

CORRELATED EVOLUTION OF MALE AND FEMALE MORPHOLOGIES IN WATER STRIDERS

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Abstract.—Sexually antagonistic coevolution may be an important force in the evolution of sexual dimorphism. We undertake a comparative study of correlated evolution of male and female morphologies in a clade of 15 water strider species in the genus *Gerris* (Heteroptera: Gerridae). Earlier studies have shown that superfluous matings impose costs on females, including increased energetic expenditure and predation risk, and females therefore resist males with premating struggles. Males of some species possess grasping structures and females of some species exhibit distinct antigrasping structures, which are used to further the interests of each sex during these premating struggles. We use this understanding, combined with coevolutionary theory, to derive a series of a priori predictions concerning both the types of traits in the two sexes that are expected to coevolve and the coevolutionary dynamics of these traits expected under sexually antagonistic coevolution. We then assess the actual pattern of correlated evolution in this clade with new morphometric methods combined with standard comparative techniques. The results were in agreement with the a priori predictions. The level of armament (different abdominal structures in the two sexes) was closely correlated between the sexes across species. Males are well adapted to grasping females in species in which females are well adapted to thwart harassing males and vice versa. Furthermore, our comparative analyses supports the prediction that correlated evolution of armament in the two sexes should be both rapid and bidirectional.

Key words.—Coevolution, evolutionary arms race, evolutionarily stable strategy, geometric morphometrics, Gerridae, sexual conflict, sexual selection.

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Conflicts in the evolutionary interests of males and females result in sexually antagonistic coevolution between genes or sets of genes residing in the same genome (Rice and Holland 1997). Such coevolutionary interactions may, in theory, result in evolutionary arms races between those traits in males and females that mediate sexual conflict (Parker 1979, 1983a). This form of intragenomic conflict has recently received much attention and may be of fundamental importance for a wide range of biological phenomena. For example, sexually antagonistic coevolution has been implied in explanations of the rapid evolution of various gamete recognition and gonadal proteins (Civetta and Singh 1995; Palumbi 1998; Rice 1998; Swanson et al. 2001); evolution of male accessory seminal substances and female receptors to these (Chapman et al. 1995; Rice 1996; Civetta and Clark 2000; Pitnick et al. 2001a,b); female infertility, mate choice, and cryptic mate choice (e.g., Parker 1979, 1983b; Eberhard 1996; Holland and Rice 1998; Gavrillets et al. 2001); and the correlated evolution of male and female reproductive morphologies (Presgraves et al. 1999; Ilango and Lane 2000; Bergsten et al. 2001). Because antagonistic coevolution should be unusually rapid and involve traits related to reproduction, theory also suggests that it may promote speciation (Parker and Partridge 1998; Rice 1998) and comparative evidence has recently provided some support for this suggestion (Arnqvist et al. 2000).

Despite the potential significance of sexual conflict in the large-scale dynamics of secondary sexual traits, very few empirical studies address sexually antagonistic coevolution at higher temporal or taxonomic scales. For example, much of our understanding of sexual conflict concerns the repro-

ductive physiology of *Drosophila* and rests on intraspecific patterns of sperm competition and mating costs (e.g., Fowler and Partridge 1989; Chapman et al. 1995; Clark et al. 1999; Civetta and Clark 2000) or short-term artificial selection experiments (Rice 1996; Holland and Rice 1999; Pitnick et al. 2001a,b). Although these studies have elegantly demonstrated that sexual conflict in this system is intense and that antagonistic coevolution can apparently be very rapid, they do not adequately address the long-term coevolutionary dynamics of male and female traits. Necessary studies would require the identification of a pair or a suite of interacting traits whose function is reasonably well understood and an analysis of their correlated evolution with standard comparative methods (Brooks and McLennan 1991; Harvey and Pagel 1991).

The general shortage of comparative studies of sexually antagonistic coevolution may be attributed to one or more of several inadequacies in our typical datasets: (1) the true identity and nature of the antagonistically evolving traits in the two sexes is unknown; (2) male and female adaptations and counteradaptations cannot be quantified in a tractable way; and/or (3) robust phylogenies are not at hand. For example, one of the few documented cases of correlated evolution in male and female morphologies to date in which a role for sexual antagonism has been implied concerns the correlated evolution of female reproductive tract morphology and either sperm size (Briskie and Montgomery 1993; Briskie et al. 1997; Pitnick et al. 1999; Presgraves et al. 1999; Morrow and Gage 2000) or male genital size (Ilango and Lane 2000). Yet, our knowledge of how sperm size and reproductive tract morphology interact is limited, and it remains to be demonstrated that sexual conflict is actually involved in their interaction (Pitnick et al. 1999; Presgraves et al. 1999).

