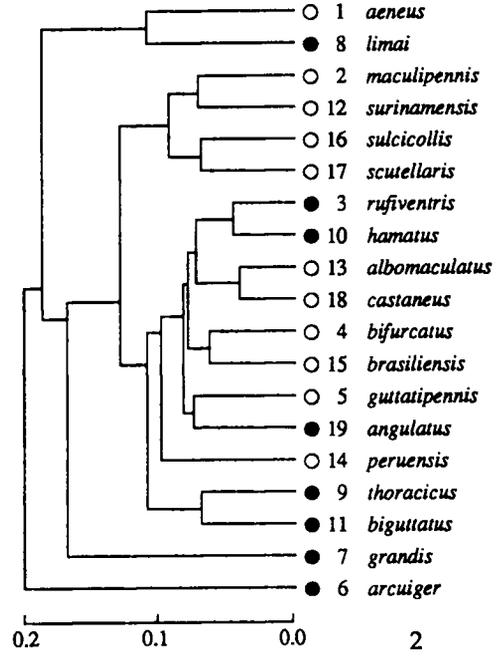
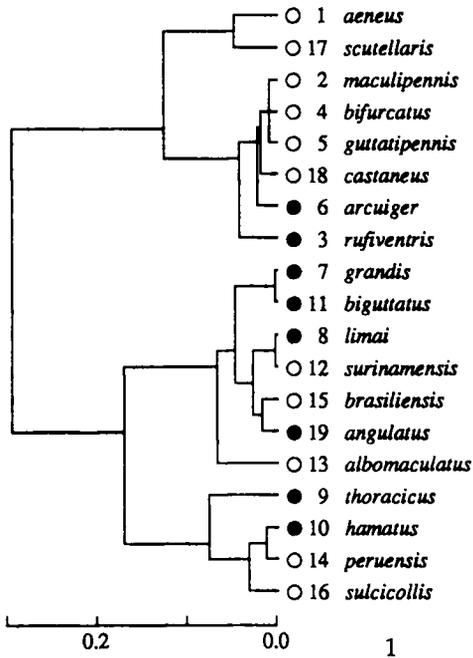
Of the male genitalia no information was available of *aeneus* (OTU 1). Except for the ratios of character 4 (table 2, 4), which has been ranged between 0-2, all the characters are binary. A UPGMA dendrogram ($CC_{sim/ult} = 0.99$) of D of the male genitalia

Fig. 1. UPGMA dendrogram of size differences between members of the *scutellaris*- (o) and *hamatus*-group (●), using Euclidean D of the first main axis (94%) of a PCA ($CC_{sim/ult} = 0.81$).

Fig. 2. UPGMA dendrogram ($CC_{sim/ult} = 0.82$) of Euclidian D based on shape differences.

Fig. 3. UPGMA dendrogram of Euclidian D based on characters of the body. ($CC_{sim/ult} = 0.87$)

Fig. 4. UPGMA dendrogram ($CC_{sim/ult} = 0.99$) of Euclidian D based on characters of the male genitalia.



shows two main clusters, one containing all the *hamatus*-group members, and the other all those of the *scutellaris*-group (fig. 4).

The *hamatus*-group is distinguished from the *scutellaris*-group by a pygophore which is rounded, has a straight inferior edge, and of which the median distal region of the medial process is not curved. Moreover, the group has subrectangular parameres (table 2, 4). Within the *scutellaris*-group *R. maculipennis* has an extreme position which is caused by the length/width ratio of the medial process of the pygophore.

Of the female genitalia a UPGMA-dendrogram ($CC_{sim/ult} = 0.99$) shows four clusters of identical OTUs because the characters allow no further differentiation (fig. 5). There are two main branches, one containing all the members of the *hamatus*-group, whereas the other branch can be divided into three subclusters of identical *scutellaris*-group members.

