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INTERSPECIFIC MORPHOMETRIC AFFINITIES IN *AMBRYSUS* (HEMIPTERA: NAUCORIDAE)

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Abstract.—Morphometric variation in 15 characters was assessed among adults of 22 species of *Ambrysus.* Generally, 10 individuals of each sex were measured for each species, although fewer than 10 specimens were available for some species. Because a multivariate analysis of variance revealed that interspecific differences were dependent on sex, subsequent analyses were conducted on males and females separately. All characters were individually significant in distinguishing among species based on univariate statistics. Moreover, each of the 22 species formed a species-specific cluster in multidimensional space (Discriminant Function Analysis) and was distinct from the others based on pairwise *F*-tests. With Principal Components Analysis, the first principal component was represented by positive loadings associated with aspects of length. Thus, most of the morphometric distinction among *Ambrysus* species is represented by factors associated with size. Five additional components were important (each component >0.5% of variation) and provided additional interspecific resolution based on shape. In general, we identified a group of 13 core species with similar shape, surrounded by 9 peripheral species. Clear distinction of the four currently-recognized subgenera did not occur, and the inclusion of additional species would likely blur these already tenuous distinctions. Moreover, continued recognition of current subgeneric groupings may represent an anachronism. Nonetheless, a number of *Ambrysus* species occupying currently-recognized infrageneric groups (*Acyttarus, Picrops, signoreti* group) do exhibit extreme morphologies, which may correspond to unusual habitats. Based on inconsistencies in morphometric affinities of other currently recognized taxa within the genus (subgenera *Syncollus* and *Ambrysus*), the small number of characters defining the subgenera, and wide ecological variation within the nominate subgenus, we recommend a phylogenetic analysis of the genus. A cladistic analysis of discrete characters is required to conclusively evaluate phylogenies and arrive at a natural infrageneric classification of *Ambrysus*.

Key Words: Naucoridae, *Ambrysus,* morphometrics, phenetics

The Naucoridae, or creeping water bugs, are predacious insects common in both temperate and tropical aquatic systems. The genus *Ambrysus* is one of the most species-rich in the family (Usinger 1946), although it is restricted to the New World. La Rivers (1971, 1974, 1976) listed 69 species in his catalog of the world naucorid fauna, and four additional species have been described (Polhemus and Polhemus 1981, 1983). Moreover, many undescribed species from Latin America and one from the western United States are represented in collections (J. T. Polhemus, pers. comm.). Ecologically,

Table 1. Naucorid taxa[a] used in morphometric analyses; asterisk indicates member of *signoreti* group.

Picrops
Ambrysus usingeri La Rivers (A)
Acyttarus
Ambrysus funebris La Rivers (B)
Syncollus
Ambrysus circumcinctus Montandon (C)
Ambrysus maldonadus La Rivers (D)
Ambrysus montandoni La Rivers (E)
Ambrysus
Ambrysus arizonus La Rivers (F)
Ambrysus buenoi Usinger (G)
Ambrysus californicus Montandon (H)
Ambrysus crenulatus Montandon (I)
Ambrysus guttatipennis Stål (J)
Ambrysus inflatus La Rivers (K)
Ambrysus lunatus Usinger* (L)
Ambrysus mexicanus Montandon (M)
Ambrysus mormon Montandon (N)
Ambrysus occidentalis La Rivers* (O)
Ambrysus parviceps Montandon (P)
Ambrysus portheo La Rivers* (Q)
Ambrysus pudicus Stål (R)
Ambrysus pulchellus Montandon (S)
Ambrysus puncticollis Stål (T)
Ambrysus thermarum La Rivers (U)
Ambrysus woodburyi Usinger (V)

[a] Letter following species corresponds with code in PCA diagrams (see Fig. 1).

species of *Ambrysus* are diverse, occurring in habitats ranging from among rocks in swift current of cold montane streams (*A. thermarum* La Rivers), to among algae and submerged vegetation of warm pools (e.g. *A. portheo* La Rivers).

Ambrysus has been classified into four subgenera on the basis of relatively few characters (see La Rivers 1965). The subgenera *Acyttarus* and *Picrops* are monotypic, *Syncollus* contains 10 species, and the remaining 61 species compose the nominate subgenus. Because of the tremendous disparity in the number of species defining these subgenera, and wide ecological variation in the species-rich nominate subgenus, the evolutionary significance of the currently established subgeneric taxa appears equivocal. In fact, La Rivers (1965) questioned the phylogenetic accuracy of the entire subfamily Ambrysinae because 73 of the 77 species described at that time were in the genus *Ambrysus*. Subsequently, Ambrysinae was downgraded to tribal rank (Popov 1970) and transferred to the subfamily Cryphocricinae (Štys & Jansson 1988).

