Efficacy of Mensural Characters in Discriminating Among Species of Naucoridae (Insecta: Hemiptera): Multivariate Approaches and Ontogenetic Perspectives

ROBERT W. SITES[1] AND MICHAEL R. WILLIG[2]

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ABSTRACT The efficacy of a suite of 15 morphometric variables was evaluated as a species-specific discriminator throughout the ontogeny of eight species of New World Naucoridae. In concert, multivariate analysis of variance (MANOVA), discriminant function analysis, and univariate analysis of variance (ANOVA, a posteriori contrasts) statistical tests demonstrated that each species is morphometrically distinguishable from all other species within age–sex groups. Although females are larger than males with respect to all characters that exhibit significance from a univariate perspective, the magnitude of dimorphism in adults is species-specific (significant species by sex interaction in the two-way MANOVA and in 7 of 15 two-way ANOVAs). Assessment of morphological trajectories during ontogeny (vectors connecting centroids for age–sex groups in each species) suggests that morphogenesis can provide critical diagnostic information of systematic importance. On average, only 8.1 characters per instar (15 maximum) differed significantly between *Usingerina moapensis* La Rivers and *Limnocoris lutzi* La Rivers, whereas the congeners *Limnocoris* sp. and *L. lutzi* were different on average for 14.3 characters per instar. Moreover, considerable morphometric overlap (principal components analysis) occurred between *U. moapensis* and *L. lutzi* throughout ontogeny. On the basis of these and other factors, the genus *Usingerina* La Rivers is placed in synonymy with *Limnocoris* Stål.

KEY WORDS Naucoridae, morphometrics, developmental trajectories

THE NAUCORIDAE, or creeping water bugs, are predacious aquatic Hemiptera that achieve their highest diversity in the tropics. The currently recognized higher classification of New World naucorids has received recent systematic contributions from La Rivers (1951, 1953, 1971, 1974, 1976), Polhemus (1991), and Usinger (1946, 1947) and was included in a world checklist of the Nepomorpha at and above the generic level (Štys & Jansson 1988). Although generic and specific groups are recognized for some of the New World fauna, relationships still are poorly understood, and contemporary systematic specialists generally agree that generic revisions are needed in the Naucoridae.

A modicum of information is available concerning naucorid morphology, and molecular studies of these taxa have not been reported. Most descriptive morphological data are associated with systematic contributions that focus on alpha taxonomy. In addition, naucorid morphology has been treated by Parsons (1966, 1974a, b), Parsons & Hewson (1974), and Sites (1990a). No work has addressed the utility of particular morphological characters as diagnostic tools in systematic studies of Naucoridae.

Specific and generic diagnoses within the Naucoridae usually have been based on a small number of gross morphological features of adults. Immature stages have been described for only a few New World naucorids (*Ambrysus lunatus* Usinger, Sites & Nichols [1990]; *A. mormon* Montandon, Usinger [1946]; *Cryphocricos hungerfordi* Usinger, Sites & Nichols [1993]; *Pelocoris femoratus* [Palisot de Beauvois], Torre Bueno [1903], Hungerford [1927] as *P. carolinensis* [see La Rivers 1948], and McPherson et al. [1987]; *Pelocoris poeyi* [Guérin Méneville], Sites [1991]; and several species of *Cryphocricos*, Lopez Ruf [1991] and *Pelocoris*, Lopez Ruf [1992] from Argentina). Several of these descriptions (*A. lunatus*, *C. hungerfordi*, *P. femoratus*, *P. poeyi*) have been based, in part, on a limited, quantitative assessment of a standard suite of morphological characters that have been used in systematic evaluations of a variety of other aquatic and terrestrial Hemiptera. Although it has been assumed that these characters generally are useful in describing immature stages, no study has verified that these characters are diacritical in diagnosing species.

Conceptual Background. Phenotypic variation in a population is the raw material on which

[1] Wilbur R. Enns Entomology Museum, Department of Entomology, University of Missouri, Columbia, MO 65211.
[2] Ecology Program, Department of Biological Sciences and The Museum, Texas Tech University, Lubbock, TX 79409–3131.

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natural selection operates. In general, the efficacy of selection is predicated on the degree to which phenotypic variation is a consequence of genetic variation (Falconer 1960). For characters that vary in a continuous fashion and are inherited in a polygenic fashion, the correspondence between phenotype and genotype is a product of direct selection on the character in question, as well as the indirect effects of selection on a suite of other phenotypic characters to which the character in question is linked through epistatic or pleiotropic gene interactions (Pearson 1903, Lande & Arnold 1983). As a consequence, mensural characters exhibit different degrees of intercorrelation, simultaneously representing challenges for analyses of mean differences among populations (Willig et al. 1986, Corruccini 1987, Willig & Owen 1987) while potentially offering additional information (e.g., the structure of character correlation matrices) on which to base systematic decisions (Corruccini 1992, Willig & Hollander 1995). The former has long been a concern of phenetics (Pimentel 1979, 1992; Reyment et al. 1984), whereas the latter has become a growing focus of contemporary morphometrics (Lande 1979, Bookstein et al. 1985, Crespi 1992). A growing consensus is emerging that some multivariable morphometric analyses can provide phylogenetic resolution because, as with cladistic methods, they evaluate partitioned variance and reflect polarity or apomorphic character states (Sorensen 1987a, b; 1992; Foottit 1992; Foottit & Sorensen 1992; Sorensen & Foottit 1992). Although a wealth of evidence suggests that developmental regulation has considerable effect on phenotypic variation (Raff & Kaufman 1983), considerable controversy surrounds issues about the manner in which ontogenetic pathways translate intraspecific variation into interspecific evolution (Cock 1966, Gould 1977, Lande 1979, Zelditch et al. 1993). Much of the theory and its linkage to principles of quantitative genetics are discussed from a variety of perspectives elsewhere (Lande 1979, Lande & Arnold 1983). Nonetheless, it remains to be documented if developmental trajectories, as evidenced by correlated morphometric characters, can provide resolution to systematic questions.

The objective of this study was to validate the interspecific diagnostic utility of a suite of 17 mensural characters that have been used in instar-specific naucorid descriptions, and to evaluate morphometric trajectories during ontogeny. To address these objectives, eight New World species representing five genera and three subfamilies were chosen for morphometric analysis. Taxa were selected to maximize diversity within two constraints: representation by two or more species within several genera, and availability of a sufficient number of individuals of each instar to facilitate quantitative analyses.