The uniform *hamatus*-group differs from the *scutellaris*-group by the ninth gonocoxite which has an elongated distal edge, its internal edge hairs are not reaching the distal edge, and of which the sclerotization area is internally unsclerotized (table 2, 4). The first subcluster, containing *peruensis*, *brasiliensis* and *castaneus*, is characterized by the shape of the ninth gonocoxite which is as wide as long, and of which the ninth and tenth tergite is also as wide as long. The subcluster with *surinamensis* and *albomaculatus* has a medial sclerotization on the sclerotization area of the ninth gonocoxite, whereas the intersegmental line of the ninth and tenth tergites is unsclerotized and incomplete.

The table with cophenetic correlations between the D-matrices (table 3; below diagonal), shows a high correlation between the genitalia of both sexes, and a moderate correlation between the binary coded characters of the body and the genitalia. Body size and ratios show also very low correlations with the other characters. An almost similar picture is shown by the UPGMA dendrograms, viz., except for the dendrograms of the male and female genitalia (figs. 4 & 5, respectively), there is little resemblance or congruence between the classifications of figs. 1-3. The amount of similarity between the UPGMA dendrograms has been given by the cophenetic correlations between their ultrametric matrices (table 3; above diagonal). Here again the highest correlations are between the genitalia of both sexes, followed by the characters of the body. All other correlations are very low.

Table 3. Table of the cophenetic correlations. Below diagonal the correlations between the five Euclidean dissimilarity matrices, the combination of these five into a Distance Matrix of All Factors (DAF) and its UPGMA-ultrametric matrix (ultrametric DAF). Above diagonal the correlations between the UPGMA ultrametric matrices.

size body	1.	.05	.23	.03	.04	-	.12
ratios body	.07	1.	.00	.04	-.02	-	.11
binary characters body	.22	.05	1.	.25	.38	-	.56
male genitalia	.00	.05	.32	1.	.81	-	.85
female genitalia	.05	.03	.44	.81	1.	-	.90
DAF	.31	.26	.65	.83	.84	1.	-
ultrametric DAF	.15	.10	.54	.85	.89	.91	1.

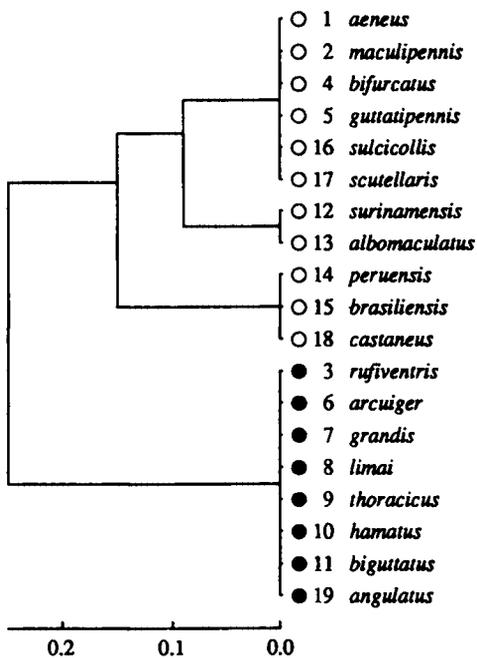


Fig. 5. UPGMA dendrogram ($CC_{sim/ult} = 0.99$) of Euclidian D based on characters of the female genitalia.

analysis (PCO) (fig. 8). The first main axis of the PCO scatterplot explains 47%, and the second 17% of the total variation. The separation into two main groups can be readily understood from the scatterplot, however, only part of the total information is shown in this two-dimensional space (64%). Therefore the pattern within each of the two main groups of fig. 8 does not fit the shortest distances as shown by the minimal spanning tree of fig. 7, e.g., 6 *R. arcuiger* - 9 *R. thoracicus*, 8 *R. limai* - 11 *R. biguttatus*, 10 *R. hamatus* - 19 *R. angulatus*, 3 *rufiventris* - 10 *R. hamatus* of the *hamatus*-group and 1 *R. aeneus* - 5 *R. guttatipennis*, 16 *R. sulcicollis* - 17 *R. scutellaris*, 15 *R. brasiliensis* - 16 *R. sulcicollis*, 12 *R. surinamensis* - 13 *R. albomaculatus*, 13 *R. albomaculatus* - 16 *R. sulcicollis* of the *sulcatus*-group.