Water striders (Heteroptera: Gerridae) are a group of semi-aquatic insects that has become a model system for testing various hypotheses about sexually antagonistic coevolution. A large number of experimental studies have demonstrated that there is intense and overt sexual conflict over mating rate, resulting from a strong asymmetry between the sexes in the costs and benefits of mating (for reviews see Rowe et al. 1994; Arnqvist 1997). Superfluous matings are costly to females (e.g., in terms of increased energetic expenditure, reduced mobility, and increased predation risk), and females consequently employ premating struggles to resist harassing males. Sexually antagonistic coevolution has earlier been implicated in the evolution of morphological adaptations in males that increase their ability grasp females efficiently and distinct morphological counteradaptations in females that increase the efficiency with which females dislodge males during these struggles (see below). The relative ability of one sex to impose its interest on the other during the struggle also shapes many aspects of the mating system and secondarily influences sexual selection (Arnqvist 1992a,b; Rowe 1992, 1994; Rowe et al. 1994; Arnqvist and Rowe 2002; Rowe and Arnqvist 2002).

We undertake a comparative analysis of correlated evolution in male and female morphologies in the largest temperate water strider genus (Andersen 1993). Earlier attempts to assess correlated evolution of male and female morphologies in this group of insects have relied on discrete coding of quantitative character states and have been unsuccessful in establishing patterns (i.e., Andersen 1997). In contrast, we treat characters as continuous, with the use of recently developed geometric morphometric techniques. Using 15 congeneric *Gerris* species, we first identify a series of a priori predictions regarding which traits in males and females should function as arms in premating conflicts and thus co-evolve and which coevolutionary dynamics would be expected under sexually antagonistic coevolution. We then test for and describe the actual pattern of correlated evolution between such traits in the two sexes and use an existing phylogenetic reconstruction and standard, quantitative comparative techniques to assess coevolutionary dynamics.

MATERIALS AND METHODS

Species and Their Evolutionary History

This study forms an integral part of a larger comparative analysis of the morphology and behavior of 15 congeneric holarctic and palearctic water strider species of the genus *Gerris* (see Appendix for species and collection data). These species share a similar ecology: All are semiaquatic predators and/or scavengers, which typically inhabit water surfaces of various ponds, pools, and lakes (Andersen 1993).

The genus *Gerris* has been the subject of extensive systematic investigations, and its evolutionary history is relatively well resolved. The total evidence phylogeny we use here (see Fig. 1) is based on an analysis of molecular and morphological characters by Damgaard and Sperling (2001) and is largely congruent with an earlier morphological analysis by Andersen (1993).

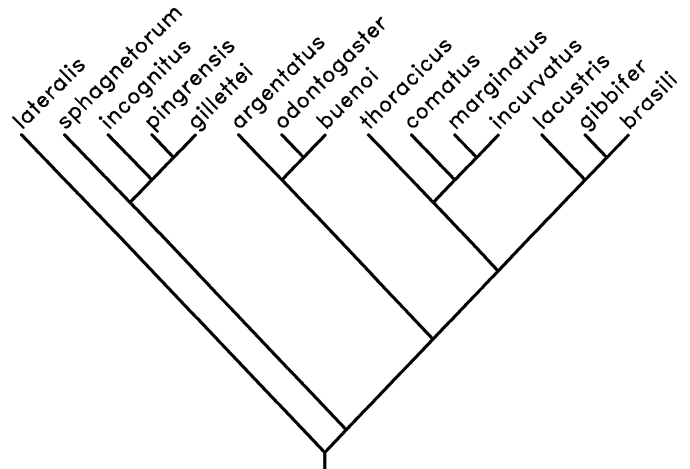


FIG. 1. Phylogenetic reconstruction of the 15 congeneric *Gerris* species used in the current study. The phylogeny used is a total evidence reconstruction, based on a large amount of molecular and morphological data (Andersen 1993; Damgaard and Sperling 2001; J. Damgaard and N. M. Andersen, unpubl. data).