Table 1. Classification of species of Naucoridae used in morphometric analyses (*sensu* Stys & Jansson 1988) and collection localities

Taxa	Locality
Cryphocricinae	
Cryphocricini	
Cryphocricos hungerfordi Usinger	Texas: Kimble County
Ambrysini	
Ambrysus circumcinctus Montandon	Texas: Kimble County
Ambrysus lunatus Usinger	Texas: Kimble County
Limnocorinae	
Limnocoris lutzi La Rivers	Texas: Kimble County
Limnocoris sp.	Ecuador: Napo Province
Usingerina moapensis La Rivers	Nevada: Clark County
Naucorinae	
Pelocoris femoratus (Palisot de Beauvois)	Illinois: Union County
Pelocoris poeyi (Guérin Méneville)	Ecuador: Napo Province

Materials and Methods

Specimens of eight species of Naucoridae (Table 1) were obtained throughout the United States and in Amazonian Ecuador, and are deposited in the Wilbur R. Enns Entomology Museum, University of Missouri-Columbia. Pending systematic revisions in the genus, a specific name may not be assigned to specimens of *Limnocoris* from Ecuador (Sites 1990b); as a consequence, we refer to them as *Limnocoris* sp. Morphometric data for 15 characters (Table 2) were obtained from 10 individuals of each group (instars one through five, adult males, and adult females). The only exception was the second instar of *Usingerina moapensis* La Rivers, which was represented by six specimens. 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 greatest distances; pronotum length was measured along the midline (see Sites & Nichols 1990). 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. Our measurements estimated aspects of shape by including various body length and width characters, as well as measurements of leg segments. In all cases, characters were measured with an ocular micrometer and subjected to a series of multivariate and univariate analyses (SPSS 1988) to establish the efficacy of these characters in distinguishing among species within age groups.

To avoid problems associated with character correlation, our approach was to establish the existence of statistically significant differences among groups based on multivariate analyses (Willig et al. 1986, Willig & Owen 1987) and to

quantify the contribution of particular characters to group differences based on both multivariate and univariate analyses. For instars one through five separately, a one-way multivariate analysis of variance (MANOVA) was performed to determine if significant differences exist among species based on the suite of 15 mensural characters. Because intersexual variation could obscure the detection of morphological differences among species, two-way MANOVA (species and sex) was performed on adults.

When a MANOVA was significant, corresponding one- or two-way analyses of variance (ANOVAs) subsequently were performed for each character alone to evaluate its potential contribution to differences among the eight species. To avoid the biases of overestimating the significance of particular characters that compose a large suite of attributes (Holm 1979, Rice 1989), we applied the sequential Bonferroni test to each univariate character before ascribing statistical significance. For each character, pair-wise differences between species were evaluated by the Student–Neuman–Kuels test (Sokal & Rohlf 1981). Characters with high discriminatory ability should yield significant differences in most pair-wise comparisons of species (28 comparisons compose the possible pair-wise contrasts involving eight species).

Discriminant function analysis (DFA) simultaneously maximizes differences among species and minimizes intraspecific variation among individuals. This assessment provides an efficacious algorithm to distinguish among a priori groups. In addition, pair-wise F-tests associated with DFA were used to determine patterns of interspecific morphological differentiation. More specifically, the overall interspecific discriminatory power of each character was estimated as the sum of the product of its squared correlation with a particular discriminant function and the percentage of variation associated with that axis (Lacher & Willig 1993, Willig & Hollander 1994). In this fashion, a single index for each age group estimated the overall contribution of a character to species-specific differences.

The degree to which variation among individuals within a species is expressed as species-specific differences can be visualized with principal components analysis (PCA). If the character suite is effective in discriminating among taxa, individuals of the same species should form distinct clusters in multidimensional space. If the clusters of species overlap greatly, then the suite of mensural characters may not be sufficiently diagnostic of taxonomic affiliations. The classification phase of DFA also can address the utility of morphological characters in discriminating among species. More specifically, the proportion of individuals classified to the appropriate species is a measure of the diagnostic value of the character suite.

Regardless of taxon or developmental stage, a single PCA on the suite of 15 mensural characters was conducted on all naucorid specimens to evaluate interspecific similarities and differences among morphometric trajectories during ontogeny. A morphometric trajectory comprises the vector that passes through the centroid of each immature stage, and bifurcates between fifth instar and adults, terminating in adult male and female groups. We chose PCA rather than DFA to define morphometric trajectories because we did not wish to distort phenetic space so as to optimize differences in taxa, per se. Our approach recognized groups based on taxonomic affiliation and developmental stage; consequently, the apomorphic nature of vectors derived by DFA (Sorensen & Foottit 1992) would be confounded by the indiscriminant attempt to distinguish taxa and developmental stages simultaneously. Herein, we contend that the trajectory of morphogenesis, rather than the nature of morphometric affinities among groups, can provide systematic resolution. Because of phylogenetic constraints during ontogeny, taxa with similar morphological trajectories are more likely to be allied with each other than would be taxa with dissimilar trajectories. Most of the interindividual variation existed as differences among instars or among species; consequently, only group centroids for each instar of each species were included in multivariate representations of morphological change during ontogeny.

Results

Highly significant differences ($P < 0.001$) existed among species within each immature age class based on the multivariate analyses of 15 morphometric variables (Table 2). Moreover, highly significant differences ($P < 0.001$) were detected for the interaction between sex and species in the two-way MANOVA for adults; morphometric differences among species depend on the sex of the individuals. Significance for each of the main effects (species and sex) in the MANOVA and examination of the means for each character strongly suggest that the interaction was one of magnitude rather than direction. Females were consistently larger than males, but the magnitude of dimorphism was species-specific.

From the univariate perspective, highly significant differences ($P < 0.001$) consistently existed among species within each immature age class for each character; these effects remained significant ($\alpha = 0.05$) after adjustments based on the sequential Bonferroni test (Table 2). Similarly, significant differences occurred among species in adults for all characters (Table 2). For all 15 characters, except body length and body width, the differences among species were consistent regardless of sex. Although significant, the two-

Table 2. Significance levels (*P*) of the character suite and each character separately in distinguishing among eight species of naucorids

Statistical test	One-way comparisons (nymphal instars[a,b])	Two-way comparisons (adults)[b]		
		Species	Sex	Species by sex
MANOVA	<0.000	<0.001	<0.001	<0.001
ANOVA				
Body length	<0.001	<0.001	<0.001	<0.001
Body width	<0.001	<0.001	<0.001	<0.001
Head length	<0.001	<0.001	<0.001	0.523NS
Head width	<0.001	<0.001	<0.001	0.011NS
Synthlipsis	<0.001	<0.001	0.004	0.038NS
Pronotum	<0.001	<0.001	<0.001	0.035NS
Profemur length	<0.001	<0.001	<0.001	0.428NS
Protibia length	<0.001	<0.001	<0.001	0.098NS
Protarsus length	<0.001	<0.001	<0.001	0.999NS
Mesofemur length	<0.001	<0.001	<0.001	0.396NS
Mesotibia length	<0.001	<0.001	<0.001	0.373NS
Mesotarsus length	<0.001	<0.001	0.012	0.128NS
Metafemur length	<0.001	<0.001	<0.001	0.005NS
Metatibia length	<0.001	<0.001	<0.001	0.094NS
Metatarsus length	<0.001	<0.001	0.001	0.015NS

[a] Identical statistical tests were performed for each of the five instars separately and resulted in identical levels of significance.
[b] Sequential Bonferroni tests within a column for the 15 univariate characters corroborated significant ($\alpha = 0.05$) group differences in all situations except those marked NS.

way interaction that was detected for body length and for body width was one of magnitude rather than direction. The difference between sexes varied among species; however, females were larger than males with respect to each character.