Discussion

The dendrogram of fig. 1 demonstrates that, although most members of the *hamatus*-group have a large body size, the *hamatus*- and *scutellaris*-group are not characterized by a constant difference in size. This is also shown by the pattern of shape differences as displayed in fig. 2. The characters of the body which are almost all binary (fig. 3) display a segregation of the species into two more or less distinct groups. The largest difference between both groups, however, is displayed by the characters of the genitalia of both sexes (figs. 4 and 5). An explanation for the low resemblance

To obtain a generalized classification with high predictive value, the information of the species should be combined. Because the various matrices represent different factors, viz., size and shape, and different kinds of characters, viz., continuous, multistate and binary, this was not done with the initial data sets, but with the D-matrices. These represent the various generalized aspects of different parts of the phenotype of the body. For this reason the variability of each similarity matrix is ranged, and squared, after which the matrices are summed by which a single Distance matrix of All Factors (DAF) is gained (Povel, 1987). A UPGMA dendrogram of the DAF ($CC_{sim/ult} = 0.91$) revealed a pattern of two main clusters, each of which is exclusively composed of the two taxonomic groups (fig. 6). The patterns within the DAF are also shown by means of a minimal spanning tree (fig. 7), and a scatterplot of the species according to the first two main axes of a Principal Coordinate

Table 4. Data set with character values of the species. The species are ordered according to the UPGMA dendrogram shown in fig. 6. Values between brackets indicate the percentage of that score.
 A = data set of the body; B = data set of the male genitalia; C = data set of the female genitalia; char. nr. = character number (see: table 2); max. = maximum; min. = minimum; - = no information; max. = maximum character value; min. = minimum character value.

A: char. nr.:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
<i>scutellaris</i> -group																			
1 R. <i>aeneus</i>	9.10	2.50	2.80	.9	2.7	.5	1.95	1.30	.81	2	2	1	1	2	0	1	2	-	
2 R. <i>maculipennis</i>	13.85	3.30	3.60	1.0	1.8	.6	1.15	1.19	.86	2	2	1	1	2	0	1	2	0	
4 R. <i>bifurcatus</i>	13.30	3.10	4.00	.7	1.6	.4	1.46	1.12	.71	2	2	1	1.5	2	0	1	2	0	
5 R. <i>guttatipennis</i>	13.05	3.30	3.95	.8	1.6	.5	1.82	1.39	.68	2	2	1	1	2	0	1	2	1	
17 R. <i>scutellaris</i>	10.30	2.80	3.00	.8	1.5	.4	.89	.89	.71	2	2	1	1	2	0	1	2	1	
18 R. <i>castaneus</i>	13.10	3.30	3.60	.6	1.7	.4	1.83	.91	.86	2	2	1	1	2	0	1	2	0	
16 R. <i>sulcicollis</i>	16.85	4.30	4.65	.6	1.5	.3	1.21	.86	.87	1	2	1	1	2	1	1	2	1	
12 R. <i>surinamensis</i>	16.55	5.85	6.60	.8	1.8	.6	1.31	.85	.75	2	2	1	1.5	2	0	1	2	1	
13 R. <i>albomaculatus</i>	23.20	5.70	5.80	.6	1.5	.3	1.86	1.00	.79	1	2	1	1.5	2	0	1	2	1	
14 R. <i>peruensis</i>	16.60	4.10	4.50	.7	1.1	.4	1.82	1.39	.70	2	2	2	1.5	1	0	1	1	1	
15 R. <i>brasiliensis</i>	21.65	5.30	5.60	.7	1.3	.4	1.46	1.10	.95	1	2	2	1	2	0	1	1	1	
min.	9.10	2.50	2.80	.6	1.1	.3	.89	.85	.68	1(33)	-	-	1(82)	1(64)	1(25)	0(100)	-	1(67)	0(43)
max.	23.20	5.85	6.60	1.0	2.7	.6	1.95	1.39	.95	2(80)	2(79)	2(25)	1.5(50)	2(67)	1(11)	1(65)	2(56)	1(64)	
<i>hamatus</i> -group																			
3 R. <i>rufiventris</i>	13.60	3.00	3.30	.7	1.5	.4	1.76	1.16	1.02	2	2	2	1	2	1	2	2	0	
10 R. <i>hamatus</i>	15.45	4.05	4.60	.7	1.3	.4	1.85	1.32	1.06	1	2	2	1	2	1	1	2	0	
7 R. <i>grandis</i>	20.15	5.00	5.50	.8	1.5	.2	1.66	1.90	1.27	1	1	2	1	1	1	2	1	1	
8 R. <i>limai</i>	23.65	5.30	5.45	1.0	2.1	.4	2.20	1.40	.90	1	1	2	1.5	1	1	1	2	0	
9 R. <i>thoracicus</i>	18.80	4.35	5.15	.3	1.8	.3	1.48	1.20	.69	1	1	2	1.5	1	1	1	2	1	
19 R. <i>angulatus</i>	22.10	5.05	5.50	.8	1.8	.6	1.66	1.12	.93	1	1	2	1	2	1	1	2	1	
11 R. <i>biguttatus</i>	20.15	5.00	5.50	.3	1.9	.5	1.80	1.06	.78	1	1	1	1.5	2	1	1	2	0	
6 R. <i>arcuiger</i>	13.80	3.45	3.80	.7	2.4	.2	.95	.70	.70	2	2	1	1.5	2	1	1	2	1	
min.	13.60	3.00	3.30	.3	1.3	.2	.95	.70	.70	1(67)	1(100)	1(18)	1(36)	1(75)	-	1(35)	1(33)	0(57)	
max.	23.65	5.30	5.50	1.1	2.4	.6	2.20	1.90	1.27	2(20)	2(21)	2(75)	1.5(50)	2(33)	1(89)	2(100)	2(44)	1(36)	