No formal taxa above species are recognized within subgenera. However, poorly-defined groups [e.g. *pudicus* group (La Rivers 1951), *signoreti* complex (Usinger 1946)] have been referenced in the literature. Within the subgenus *Ambrysus*, the species in the *signoreti* group are ecologically distinct, commonly inhabit marginal areas of streams, and may occur in pooled water that is discontinuous from the main lotic channel.

Relatively few external morphological characters have been used to distinguish among species of *Ambrysus*, other than those associated with genitalic segments. Nonetheless, interspecific differences are evident that relate to shape. In this study, we addressed the phenetic affinities of species of *Ambrysus* to determine if patterns of morphometric similarity (specifically, shape) emulate currently accepted infrageneric taxonomy.

Materials and Methods

A suite of 15 external mensural characters (body length and width; head length and width; synthlipsis; pronotal length; lengths of pro-, meso-, and metathoracic femur, tibia, and tarsus), previously determined to be effective in discriminating among naucorid taxa (Sites and Willig 1994), was measured for adult specimens of 22 species of *Ambrysus* (Table 1). Body length was measured from the tip of the labrum to tip of the abdomen; body width, head length, head width, and all leg segments were longest distances; pronotal length was measured along the midline. Meso- and metanotal lengths were not included because it is difficult to obtain accurate measurements without dissection. Each of these nota subducts below the preceding notum, and the visible length is variable and dependent on the degree of thoracic flexion. Generally, 10 specimens of each species were measured; however, for several species, fewer than 10 specimens were available. All data were transformed to natural logarithms to more effectively evaluate the contribution of shape in defining interspecific differences. Voucher specimens are deposited in the Wilbur R. Enns Entomology Museum, University of Missouri-Columbia.

Two-way multivariate analysis of variance (MANOVA) was performed to determine whether the character suite could discriminate among species and between sexes. Because a significant species-sex interaction was detected, sexes were considered separately in subsequent analyses. Univariate analyses of variance (ANOVAs) were performed to assess the individual contribution of particular characters to interspecific distinctions. Discriminant function analysis (DFA) simultaneously maximized the differences among species and minimized intraspecific variation among individuals by altering the linear combination of variables on each of a number of orthogonal axes. Pairwise *F*-tests associated with DFA determined which species significantly differed from each of the other species. The subsequent classification phase of DFA then assigned each specimen to a taxon based on the linear combination of variables from each discriminant function axis. Percent of correct assignments may be used as a separate measure of morphometric distinction among taxa. Because DFA reconstitutes the variables to maximize differences among taxa, natural relationships can be contorted in multidimensional space. In contrast, principal components analysis (PCA) is a data reduction technique that retains distance relations among individuals in multidimensional space and disregards group affiliations.

Results and Discussion

A very highly significant two-way interaction (MANOVA, $P < 0.001$) was detected between species and sex, and for each main effect. Thus, sexes were considered separately in subsequent analyses. With ANOVA, all but four univariate characters (pronotum length, synthlipsis, protarsus length, and mesotibia length) were very highly significant ($P < 0.001$) for the interaction between species and sex. Only profemur length was not significant in distinguishing between sexes. Each character separately was very highly significant ($P < 0.001$) in distinguishing among species. Thus, this character suite is diacritical in distinguishing among congeners and reinforces the conclusions of Sites and Willig (1994) that this character suite effectively discriminates among species groups of Naucoridae.

Pairwise interspecific *F*-tests associated with DFA resulted in very highly significant differences ($P < 0.001$) between each possible species pair. These results reveal that each species of *Ambrysus* is morphometrically distinct from each of the other analyzed species. Without exception, the classification phase of DFA assigned each individual to the correct species within each sex. Intraspecific morphometric variation was considerably less than interspecific variation, and each species group was exclusive of all other groups.

Principal components analysis effectively disassociated aspects of size (PC 1) and shape (other axes) from the total morphological variation among individuals. Loading coefficients of all characters were positive on PC 1 (Table 2). The high loadings for leg lengths and body length suggest that this factor is associated strongly with size (specifically length elements), and accounted for 85.9% of the interindividual variation. Five additional axes were considered important,

Table 2. Coefficients and percentages of total- and shape-related variance for each of six principal components. Most important loadings for PC 1–4 appear in boldface.