A posteriori comparisons within age groups performed on all possible pairs of species resulted in significance for each case (*F*-test, $P < 0.05$). Clearly, based on DFA within each age group, each species was significantly different from all seven other species. Moreover, DFA within each age group was significant ($P < 0.05$) in accounting for >93% of the variation among species based on the first three canonical axes (loadings are listed in *Appendix 1*). Subsequent classification of individuals based on the linear combination of the original variables produced by DFA resulted in 100% correct assignment of individuals to the appropriate species.

Graphical results of PCA (Fig. 1) illustrate the morphological distinctiveness of naucorid taxa. Factor loadings for the first three axes are listed in *Appendix 2*. The degree of intraspecific dispersion within a species' cluster reflects the magnitude of intraspecific heterogeneity. Although the relative positions of species clusters varied throughout ontogenetic development, each cluster remained statistically distinct from all other species clusters within an age class. Nonetheless, high morphological similarity characterized *L. lutzi* and *U. moapensis* (species pair three and five) as well as *P. femoratus* and *P. poeyi* (species pair seven and eight) and was pervasive throughout ontogeny. Similarly, the distinctiveness of all other taxa was consistent regardless of age group or sex.

Clearly, most characters contain considerable diacritical information for these taxa throughout ontogeny (Tables 2 and 3). The few interspecific comparisons for which significance was not detected were usually between *U. moapensis* and *L. lutzi*, or between *P. femoratus* and *P. poeyi;* lack of significance indicates morphometric affinity between species pairs.

In the PCA performed on all stages, the first two principal components accounted for 96.1% of the variation among individuals, with the first and second components accounting for 89.6 and 6.5% of the variation, respectively. Because no other component accounted for 5% or more of the variation and each had an eigenvalue less than unity, we represent all ontogenetic trajectories in two-dimensional morphometric space (Fig. 2). Factor loadings for the first three principal components are listed in Table 4.

Discussion

Character Efficacy. General disagreement exists among systematists regarding the family-level treatment of Naucoridae. Various groups are either included with or restricted from Naucoridae; this has been cogently reviewed by Štys & Jansson (1988). We follow Štys & Jansson (1988) in treating Aphelocheiridae and Potamocoridae as families distinct from Naucoridae sensu stricto.

A traditional suite of mensural features often is used in descriptions of Hemiptera, although the diacritical nature of the characters is unsubstantiated. Herein, 15 of these morphological characters were tested and are diagnostic of interspecific differences for each instar. This assemblage

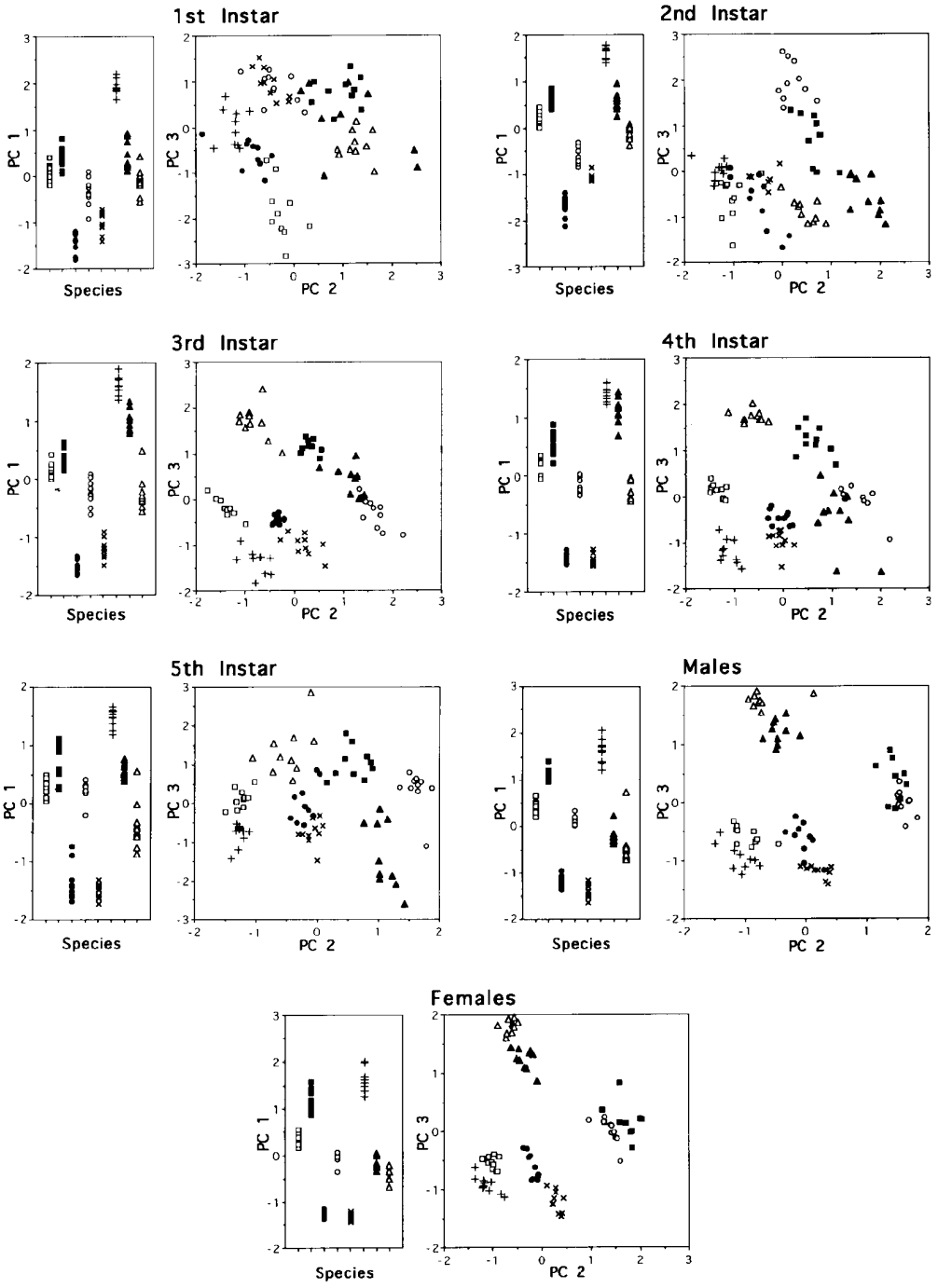

Fig. 1. Independent PCAs for each instar and sex of adult resulted in size-related variation represented primarily by PC 1 scores. Two-dimensional shape-related morphometric variation is represented by PC 2 by PC 3. Clusters of individuals representing eight naucorid species are distinctly separate from one another throughout ontogeny except for *P. femoratus and P. poeyi*, as well as *L. lutzi and U. moapensis*. □, *A. circumcinctus*; ■, *A. lunatus*; ●, *L. lutzi*; ○, *Limnocoris* sp.; ×, *U. moapensis*; +, *C. hungerfordi*; ▲, *P. femoratus*; △, *P. poeyi*.