A Priori Predictions

Background

Males of most water strider species typically pounce on top of females without prior courtship and try to secure matings by grasping females (for reviews and illustrations see Rowe et al. 1994; Arnqvist 1997). A male grasps a female anteriorly (on the pronotum) with his forelegs and posteriorly with his genital segments. The latter is achieved by pressing the ventral side of their abdomen close to the dorsum of the female, while extending and curving his genitalia around the tip of the female abdomen. Females are typically reluctant to mate and respond to male mating attempts with struggling. The biomechanics (Lauer 1996; Arnqvist 1997) and economics (Rowe 1994; Watson et al. 1998) of these premating struggles are relatively well understood. Like mating itself (see introduction), premating struggles are costly to females (Rowe 1994; Watson et al. 1998) and can be intense, involving a series of behavioral elements aimed at breaking both the males' anterior and posterior grip (Lauer 1996; Lauer et al. 1996; Weigensberg and Fairbairn 1996; Arnqvist 1997). Water striders are sexually dimorphic in abdominal morphology (Andersen 1982, 1993, 1997), body size (Fairbairn 1990, 1997), and leg size (Arnqvist 1997), and several such structural features have earlier been either shown or suggested to mediate sexually antagonistic interactions (see below). The behavioral sequence described above is common to all of the 15 species used in the current study (Rowe and Arnqvist 2002).

Male and female traits

In this section, we use the results of prior experimental studies to develop predictions concerning which traits in males and females should function as arms in premating conflicts. Male ability to grasp a female is primarily determined by the anterior and posterior grip (see above). Based on the mechanics of the premating struggle, three types of traits have

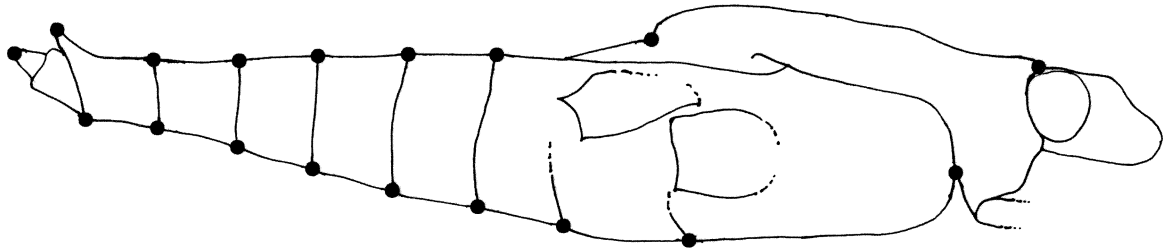


FIG. 2. Lateral view of a *Gerris* sp. female. Dots indicate the location of the 18 landmarks used to characterize body shape.

previously been suggested or demonstrated to influence male grasping ability in this group of water striders. First, physical proximity increases the stability of the male position on top of the female, and the marked dorsoventral flattened shape of the distal portion of the male abdomen observed in many species has been suggested to do so by allowing a tighter union to the female during premating struggles (Andersen 1990; Arnqvist 1997). Second, the strength of the posterior grip should be determined in large part by a male's ability to curve and reach around the tip of the female abdomen with his genital and pregenital segments, thereby securing a genital grasp of the female (Andersen 1991; Arnqvist 1997). In support, experimental manipulations of pregenital structures in *G. odontogaster* show that these improve male posterior grasping (Arnqvist 1989a), and correlational studies have shown that the length of male genital and pregenital structures is directly related to grasping ability (Arnqvist 1989a) and to male mating success (Arnqvist 1992b; Preziosi and Fairbairn 1996; but see Arnqvist et al. 1997) in several species. Third, the strength of the anterior grip should be determined largely by foreleg power, as revealed by the relative dimensions of the forelegs. In support of this suggestion, studies of several water strider species have found that relative forefemur width correlates with male mating success (Rubenstein 1984; Preziosi and Fairbairn 1996; Weigensberg and Fairbairn 1996).

Earlier discussions of females' ability to dislodge males have focused on two types of traits. First, female traits that make it more difficult for males to achieve a firm posterior grip should be beneficial for females. All water striders have a pair of posteriolateral abdominal spines (i.e., the connexival spines; Andersen 1993; see Fig. 2). Prolongation/elevation of these spines dissociates the male abdomen from the female abdomen during the struggle and impedes access to the female abdominal tip, thereby making it more difficult for the male to secure a posterior grip (Arnqvist 1997). By phenotypic manipulations of these spines in *G. incognitus*, Arnqvist and Rowe (1995) were able to demonstrate that, as expected, the ease with which females dislodged males during the premating struggle was an increasing function of spine length, thereby decreasing the frequency of superfluous and costly matings. This function was later corroborated in a study of a natural population, where the rate of superfluous mating by females was a decreasing function of both the length and elevation of abdominal spines (Arnqvist et al. 1997). A more downward-pointing abdominal tip in females may also contribute to impeding the male posterior grip by increasing the distance that the male has to extend and curl his genitalia to

reach around the female abdominal tip. Interestingly, this effect is achieved during mate rejection behavior in many other female insects with flexible abdomina (e.g., Weall and Gilburn 2000). Second, females of all species studied to date use their forelegs to dislodge those of the males that are employed to grip the female pronotum (Lauer 1996; Lauer et al. 1996; Arnqvist 1997). More powerful female forelegs should thus aid in dislodging male forelegs.