Character	Principal Component Factor					
	1	2	3	4	5	6
Protibia length	**0.952**	0.224	0.137	0.091	−0.021	0.056
Profemur length	**0.850**	0.399	0.257	0.165	−0.023	0.108
Mesotibia length	**0.841**	0.402	0.221	0.257	0.067	−0.024
Mesofemur length	**0.825**	0.406	0.237	0.229	0.190	0.027
Metatibia length	**0.750**	0.490	0.264	0.278	0.182	−0.059
Metafemur length	**0.740**	0.527	0.256	0.219	0.231	−0.024
Body length	**0.720**	0.556	0.259	0.203	0.205	0.084
Synthlipsis	0.342	**0.816**	0.359	0.247	−0.103	−0.099
Head width	0.505	**0.785**	0.263	0.127	0.099	0.129
Head length	0.519	**0.723**	0.344	0.234	0.083	0.097
Body width	0.570	**0.696**	0.293	0.138	0.257	−0.038
Metatarsus length	0.391	**0.673**	0.274	0.418	0.352	0.079
Pronotum length	0.571	**0.601**	0.338	0.295	0.061	0.303
Protarsus length	0.256	0.352	**0.873**	0.170	0.065	0.027
Mesotarsus length	0.422	0.515	0.396	**0.623**	0.048	0.030
% Variance (total)	85.9	6.7	2.6	1.6	1.2	0.9
% Variance (shape)	—	47.5	18.4	11.3	8.5	6.4

each accounting for at least 0.5% of the variation and included aspects of shape in addition to size. Of these five "shape" axes, PC 2 accounted for 47.5% of the shape-related variation, with high character loadings for head length and width, body width, synthlipsis, pronotum length, and metatarsus length. Factors three and four included high loadings for lengths of protarsus and mesotarsus, respectively; whereas factors five and six were each characterized by many characters whose loadings were approximately equal in magnitude.

Despite significant sexual dimorphism in all species of *Ambrysus*, interspecific patterns in morphology (shape) are similar in males and females based on PC 2 through 4 (Fig. 1). Patterns of morphological dispersion, based on continuous characters, do not parallel the composition of the four currently recognized subgenera, which have been erected primarily on the basis of similarity in discrete morphological characters. Rather, our analyses identified a core of species with relatively similar morphologies, with nine species (*A. circumcinctus, A. crenulatus, A. funebris, A. inflatus, A. lunatus, A. occidentalis, A. parviceps, A. portheo,* and *A. usingeri*) dispersed about the periphery of the core group variously representing more extreme morphologies. Unusual shapes do characterize the monotypic subgenera *Picrops* and *Acyttarus*, as well as the *signoreti* group of the subgenus *Ambrysus*. However, the current constituents of these groups are not unique in that regard. For example, three species [*A.* (*Syncollus*) *circumcinctus, A.* (*Ambrysus*) *crenulatus,* and *A.* (*Ambrysus*) *parviceps*] are closely associated with *A.* (*Acyttarus*) *funebris* in morphological space. Two species in the subgenus *Syncollus* (*A. maldonadus* & *A. montandoni*) are clearly within the core group of *Ambrysus*, and *A.* (*Ambrysus*) *crenulatus* is more associated with taxa outside the subgenus *Ambrysus*.

Based on evaluation of shape, there are at best four morphological groups: the central core of 13 species and three peripheral associations (*A. inflatus, A. lunatus, A. oc-*