Table 3. Number of pairwise interspecific contrasts within each age group (28 maximum) for which a particular character exhibited significance

Character	Instar					Adult
	1	2	3	4	5	
Body length	26	25	24	23	26	25
Body width	26	26	27	27	28	24
Head length	18	17	24	24	24	26
Head width	26	28	25	26	26	27
Synthlipsis	24	22	26	26	26	25
Pronotum	17	21	26	26	27	27
Profemur	25	24	25	27	27	24
Protibia	26	28	26	26	27	27
Protarsus	17	19	23	22	24	23
Mesofemur	24	25	25	25	24	26
Mesotibia	24	27	25	26	26	28
Mesotarsus	9	17	19	23	23	25
Metafemur	26	28	27	25	26	26
Metatibia	26	26	25	26	27	26
Metatarsus	27	26	26	25	25	27

Student–Neuman–Kuels test, $P \leq 0.05$.

Table 4. Factor loadings (correlations), eigenvalues, and explained variation on each of the first three axes of the principal components analysis involving all individuals regardless of instar, sex, or species (Fig. 2)

Character	Principal components		
	1	2	3
Body length	0.991	−0.029	−0.073
Body width	0.956	0.240	0.117
Head length	0.960	0.149	−0.070
Head width	0.910	0.359	−0.153
Synthlipsis	0.885	0.432	0.081
Pronotum length	0.943	0.092	−0.279
Profemur length	0.944	−0.287	−0.126
Protibia length	0.873	−0.466	−0.120
Protarsus length	0.890	−0.208	0.353
Mesofemur length	0.985	−0.153	0.013
Mesotibia length	0.952	−0.287	0.030
Mesotarsus length	0.984	0.010	0.033
Metafemur length	0.995	−0.004	0.064
Metatibia length	0.985	−0.132	0.052
Metatarsus length	0.935	0.292	0.086
Eigenvalue	13.440	0.955	0.303
Variance explained	89.600	6.467	2.013

of eight species was chosen to represent maximal taxonomic diversity (three subfamilies, five genera), as well as to evaluate differences among congeners within *Ambrysus*, *Limnocoris*, and *Pelocoris*. Because differences among all species regardless of generic association were evident, this suite of characters is effective in species-specific discrimination. Although some of the characters may be viewed as expressing redundant information, these characters may change in a species-specific fashion during ontogeny (e.g.,

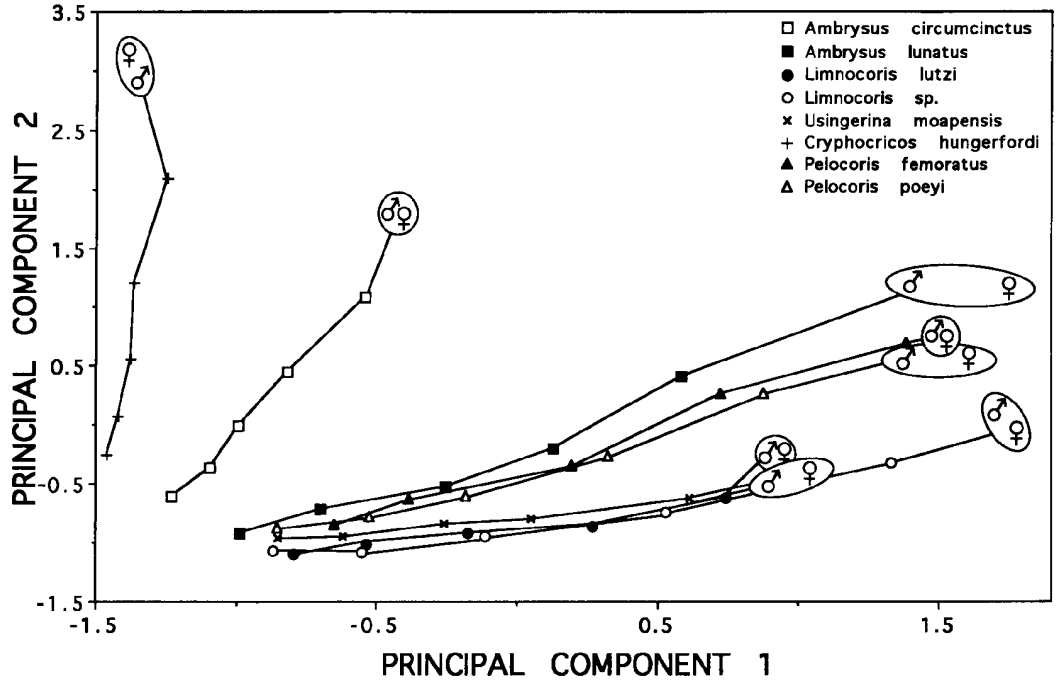

Fig. 2. For each naucorid species, the vectors connecting centroids (symbols) of instars in morphometric space defined by PCA represent ontogenetic trajectories. In *C. hungerfordi*, most of the variation during development is related to increases in body length and length of the appendages (trajectory parallels PC 2). In *A. circumcinctus*, variation during development includes those same increases, as well as changes in head length, head width, body width, synthlipsis, and pronotum length (PC 1). Most of the morphometric variation during ontogeny in the other six species is related to PC 1.

protarsus, mesofemur, and mesotibia are correlated with principal component two, along which *A. circumcinctus* and *C. hungerfordi* differentiate during development), thereby representing important aspects of systematic differentiation.

Systematic Considerations. *Ambrysus* is a diverse New World genus comprising 74 described species (Polhemus & Polhemus 1994, Sites & Willig 1994). The two species analyzed in this study (*A. circumcinctus* Montandon and *A. lunatus* Usinger) represent two of the four subgenera (*Syncollus* and *Ambrysus*, respectively). The morphometric distance separating these congeners is considerably greater than that between species representing different subfamilies; e.g., *A. lunatus* (Cryphocricinae) and *Limnocoris* sp. (Limnocorinae). This, and other evidence, e.g., only one or two characters supporting erection of the subgenera *Acyttarus* and *Picrops*, respectively (La Rivers 1965), suggests the need for systematic revision in *Ambrysus* based on phylogenetic methodologies. Moreover, given the variation among taxa, this character suite might prove valuable in phylogenetic analyses. If adequate outgroups to the Naucoridae can be identified and the morphometric data can be transformed by way of size-free (Sneath & Sokal 1973) or common-part-removed (Wood 1983) techniques, then valid phylogenetic analysis with morphometric variables is possible without deriving character polarities (Owen 1987). Either these or cladistic procedures should be performed to determine phylogenetic relationships within the genus *Ambrysus*.

Cryphocricos comprises 14 described species restricted to the New World. Currently, *Cryphocricos* is placed with *Procryphocricos* (Polhemus 1991) in the Cryphocricini, a tribe in the subfamily Cryphocricinae. Although the evolutionary relationships of the Cryphocricini with other taxa are unresolved, it may be most closely allied with members of the tribe Ambrysini (Usinger 1947). The morphometric similarity of *C. hungerfordi* and *A. circumcinctus* (Fig. 1) is consistent with this interpretation, although neither necessary nor sufficient to establish its validity. Of the taxa that we measured, *C. hungerfordi* appears to be most similar to *A. (Syncollus) circumcinctus* (Ambrysini) in terms of shared morphological attributes. Nonetheless, other candidate taxa, e.g., *Cataractocoris* (Cataractocorini) zand *Melloiella* (Ambrysini), as well as cladistic approaches should be considered before establishing systematic relationships based on morphology.