It has also been argued that the outcome of premating conflicts in water striders are determined, in part, by the relative sizes of the two interacting individuals (Fairbairn 1988, 1990; Sih and Krupa 1992; Arnqvist et al. 1996; Rowe and Arnqvist 1996). This suggestion is supported by the frequent observations of large male mating advantage and by the fact that size assortative mating has been observed in many species (see Arnqvist et al. 1996). If the body size of a male relative to that of a female indeed affects their relative abilities to grasp or thwart the other sex, then body size and/or general body elongation may coevolve.

Coevolutionary dynamics

One might intuitively expect that coevolution of armaments in the sexes would converge on some optimal level of investment in armaments by the two sexes. However, theory suggests that this is not generally the case. Game theoretical models of sexually antagonistic coevolution instead predict rapid and correlated but unstable and fluctuating cycles, where episodes of escalation may be followed by deescalation (see Parker 1979, 1983a,b, 1984; Hammerstein and Parker 1987; Härdling 1999; see also Gavrillets et al. 2001). Theory thus predicts coevolutionary arms races to yield some trajectory of adaptation and counteradaptation along which species should evolve back and forth. Along this line, any change in investment in armament by one sex may be accompanied by a corresponding change in the other. Therefore, some balance of arms level is expected along this coevolutionary trajectory.

In water striders, we can thus make three predictions relating to coevolutionary dynamics. First, the evolution of increased male investment in adaptations that increases their grasping ability should be associated with an increased female investment in counteradaptations that decrease male grasping efficiency and vice versa (i.e., correlated evolution of armament). Second, the observed level of investment in arms should vary considerably across species. Third, due to the rapid, bidirectional, and unstable nature of antagonistic

coevolution, the degree of phylogenetic inertia should be very low (cf. Losos 1999).

Morphometric Data

To assess correlated evolution in body shape, we employed some of the recently developed tools of geometric morphometric. Geometric morphometric methods offer powerful multivariate statistical methods designed for the analysis of shape data and for associated visualization of shape variation, which are in many ways superior to standard multivariate methods applied on linear distances, angles, and ratios (for general discussions see Bookstein 1991; Rohlf 1993; Rohlf and Marcus 1993; Marcus et al. 1996).

Because morphological traits suggested to be antagonistically coevolving in the sexes (see above) are most apparent when animals are viewed from the side, we chose to base our analyses on a lateral representation of the body. We collected 18 landmarks from individuals presented in lateral view on a cup stage (see Fig. 2 for location of landmarks), using a digitizing tablet (Summasketch III, GTCO CalComp, Inc., Scottsdale, AZ) under a side-mounted camera lucida attached to a dissecting microscope (Leica MZ8, Leica Microsystems, Wetzlar, Germany). This method minimizes measurement error in relative landmark location (Arnqvist and Mårtensson 1998). Because of our a priori interest in forelegs (see above), we also measured the following dimensions of the foreleg using the same method: femur width (widest point), femur length, tibia length, and tarsus length. The sum of the latter three was used as a measure of foreleg length.

We collected these data from five individuals of each species and sex. The average landmark configuration for each species and sex, estimated by a generalized least-squares Procrustes analysis (Rohlf and Slice 1990) using the software GRF-ND (Slice 1999), was used as data in subsequent statistical analyses. For all distance measures of the forelegs, average linear values were used for each species and sex.

Statistical Methods

To assess correlated evolution of body shape that is purely uniform, we estimated the two uniform shape components (Bookstein 1996) using the software TpsRelw (Rohlf 2000a) including all species and sexes in one joint analysis. The uniform shape components parameterize all shape variation that is uniform throughout the geometry, that is, large scale and neither spatially localized nor spatially disproportionate. A common example of uniform shape variation is a general extension/contraction of a whole animal along some axis. We also retained the centroid size (i.e., the square root of the sum of squared distances of all landmarks from their centroid) and used this as an integrative measure of body size (see Marcus et al. 1996).

To test for correlated evolution in components of shape that are localized and more small scaled (see a priori predictions above), we employed a two-block partial least squares analysis (2B-PLS; Rohlf and Corti 2000) of non-uniform shape variation across species. This analysis offers a powerful and tractable method for studying covariation between two sets of shapes. One of the main advantages is that

the two sets of shapes are treated equally in 2B-PLS, that is, one is not assumed to be a function of the other as in regression methods where independent variables are used to predict dependent variables. When applied to shape data, 2B-PLS finds one or more pairs of latent variables, or covariance dimensions, which account for a maximal fraction of the covariance between two sets of shapes (for a general discussion see Rohlf and Corti 2000). We employed the software TpsPls (Rohlf 2000b) to test for and characterize covariation between male and female body shapes with 2B-PLS. Because we were primarily interested in small-scale shape variation, we chose parameter of $\alpha = -0.5$.