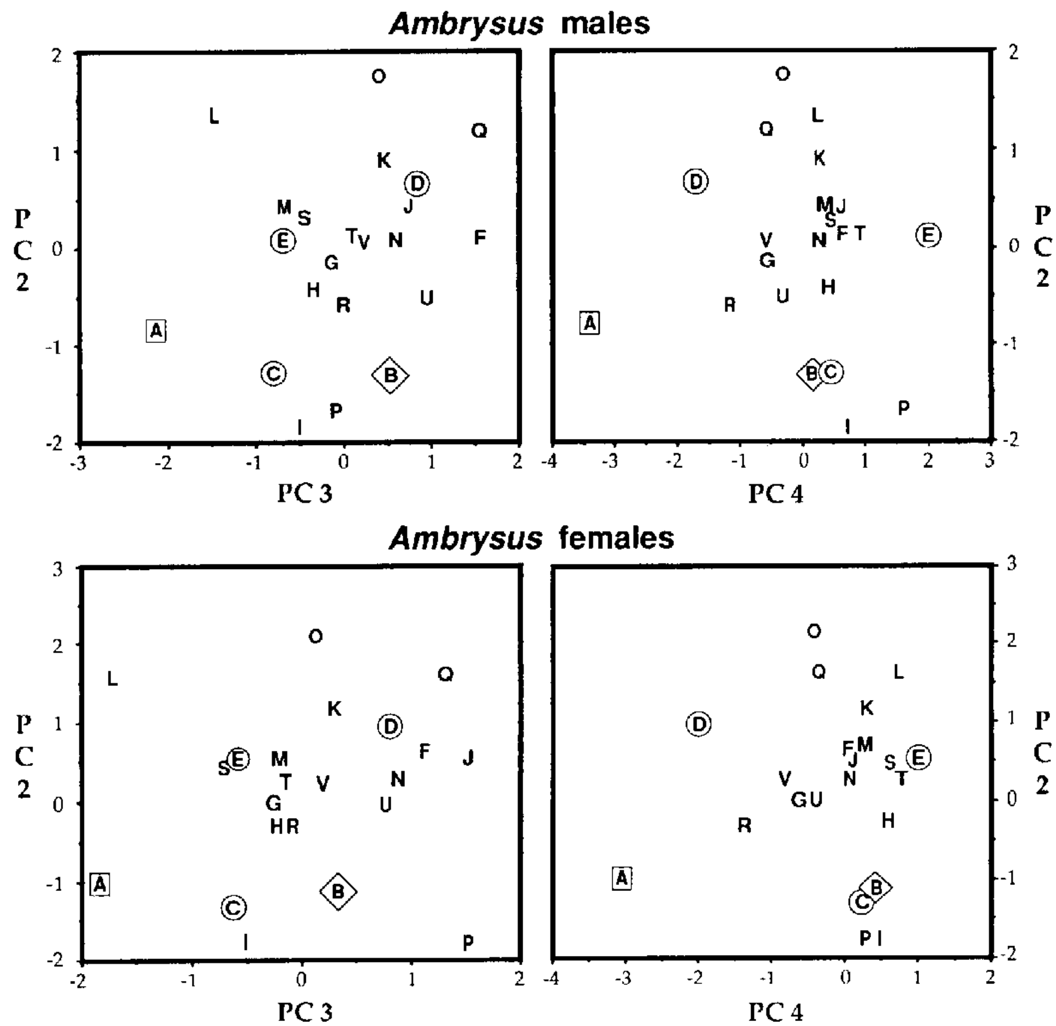

Fig. 1. Results are presented separately for naucorid males and females; nonetheless, relative positions of species centroids are similar for each. Group centroids are represented by letters and subgenera by shapes: circle, *Syncollus*; diamond, *Acyttarus*; rectangle, *Picrops*; none, *Ambrysus*. Letter abbreviations are given in Table 1. To facilitate visualization of many centroids, intraspecific dispersion of individuals is not depicted.

cidentalis, A. portheo; A. circumcinctus, A. crenulatus, A. funebris, A. parviceps; and *A. usingeri*). Examination of the morphological relationships of other *Ambrysus* is likely to further blur the already tenuous distinction among the groups. To some extent, peripheral location in morphological space appears to be related to extreme environmental conditions. For example, *A. funebris* is restricted to Furnace and Cow creeks in Death Valley where temperatures are high (36° C) (La Rivers 1949). *Ambrysus inflatus, A. lunatus, A. occidentalis,* and *A. portheo* inhabit lotic and lentic littoral zones, and forage in patches of aquatic macrophytes. Here currents are slow to non-existent and temperatures are high in the summer. Poor knowledge of the autecology of the other peripheral species prevents a more inclusive evaluation of the degree to which extreme morphology may relate to unusual habitats in Naucoridae.

Current subgenera were erected based on similarities in discrete character states and include two monotypic subgenera and a species-rich subgenus. However, our continuous-state characters do not support the current subgeneric associations. Further, the systematic value of currently recognized subgenera is compromised because they are not based on a phylogenetic approach, and continued recognition of the four established subgenera of *Ambrysus* may in fact represent an anachronism. This would best be resolved with a phylogenetic analysis based on discrete-state characters for which polarities can be established (Hennig 1966).

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