Morphological trajectories contain rich phylogenetic information reflecting the joint action of structural and regulatory genes (Raff & Kaufman 1983) during ontogeny. Indeed, modern interpretations of Haeckel's rule (ontogeny recapitulates phylogeny) are embedded in the inheritance of both regulatory and structural genetic elements. Allometry, both among instars within a species and among adults of different species in a higher taxon, is produced by alterations in the timing or duration of gene expression. Convergence results in similar morphologies among species that are derived from different genetic processes. Similar trajectories and morphologies throughout development are much less likely to be caused by convergence because of the number and types of genes required to orchestrate ontogenetic events. As such, changes during morphogenesis have the potential to provide considerable systematic resolution.

In morphometric analyses involving principal component analysis, shape is represented by the inclusion of both negatively and positively loaded characters on components two and higher. Here, the first two axes represent size-related features rather than shape, because all character loadings were positive (*Appendix 2*). More specifically, principal component 1 represents width-related features (synthlipsis, head width, and body width) as well as length elements. In contrast, principal component 2 represents body and appendage lengths without inclusion of any morphological aspects of width.

Three distinct sets of trajectories are apparent in morphological space defined by PCA: one each for *C. hungerfordi, A. circumcinctus,* and the remaining taxa (Fig. 2). The trajectory for *C. hungerfordi* is nearly vertical and achieves maximum separation of instars along principal component 2, with little differentiation along principal component 1. Several morphological features (e.g., synthlipsis, head width, and body width) of *C. hungerfordi* remain relatively narrow throughout ontogeny. Divergent trajectories are evident between *A. circumcinctus* and *A. lunatus,* further supporting our contention that generic revision is needed within *Ambrysus*. Unlike other naucorid taxa, *A. circumcinctus* exhibits appreciable morphological differentiation with respect to head and body width (principal component 1) as well as to body and appendage length (principal component 2). Developmental trajectories of all other naucorid species primarily reflect morphological differentiation of characteristics embodied in principal component 1. Trajectories for *P. femoratus* and *P. poeyi* are almost coincident throughout their length, suggesting close affinity and shared developmental constraints. Trajectories for the three species of Limnocorinae are similar during all immature instars. More specifically, the trajectory of *U. moapensis* closely approximates that of both *Limnocoris* sp. and *L. lutzi,* indicating the operation of similar genetic constraints on morphology. Because *Limnocoris* sp. attains a wider adult form than do either of the other two limnocorines, protracted development is evident with respect to principal component 1.

Status of *Usingerina*. The systematic status of the monotypic *U. moapensis* has been in question since its establishment. It was originally placed in its own tribe, the Usingerini. Nonetheless, since its establishment, this tribe has not been recognized in the literature, even in a catalog by its author (La Rivers 1971), and was formally synonymized by Štys & Jansson (1988). Retention of generic status has been questioned by several systematists. DeCarlo (1951) considered *Usingerina* to be a junior subjective synonym of *Limnocoris*, a contention subsequently supported by Nieser (1975); however, the proposed synonymy of DeCarlo (1951) was not formal and, consequently, not recognized by Polhemus & Polhemus (1988) or by Štys & Jansson (1988). Our morphometric analyses support synonymy, a contention shared by J. T. Polhemus (personal communication).

Wide pronotal and embolar flanges are among the morphological features given by La Rivers (1950) to distinguish *Usingerina* La Rivers from *Limnocoris* Stål. These structures presumably are adaptations of *U. moapensis* for existence in the thermal spring runoffs of southern Nevada, to which it is endemic. The wide lateral flanges are at least partially represented in our analyses by body width. In addition, an undescribed limnocorine from Colombia (collected by J. T. Polhemus) has similar embolar flanges; thus, this feature is not unique. Other external features including width of hemelytral membrane, antennal length, and hindwing length were also given as generic characteristics by La Rivers, but were not represented in our analyses. In the original description of *U. moapensis*, La Rivers (1950) presented comparative descriptive data with *L. signoreti* Montandon, geographically the closest-known limnocorine (Mexico). In 1957, *L. lutzi* La Rivers was described from Texas and may represent a limnocorine that is geographically and morphologically closer to *U. moapensis*. Unlike *L. signoreti*, *L. lutzi* possesses short hindwings, a feature which was given as diagnostic for the genus *Usingerina*. In addition, La Rivers (1957) described the embolium of *L. lutzi* as narrower than that of *L. signoreti*, thereby establishing interspecific variability in embolar expression within geographically proximate species of *Limnocoris*.

Usingerina moapensis and *L. lutzi* share similar morphometric attributes throughout development. The Student–Neuman–Kuels test detected an average of only 8.1 characters per instar that were significant in differentiating between these species. For other interspecific comparisons, the average number of characters that significantly distinguished between congeners was 12.4 (*Pelocoris*) and 14.1 (*Ambrysus*). In fact, the number of characters that was significant in distinguishing between the congeners *Limnocoris* sp. and *L. lutzi* was higher, averaging 14.3 characters per instar (15 maximum). Although these morphometric differences clearly support the specific distinction of *U. moapensis* from *L. lutzi*, they do not support retention of generic status for *Usingerina*. In addition, the synonymization of *Usingerina* with *Limnocoris* is supported by the results of PCA. In morphometric space, individuals of *U. moapensis* do not form a nonoverlapping cluster distinct from that comprising individuals of *L. lutzi* throughout ontogenetic development (Fig. 1). Although mean differences characterize this pair of species, those differences are small relative to interindividual variation and do not support generic recognition. In sharp contrast, clusters of *Limnocoris* sp. and *L. lutzi* are clearly distinguishable at each developmental stage, even though they are considered congeners.

We place *U. moapensis* in the genus *Limnocoris* for four reasons. First, overall morphological differences between *U. moapensis* and *L. lutzi* are less than those between other recognized species within *Limnocoris*, *Ambrysus*, or *Pelocoris*. Second, the short hindwings originally thought to be diagnostic of *Usingerina* occur in *L. lutzi*. Third, variability in embolar expression within *Limnocoris* encompasses that of *Usingerina*, and an undescribed species of *Limnocoris* from Colombia has embolar flanges similar to those of *U. moapensis*. Fourth, the morphometric trajectory of *U. moapensis* parallels those of *L. lutzi* and *Limnocoris* sp. and all three taxa exhibit similar patterns of morphological change during ontogeny, especially between immature instars. Other characters including male genitalic structure and prosternal carina morphology support synonymy (J. T. Polhemus, personal communication) as well. Therefore, we propose the following synonymy.

Limnocoris Stål 1858: 83. Type species by monotypy: *Limnocoris insignis* Stål 1858.

Usingerina La Rivers 1950: 368. Type species by original designation and monotypy: *Usingerina moapensis* La Rivers 1950. Synonymy tentatively proposed by DeCarlo 1951, supported by Nieser 1975. New Synonymy.