To test for correlated evolution of male and female morphologies, we removed phylogenetic effects by employing the independent contrast approach of Felsenstein (1985). Because reliable estimates of branch lengths were not available, all branch lengths were assumed to be equal as recommended by Harvey and Pagel (1991; see also Martins and Garland 1991). The software collection PHYLIP (Felsenstein 2001) was used to calculate independent contrasts, and SYSTAT was used for all other statistical procedures. In no case was the average value of the contrasts reported below significantly different from zero (one-sample *t*-tests, $P > 0.14$ in all cases) and regressions involving contrasts were all forced through the origin (Harvey and Pagel 1991; Garland et al. 1992).

RESULTS

Body Size and Uniform Shape Variation

Male and female body sizes were closely correlated across species ($r = 0.979$, $P < 0.001$). Analysis of the independent contrasts, in which the log of male body size contrasts were regressed on the log of female body size contrasts, showed that evolution of body size is tightly correlated in the two sexes ($R^2 = 0.939$, $P < 0.001$). The slope of this relationship, as estimated in a reduced major axis (model II) regression was $\beta = 1.019$, which did not differ significantly from unity (95% CI = 0.824–1.213; cf. Fairbairn 1997).

The two uniform shape components described a parallel shift in the dorsoventral alignment (Uni X) and an elongation/thickening of the whole body (Uni Y; see Fig. 3 for visualizations). Analysis of the independent contrasts, in which male body shape contrasts were regressed on female body shape contrasts, showed that the uniform body shape of the two sexes evolves in concert (Uni X: $R^2 = 0.812$, $P < 0.001$; Uni Y: $R^2 = 0.635$, $P < 0.001$). This was true also when controlling for the effects of body size evolution by inclusion of female body size contrasts in multiple regressions (effect of Uni X: $P = 0.002$; effect of Uni Y: $P = 0.007$; effects of body size $P > 0.5$ in both models). A whole set correlation analysis (Cohen 1982) of the 2×2 independent contrasts showed a very high correlation between male and female total uniform shape ($R^2 = 0.926$, $P < 0.001$).

Nonuniform Shape Variation

The 2B-PLS analysis of male and female body shape revealed a significant first dimension of covariation (hereafter PLS1; permutation test using 999 random permutations; $P = 0.021$; Rohlf and Corti 2000), which accounted for 77% of

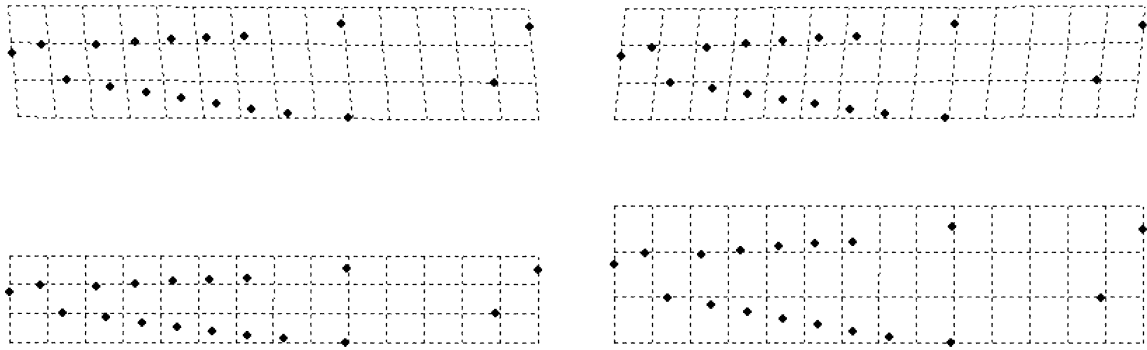


FIG. 3. Visualization of uniform shape variation across the 15 *Gerris* species studied, partitioned into the two uniform shape components (see Fig. 2 for landmark locations). Top panels show deformations resulting from a negative (left) and positive (right) loading along uniform x and bottom panels show deformations resulting from a negative (left) and positive (right) loading along uniform y .