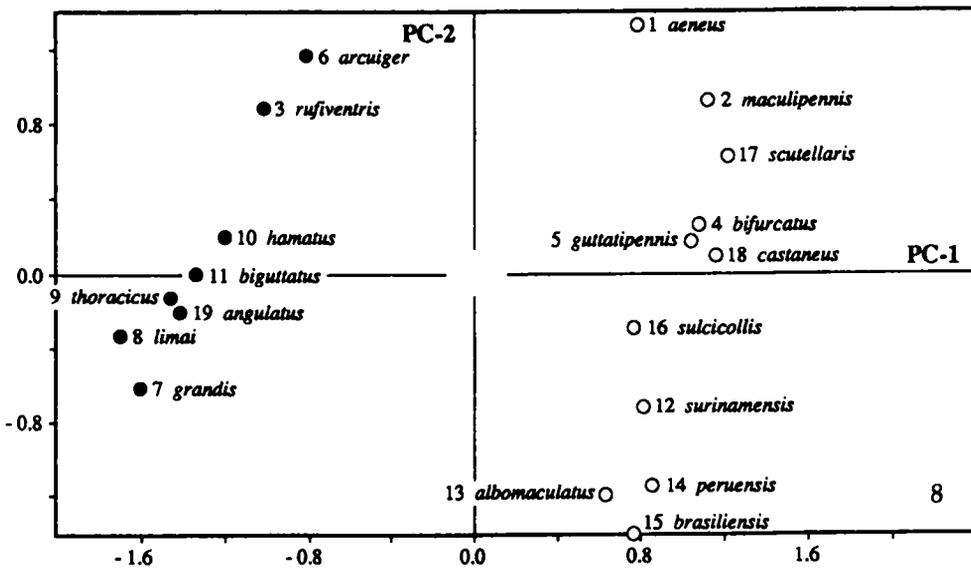
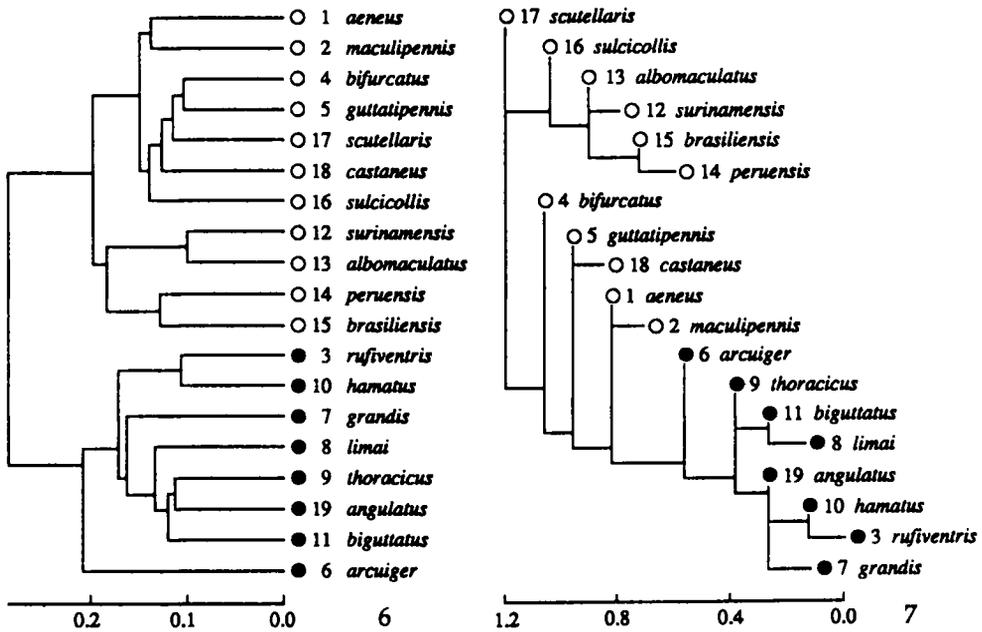