As such, *Usingerina* is a junior synonym of *Limnocoris*.

Prospectus. Morphometric characteristics, coupled with univariate and multivariate approaches, provide powerful tools in systematics if the phylogenetically useful information can be distinguished from uninformative variation (Wood 1983). Species of Naucoridae can be distinguished at all stages of development based on a suite of 15 morphological characters. Moreover, morphological trajectories during development may contribute to the arsenal of tools available in systematic research. The degree of interspecific morphological variation exhibited by Naucoridae and its diacritical nature suggest that a cladistic

approach to the revision of the family may provide a phylogenetically based classification of the group. We recommend the application of size-free or common-part-removed techniques as well as cladistic procedures to determine phylogenies within Naucoridae.

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References Cited

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, G. R. Smith & R. E. Strauss. 1985. Morphometrics in evolutionary biology. Spec. Publ. Acad. Natl. Sci. Philadelphia 15.

Cock, A. G. 1966. Genetical aspects of metrical growth and form in animals. Q. Rev. Biol. 41: 131–190.

Corruccini, R. S. 1987. Univariate versus multivariate morphometric variation: an alternative viewpoint. Syst. Zool. 36: 396–397.

1992. Aspects of covariance matrix heterogeneity in morphometrics. Int. J. Anthropol. 7: 51–60.

Crespi, B. J. 1992. Natural selection and morphometrics, pp. 55–64. *In* J. T. Sorensen & R. G. Foottit [eds.], Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales. Elsevier, New York.

DeCarlo, J. A. 1951. Género *Limnocoris* Stål (Hem. Naucor.). *Usingerina* Ira La Rivers igual a *Limnocoris* Stål; descripcion de especies nuevas y datos sobre otras poco conocidas. Mision Estudios Patologia Regional Argentina 15: 69–72.

Falconer, D. S. 1960. Introduction to quantitative genetics. Robert MacLehose, Glasgow.

Foottit, R. G. 1992. The use of ordination methods to resolve problems of species discrimination in the genus *Cinara* Curtis (Homoptera: Aphidoidea: Lachnidae), pp. 193–221. *In* J. T. Sorensen & R. G. Foottit [eds.], Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales. Elsevier, New York.

Foottit, R. G. & J. T. Sorensen. 1992. Ordination methods: their contrast to clustering and cladistic techniques, pp. 1–10. *In* J. T. Sorensen & R. G. Foottit [eds.], Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales. Elsevier, New York.

Gould, S. J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, MA.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Stand. J. Stat. 6: 65–70.

Hungerford, H. B. 1927. The life history of the creeping water bug, *Pelocoris carolinensis* Bueno (Naucoridae). Bull. Brooklyn Entomol. Soc. 22: 77–83.

Lacher, Jr., T. E. & M. R. Willig. 1993. Univariate and multivariate approaches to the analysis of ecotoxicological data, pp. 425–437. *In* R. J. Kendall & T. E. Lacher, Jr. [eds.], Wildlife toxicology and population modeling: Integrated studies of agroecosystems. Lewis, Chelsea, MI.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evolution 33: 402–416.

Lande, R. & S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37: 1210–1226.

La Rivers, I. 1948. A new species of *Pelocoris* from Nevada, with notes on the genus in the United States (Hemiptera: Naucoridae). Ann. Entomol. Soc. Am. 41: 371–376.

1950. A new naucorid genus and species from Nevada (Hemiptera). Ann. Entomol. Soc. Am. 43: 368–373.

1951. A revision of the genus *Ambrysus* in the United States (Hemiptera: Naucoridae). Univ. Calif. Publ. Entomol. 8: 277–338.

1953. The *Ambrysus* of Mexico (Hemiptera, Naucoridae). Univ. Kans. Sci. Bull. 35: 1279–1349.

1957. A *Limnocoris* for the United States (Hemiptera: Naucoridae). Pan-Pac. Entomol. 33: 71–75.

1965. The subgenera of the genus *Ambrysus* (Hemiptera, Naucoridae). Biol. Soc. Nev. Occas. Pap. 4: 1–7.

1971. Studies of Naucoridae (Hemiptera). Biol. Soc. Nev. Mem. 2: iii and 120.

1974. Catalogue of taxa described in the family Naucoridae (Hemiptera) supplement no. 1: corrections, emendations and additions, with descriptions of new species. Biol. Soc. Nev. Occas. Pap. 38: 1–17.

1976. Supplement no. 2 to the catalogue of taxa described in the family Naucoridae (Hemiptera), with descriptions of new species. Biol. Soc. Nev. Occas. Pap. 41: 1–17.

Lopez Ruf, M. L. 1991. El genero *Cryphocricos* en la Argentina (Hemiptera-Limnocoridae). Rev. Soc. Entomol. Argent. 49: 103–120.

1992. El genero *Pelocoris* Stål en la Argentina (Heteroptera-Limnocoridae). III. Descripcion de las ninfas. Rev. Soc. Entomol. Argent. 50: 353–365.

McPherson, J. E., R. J. Packauskas & P. P. Korch, III. 1987. Life history and laboratory rearing of *Pelocoris femoratus* (Hemiptera: Naucoridae), with descriptions of immature stages. Proc. Entomol. Soc. Wash. 89: 288–295.

Nieser, N. 1975. The water bugs (Heteroptera: Nepomorpha) of the Guyana region. Studies on the fauna of Suriname and other Guyanas no. 59. Foundation for Scientific Research in Surinam and the Netherlands Antilles, Utrecht.

Owen, R. D. 1987. Phylogenetic analyses of the bat subfamily Stenodermatinae (Mammalia: Chiroptera). Special Publication of The Museum, Texas Tech University, Lubbock.

Parsons, M. C. 1966. Studies on the cephalic anatomy of Naucoridae (Heteroptera). Trans. R. Entomol. Soc. Lond. 118: 119–151.

1974a. Anterior displacement of the metathoracic spiracle and lateral intersegmental boundary in the pterothorax of Hydrocorisae (Aquatic Heteroptera). Z. Morphol. Tiere 79: 165–198.

1974b. Modification of the intersegmental region in the pterothorax of *Cryphocricos* (Heteroptera: Naucoridae). Psyche 81: 42–50.

Parsons, M. C. & R. J. Hewson. 1974. Plastral respiratory devices in adult *Cryphocricos* (Naucoridae: Heteroptera). Psyche 81: 510–527.

Pearson, K. 1903. Mathematical contributions to the theory of evolution. XI. On the influence of natural selection on the variability and correlation of organs. Philos. Trans. R. Soc. Lond. A 200: 1–66.

Pimentel, R. A. 1979. Morphometrics, the multivariate analysis of biological data. Kendall/Hunt, Dubuque, IA.

1992. An introduction to ordination, principal components analysis and discriminant analyses, pp. 11–28. *In* J. T. Sorensen & R. G. Foottit [eds.], Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales. Elsevier, New York.

Polhemus, J. T. 1991. A new and primitive genus of Cryphocricinae (Heteroptera: Naucoridae). Pan-Pac. Entomol. 67: 119–123.