the squared covariance between male and female nonuniform body shape across species. None of the lower-order covariance dimensions were statistically significant ($P > 0.788$ in all cases). Male and female body shapes were tightly correlated along PLS1 ($r = 0.924$). Figure 4 shows ordinations of the 15 species along PLS1 as well as visualizations of the shape changes that occur along this dimension. The morphology of the distal part of the abdomen of both sexes covaries markedly, but shape change along PLS1 is highly specific to each sex. This variable thus describes variation in different abdominal traits in the two sexes. A negative loading on PLS1 describes females with long and erect abdominal spines and a downward-oriented genital tip. The same loading in males instead describes males with long genital and pregenital seg-

ments and an abruptly flattened distal relative to the proximal part of the abdomen. Positive loadings describe the opposite morphology, relative to the average landmark configuration, in both sexes. An animated visualization of the shape changes in the two sexes that occur along PLS1 can be viewed at <http://www.ebc.uu.se/zoeko/GoranA/pls.htm>.

The covariance described by the 2B-PLS analysis above is purely phenotypic and does not account for similarities that are due to common descent (Harvey and Pagel 1991). However, an analysis of phylogenetically independent contrasts, in which male body shape contrasts (male PLS1 score) were regressed on female body shape contrasts (female PLS1 score), showed that evolution of body shapes in the two sexes is closely correlated along PLS1 (Fig. 5; $R^2 = 0.722$, $P <$

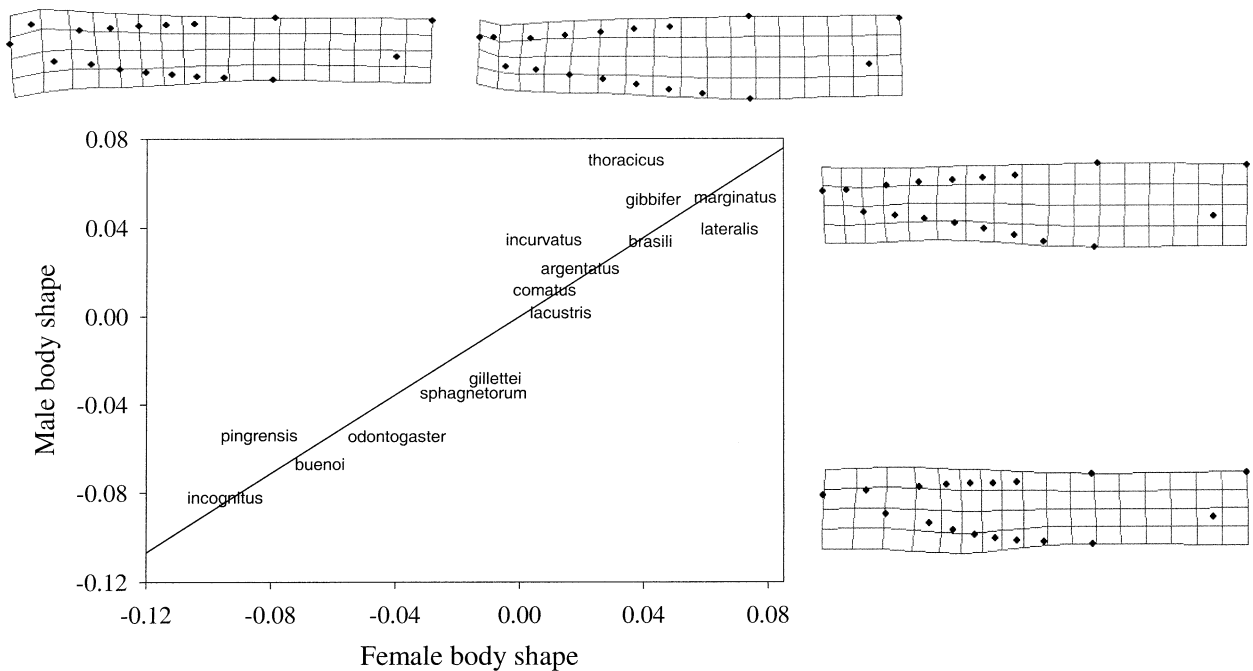


FIG. 4. Ordination of the 15 species along the first covariance dimension of the nonuniform shape space (PLS1), where species names are centered over their exact position. The different shape changes that occur in males (right panels) and females (top panels) along this dimension are shown as thin-plate spline deformations of average shape. Note that this variable describes variation in different traits in the two sexes, so that females have long and erect abdominal spines in species where males show markedly prolonged genital and pregenital segments (see Fig. 2 for landmark locations, Fig. 6 for examples and <http://www.ebc.uu.se/zoeko/GoranA/pls.htm> for an animated visualization of correlated shape change in the two sexes).