Fig. 6. UPGMA dendrogram ($CC_{sim/ult} = 0.91$) of the combination of the five D-matrices used in figs. 1-5 into a Distance Matrix of All Factors (DAF).

Fig. 7. Minimal Spanning Tree of the DAF.

Fig. 8. Scatterplot of the members of the *scutellaris*- (o) and *hamatus*-group (•), according to the first two main axes of a Principal Coordinate analysis (PCO). The first two main axes of the PCO explain 47 and 17% of the total variation, respectively.

between some similarity matrices and the classifications is that there is much difference in information of the character complexes. Next to this also the low dimensionality or amount of characters may play a role in the variability of the overall similarity.

When the five dendrograms, which contain the optimal structure derived from the similarity matrix by an agglomerative strategy and the UPGMA criterion, should be combined into a single classification, this would give no solution for most of the branches. Moreover, the result does not match the goal of performing a phenetic classification with high predictive value (Sneath & Sokal, 1973; Sneath, 1991). Therefore, another approach is used to arrive at a general classification, i.e. by not combining the OTUs in a single classification on the level of the dendrograms but on the next lower and more general level of the similarity matrices. As explained above, each similarity matrix is considered as the description of the similarity between the OTUs on the basis of a single factor.

Table 3 shows that of the cophenetic correlation between the five similarity matrices, which for most are very low, only those of the genitalia and, to a lesser degree, the characters of the body contain corresponding information. The combination of the various factors produces a similarity matrix (DAF) which displays a general increase of cophenetic correlation with all five data sets. It furthermore contains sufficient information to demonstrate the subdivision of the various species into the two main taxonomic groups (fig. 6). However, the classification of the species within these groups, however, remains inconsistent.

In addition to the increased cophenetic correlation between the DAF and the five similarity matrices the correlations of the ultrametric matrices of the various UPGMA dendrograms show a similar increase of affinity with the UPGMA dendrogram of the DAF. A Minimal Spanning tree (fig. 7), and a PCO scatterplot (fig. 8) of the DAF also demonstrate this gap between the distribution of the *R. hamatus*- and *R. scutellaris*-group members. It means that in order to obtain a phenetic classification with high information it seems reasonable to collect characters from several parts of the body, derive various aspects of information from them and combine these into a single generalized similarity matrix to be used for further taxonomical analyses.

Acknowledgements

This work was partially supported by a grant of the National Council of Scientific and Technological Research (CONICET) of Argentina.

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Received: 17.i.1994

Accepted: 24.i.1994

Edited: R. de Jong