Polhemus, D. A. & J. T. Polhemus. 1988. Family Naucoridae Leach, 1815: the creeping water bugs, pp. 521–527. *In* T. J. Henry & R. C. Froeschner [eds.], Catalog of the Heteroptera, or true bugs, of Canada and the continental United States. Brill, New York.

Polhemus, J. T. & D. A. Polhemus. 1994. A new species of *Ambrysus* Stål from Ash Meadows, Nevada (Naucoridae, Heteroptera). J. N.Y. Entomol. Soc. (in press).

Raff, R. A. & T. C. Kaufman. 1983. Embryos, genes, and evolution: the developmental-genetic basis of evolutionary change. Macmillan, New York.

Reyment, R. A., R. E. Blacklith & N. A. Campbell. 1984. Multivariate morphometrics, 2nd ed. Academic, New York.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43: 223–225.

Sites, R. W. 1990a. Morphological variations in the hemelytra of *Cryphocricos hungerfordi* Usinger (Heteroptera: Naucoridae). Proc. Entomol. Soc. Wash. 92: 111–114.

1990b. Naucorid records from Amazonian Ecuador. Fla. Entomol. 73: 334–335.

1991. Egg ultrastructure and descriptions of nymphs of *Pelocoris poeyi* (Guérin Méneville) (Hemiptera: Naucoridae). J. N.Y. Entomol. Soc. 99: 622–629.

Sites, R. W. & B. J. Nichols. 1990. Life history and descriptions of immature stages of *Ambrysus lunatus lunatus* (Hemiptera: Naucoridae). Ann. Entomol. Soc. Am. 83: 800–808.

1993. Voltinism, egg structure, and descriptions of immature stages of *Cryphocricos hungerfordi* (Hemiptera: Naucoridae). Ann. Entomol. Soc. Am. 86: 80–90.

Sites, R. W. & M. R. Willig. 1991. Microhabitat associations of three sympatric species of Naucoridae. Environ. Entomol. 20: 127–134.

1994. Interspecific morphometric affinities in *Ambrysus* (Hemiptera: Naucoridae). Proc. Entomol. Soc. Wash. 96: 527–532.

Sneath, P.H.A. & R. R. Sokal. 1973. Numerical taxonomy: the principles and practice of numerical classification. Freeman, San Francisco.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research, 2nd ed. Freeman, San Francisco.

Sorensen, J. T. 1987a. Multivariate statistical approach to deduction of phylogeny within *Essigiella* (Aphididae: Lachninae), pp. 243–260. *In* J. Holman, J. Pelikan, A.F.G. Dixon & L. Weismann [eds.], Population structure, genetics and taxonomy of aphids and Thysanoptera. VEDA, House of the Slovak Academy of Sciences, Bratislava, Czechoslovakia.

1987b. The multivariate evolution and taxonomic analyses of leafhopper biotypes and species complexes: use of character correlations and quantitative genetics methods, pp. 217–234. *In* M. R. Wilson & L. R. Nault [eds.], Proceedings, Second International Workshop on Leafhoppers and Planthoppers of Economic Importance, 28 July–1 August 1986, Provo, UT. CIE, London.

1992. The use of discriminant function analysis for estimation of phylogeny: partitioning, perspective and problems, pp. 65–93. *In* J. T. Sorensen & R. G. Foottit [eds.], Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales. Elsevier, New York.

Sorensen, J. T. & R. G. Foottit. 1992. The evolutionary quantitative genetic rationales for the use of ordination analyses in systematics: phylogenetic implications, pp. 29–53. *In* J. T. Sorensen & R. G. Foottit [eds.], Ordination in the study of morphology, evolution and systematics of insects: applications and quantitative genetic rationales. Elsevier, New York.

SPSS. 1986. SPSS user's guide, 2nd ed. SPSS, New York.

Stål, C. 1858. Bidrag till Rio Janeiro-traktens Hemipter-fauna. K. Sven. Vetenskapsakad. Handl. 2: 1–84.

Štys, P. & A. Jansson. 1988. Check-list of recent family-group and genus-group names of Nepomorpha (Heteroptera) of the world. Acta Entomol. Fenn. 50: 1–44.

Torre Bueno, J. R. de la. 1903. Brief notes toward the life history of *Pelocoris femorata* Pal. B. with a few remarks on habits. J. N.Y. Entomol. Soc. 11: 166–173.

Usinger, R. L. 1946. Notes and descriptions of *Ambrysus* Stal with an account of the life history of *Ambrysus mormon* Montd. (Hemiptera, Naucoridae). Univ. Kans. Sci. Bull. 31: 185–210.

1947. Classification of the Cryphocricinae (Hemiptera: Naucoridae). Ann. Entomol. Soc. Am. 40: 329–343.

Willig, M. R. & R. R. Hollander. 1995. Phylogenetic constraints on the expression of sexual dimorphism in bats: a statistical approach. J. Mammal. (in press).

Willig, M. R. & R. D. Owen. 1987. Univariate analyses of morphometric variation do not emulate the results of multivariate analyses. Syst. Zool. 36: 398–400.

Willig, M. R., R. D. Owen & R. L. Colbert. 1986. Assessment of morphometric variation in natural populations: the inadequacy of the univariate approach. Syst. Zool. 35: 195–203.

Wood, D. S. 1983. Character transformations in phenetic studies using continuous morphometric variables. Syst. Zool. 32: 125–131.

Zelditch, M. L., F. L. Bookstein & B. L. Lundrigan. 1993. The ontogenetic complexity of developmental constraints. J. Evol. Biol. 6: 621–641.

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Appendix 1. Factor loadings (correlations), eigenvalues, and explained variation on each of the first three axes of the discriminant function (DF) analyses performed separately for each instar or sex of adult