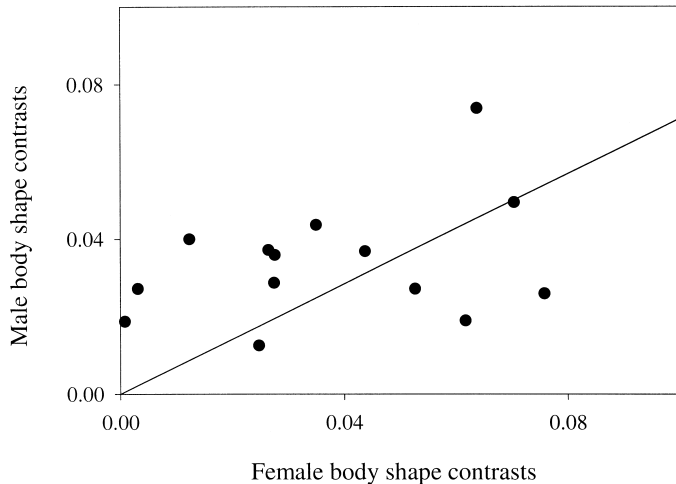


FIG. 5. Correlated evolution of male and female body shape along the first covariance dimension of the nonuniform shape space (PLS1). The figure shows phylogenetically independent contrasts of male and female body shapes along this dimension (see Fig. 4 for a visualization), made positive for female body shape contrasts (see Garland et al. 1992). There is a highly significant linear ($R^2 = 0.722$, $P < 0.001$), but not nonlinear (partial F -test of addition of quadratic component: $F_{1,11} = 4.77$, $P = 0.051$), relationship between the paired set of phylogenetically independent contrasts.

0.001). The correlation between the two independent contrasts was $r = 0.849$. Furthermore, a multiple regression analysis of male body shape contrasts, including both female body size (standardized partial regression coefficient $\beta_i = 0.264$, $P > 0.1$) and female body shape (standardized partial regression coefficient $\beta_j = 0.729$, $P < 0.001$) contrasts, showed that evolution of male body shape is correlated with female body shape rather than with female size (cf. Price 1997).

As an a posteriori validation of the pattern of correlated evolution between female abdominal spines and male genitalia detected here (see Discussion), we extracted spine length in females and genital length in males from our data as simple linear interlandmark distances. We tested both absolute lengths and relative lengths, the latter being the residuals from a regression of spine and genital length on body size. Both absolute and relative lengths of these structures were highly correlated between sexes across species when ignoring phylogenetic effects (absolute lengths: $r = 0.81$, $P < 0.001$; relative lengths: $r = 0.80$, $P < 0.001$). Furthermore, the correlation of independent contrasts was substantial (absolute lengths: $r = 0.81$, $P < 0.001$; relative lengths: $r = 0.80$, $P < 0.001$), and a regression analysis of the phylogenetically independent contrasts (relative lengths: $R^2 = 0.679$, $P < 0.001$) showed that evolution of spine length in females is correlated with genital length in males. A multiple regression analysis of absolute genital length contrasts, including female body size (standardized partial regression coefficient $\beta_i = 0.005$, $P = 0.976$) and absolute spine length (standardized partial regression coefficient $\beta_j = 0.118$, $P < 0.001$) contrasts, showed that evolution of male genital length is correlated with evolution of female abdominal spine length rather than with evolution of female body size.

Foreleg Morphology

We assessed correlated evolution in two different measures of foreleg morphology: relative foreleg length and relative forefemur width (see a priori predictions above). Relative foreleg length was the residual total foreleg length extracted from an ANCOVA including body size, sex, and their interaction (effects: $F_{1,26} = 117.79$, $P < 0.001$; $F_{1,26} = 0.08$, $P = 0.779$; $F_{1,26} = 0.28$, $P = 0.599$, respectively). The independent contrasts, in which male relative foreleg length contrasts were regressed on female relative foreleg length contrasts, showed that the evolution of relative leg length is significantly correlated between the sexes ($R^2 = 0.725$, $P < 0.001$). Relative forefemur width was the residual forefemur width extracted from an ANCOVA including forefemur length, sex, and their interaction (effects: $F_{1,26} = 17.02$, $P < 0.001$; $F_{1,26} = 0.04$, $P = 0.835$; $F_{1,26} < 0.01$, $P = 0.963$, respectively). Again, an analysis of the independent contrasts, in which male relative forefemur width contrasts were regressed on female relative forefemur width contrasts, showed that evolution of relative forefemur width is correlated between the sexes ($R^2 = 0.409$, $P = 0.010$).