Character	DF 1							DF 2							DF 3						
	1	2	3	4	5	M	F	1	2	3	4	5	M	F	1	2	3	4	5	M	F
Body length	−0.001	−0.125	0.108	0.069	0.020	0.019	0.013	0.650	0.731	0.467	0.359	−0.209	−0.162	0.342	−0.139	−0.120	0.486	0.425	0.685	0.719	0.744
Body width	0.313	0.190	−0.252	−0.156	−0.163	−0.198	0.213	0.445	0.455	0.358	0.185	−0.023	0.196	−0.043	−0.027	0.122	0.644	0.501	0.650	0.554	0.723
Head length	0.067	0.030	−0.076	−0.052	−0.049	−0.078	0.087	0.221	0.177	0.313	0.163	−0.032	−0.140	0.190	−0.155	0.014	0.118	0.268	0.287	0.418	0.305
Head width	0.361	0.325	−0.304	−0.227	−0.276	−0.294	0.295	0.310	0.614	0.769	0.607	−0.334	−0.320	0.399	−0.256	−0.492	0.201	0.288	0.649	0.487	0.320
Synthlipsis	0.161	0.167	−0.204	−0.136	−0.170	−0.207	0.193	0.023	0.073	0.196	0.082	0.026	0.067	−0.029	−0.104	−0.028	0.147	0.156	0.300	0.234	0.260
Pronotum length	0.071	−0.008	0.156	0.114	0.011	−0.121	0.169	0.209	0.338	0.571	0.473	−0.375	−0.357	0.572	−0.019	0.029	0.246	0.198	0.524	0.547	0.373
Profemur length	−0.220	−0.365	0.391	0.336	0.203	0.146	−0.148	0.371	0.432	0.342	0.334	−0.238	−0.111	0.293	0.046	0.064	0.482	0.340	0.532	0.396	0.454
Protibia length	−0.469	−0.459	0.484	0.436	0.329	0.296	−0.266	0.529	0.280	0.203	0.204	−0.226	−0.126	0.298	0.014	−0.018	0.291	0.261	0.486	0.460	0.529
Protarsus length	0.006	−0.005	0.036	0.044	0.031	0.052	−0.037	0.124	0.122	0.013	−0.092	0.068	0.083	−0.033	0.135	0.264	0.289	0.295	0.250	0.156	0.173
Mesofemur length	−0.182	−0.120	0.180	0.170	0.092	0.108	−0.073	0.341	0.273	0.121	0.159	−0.058	0.016	0.130	0.283	0.125	0.494	0.563	0.632	0.532	0.578
Mesotibia length	−0.196	−0.184	0.276	0.188	0.160	0.204	−0.133	0.296	0.242	0.143	0.123	−0.049	0.041	0.087	0.121	0.240	0.503	0.454	0.566	0.511	0.514
Mesotarsus length	0.066	0.120	0.043	−0.004	−0.019	0.005	0.002	−0.033	0.135	0.117	0.150	−0.057	0.033	0.054	0.048	0.260	0.360	0.345	0.590	0.313	0.297
Metafemur length	0.012	−0.014	0.002	0.022	−0.013	0.017	0.018	0.413	0.456	0.225	0.196	−0.023	0.122	0.065	0.351	0.414	0.669	0.653	0.797	0.825	0.607
Metatibia length	−0.011	−0.056	0.064	0.102	0.064	0.113	−0.061	0.580	0.522	0.229	0.193	−0.031	0.061	0.087	0.351	0.462	0.655	0.758	0.704	0.634	0.621
Metatarsus length	0.338	0.224	−0.209	−0.131	−0.161	−0.146	0.128	0.040	0.229	0.065	0.099	0.016	0.068	0.007	0.475	0.424	0.419	0.353	0.603	0.437	0.407
Eigenvalue	108.580	252.519	192.191	319.096	331.675	259.043	451.206	32.409	65.551	58.055	88.649	137.153	73.721	102.117	19.463	25.291	32.154	38.842	27.927	42.929	51.100
Variance explained	64.460	70.340	63.340	66.940	62.170	66.700	72.580	19.240	18.260	19.130	18.600	25.710	18.980	16.430	11.550	7.040	10.600	8.150	5.230	11.050	8.220

Appendix 2. Factor loadings (correlations), eigenvalues, and explained variation on each of the first three axes of the principal components (PC) analyses performed separately for each instar or sex of adult

Character	PC 1							PC 2							PC 3						
	1	2	3	4	5	M	F	1	2	3	4	5	M	F	1	2	3	4	5	M	F
Body length	0.840	0.880	0.949	0.948	0.945	0.956	0.953	0.307	−0.067	−0.079	−0.021	−0.061	0.041	0.005	−0.372	0.388	0.254	−0.265	−0.233	−0.236	0.226
Body width	0.275	0.557	0.637	0.615	0.710	0.652	0.697	0.898	0.775	0.727	0.758	0.683	0.623	0.592	−0.189	0.136	−0.063	0.135	0.099	0.370	−0.328
Head length	0.386	0.592	0.601	0.618	0.579	0.795	0.789	0.528	0.335	0.496	0.426	0.303	0.453	0.489	−0.571	0.443	0.428	−0.073	0.249	−0.303	0.266
Head width	0.026	0.320	0.482	0.504	0.579	0.480	0.505	0.930	0.803	0.742	0.720	0.668	0.801	0.792	−0.251	0.430	0.423	−0.438	−0.397	−0.320	0.315
Synthlipsis	−0.264	−0.058	0.260	0.236	0.356	0.350	0.412	0.774	0.930	0.873	0.913	0.884	0.874	0.853	−0.031	0.033	0.108	0.041	0.011	0.235	−0.258
Pronotum length	0.507	0.854	0.796	0.782	0.766	0.704	0.654	0.655	0.192	−0.191	−0.172	−0.079	0.465	0.479	−0.089	0.212	0.551	−0.565	−0.577	−0.493	0.544
Profemur length	0.809	0.687	0.686	0.696	0.681	0.770	0.721	−0.451	−0.656	−0.657	−0.645	−0.647	−0.536	−0.583	−0.139	0.097	0.162	−0.224	−0.282	−0.274	0.330
Protibia length	0.754	0.506	0.506	0.531	0.511	0.603	0.575	−0.603	−0.838	−0.842	−0.831	−0.838	−0.742	−0.765	−0.139	0.138	0.139	−0.123	−0.161	−0.255	0.262
Protarsus length	0.530	0.734	0.669	0.483	0.544	0.581	0.576	0.248	0.109	−0.172	−0.265	−0.216	−0.479	−0.507	0.358	−0.463	−0.485	0.744	0.750	0.481	−0.481
Mesofemur length	0.852	0.823	0.825	0.888	0.902	0.909	0.914	−0.334	−0.491	−0.494	−0.390	−0.358	−0.377	−0.375	0.248	−0.125	−0.172	0.127	0.075	0.047	−0.048
Mesotibia length	0.832	0.749	0.746	0.786	0.748	0.754	0.757	−0.451	−0.593	−0.621	−0.550	−0.608	−0.627	−0.623	0.005	−0.058	−0.097	0.115	0.141	0.038	−0.051
Mesotarsus length	0.273	0.677	0.783	0.868	0.902	0.901	0.936	0.404	0.348	0.396	0.266	0.184	0.020	−0.031	0.697	−0.459	−0.303	0.049	−0.030	0.181	−0.113
Metafemur length	0.823	0.937	0.943	0.956	0.957	0.958	0.965	0.289	0.172	0.156	0.148	0.125	−0.004	0.016	0.253	−0.149	−0.235	0.183	0.188	0.235	−0.217
Metatibia length	0.889	0.940	0.955	0.950	0.941	0.927	0.923	0.253	0.052	−0.035	−0.115	−0.212	−0.325	−0.324	0.104	−0.085	−0.167	0.224	0.196	0.101	−0.121
Metatarsus length	−0.108	0.308	0.401	0.484	0.613	0.671	0.709	0.798	0.840	0.796	0.788	0.708	0.625	0.577	0.464	−0.382	−0.383	0.195	0.047	0.260	−0.291
Eigenvalue	5.733	7.089	7.585	7.791	8.164	8.548	8.619	4.963	4.859	4.745	4.495	4.057	4.314	4.325	1.576	1.244	1.388	1.379	1.388	1.226	1.263
Variance explained	38.220	47.257	50.567	51.939	54.423	56.984	57.462	33.086	32.394	31.630	29.966	27.047	28.762	28.833	10.507	8.295	9.255	9.192	9.251	8.171	8.420