Correlated Evolution across Trait Types

Several of traits investigated above also showed fairly high levels of correlated evolution across trait types. There are four patterns in the correlation matrix (see Table 1) that we wish to emphasize. First, evolution of body size and uniform shape is correlated in both sexes, so that the evolution of larger size is accompanied by the evolution of a more slender body shape and vice versa. Second, evolutionary change in relative forefemur width in both sexes appears to be relatively independent of any other trait investigated in this study. Third, evolutionary change in female foreleg length seems more closely correlated with change in body shape than does change in male foreleg length. Finally, nonuniform shape changes that occur along the first covariance dimension from the 2B-PLS analysis appear more closely correlated with evolution of body size, foreleg length, and uniform shape in males relative to females.

DISCUSSION

The results of our comparative analyses were in close accord with the a priori predictions, based on the process of sexually antagonistic coevolution. This was true both for predictions regarding the types of traits in males and females that should exhibit correlated evolution and with regard to coevolutionary dynamics. In this discussion, we note that correlated evolution of morphology between the sexes can be attributed to a variety of evolutionary processes, and therefore a pattern of covariance is not enough to infer process. Below, we suggest that the results of prior experimental studies of the function of key morphological traits in this clade, combined with recent comparative studies of behavior, point to sexually antagonistic coevolution as the most likely cause for the correlated morphological evolution observed here.

Detecting Sexually Antagonistic Coevolution with Comparative Data

Correlated evolution between the sexes in morphology, physiology, and/or behavior is a rule rather than an exception.

TABLE 1. Correlation matrix for all across-trait Pearson product-moment correlations between sets of independent contrasts. Values in bold are significant at $\alpha = 0.05$ (uncorrected for multiple tests, $N = 14$ in all cases).

	Male body size	Female body size	Male foreleg length	Female foreleg length	Male foreleg width	Female foreleg width	Male uniform shape x	Female uniform shape x	Male uniform shape y	Female uniform shape y
Male foreleg length	-0.17952	-0.20314								
Female foreleg length	-0.4715	-0.48671								
Male foreleg width	0.03608	0.04584	0.08751	0.16471						
Female foreleg width	0.40578	0.34339	-0.41668	-0.33452	0.17038	-0.34259				
Male uniform shape x	-0.81946	-0.77454	0.40631	0.55448	0.06151	-0.28567				
Female uniform shape x	-0.83625	-0.8346	0.44193	0.67117	0.09651	-0.34966	0.41709	0.359		
Male uniform shape y	-0.57379	-0.58347	0.46268	0.57661	0.42649	-0.01345	0.50992	0.47177		
Female uniform shape y	-0.60109	-0.62431	0.43412	0.65751	-0.28891	0.36109	-0.56505	-0.47956	-0.80596	-0.7371
Male first covariance dimension	0.60725	0.63848	-0.5726	-0.56526	-0.1459	0.33302	-0.39743	-0.30926	-0.67287	-0.61663
Female first covariance dimension	0.43869	0.49417	-0.43055	-0.36978						

Such correlated evolution can result from at least three very different mechanisms, and our understanding of the relative importance of these is limited in most cases (cf. Fairbairn 1997; Emerson 2000). For example, any restriction on the degree of sex-limited gene expression will lead to correlated evolution between the sexes, because evolutionary forces and responses will be shared between the sexes (e.g., Lande 1980; Halliday and Arnold 1987; Arnold and Halliday 1992; Parker and Partridge 1998; Cuervo and Møller 1999). Even in the absence of such genetic constraints, correlated evolution will result if both sexes evolve in response to a common natural selection regime, dictated by, for example, parasite and predator avoidance and food acquisition. Although these two processes describe correlated evolution, the sexes may also be truly coevolving such that evolution in one sex to some extent represents a response to evolutionary change in the other. This process will result from intersexual selection (for a review see Andersson 1994), of which sexually antagonistic coevolution is one of several forms (Kirkpatrick 1989; Andersson 1994; Holland and Rice 1998; Getty 1999; Rosenthal and Servedio 1999; Gavrillets et al. 2001).

Although comparative studies are critical in detecting and characterizing correlated evolution, reliable inferences about underlying evolutionary mechanisms cannot be made based on such patterns alone (cf. Prum 1997; Pitnick et al. 1999; Presgraves et al. 1999; Emerson 2000). Instead, such inferences must rest on detailed experimental studies of extant species (Fairbairn 1997; Martins 2000). This combination of experimental and comparative approaches to correlated evolution has been used to distinguish processes in the coevolution of male and female sexual traits (e.g., Basolo 1996, 1998; McLennan 1996; Ryan 1998), but sexual antagonism has not been among these processes.

The Footprints of Sexual Antagonisms in Water Striders

The details of the mating system varies among *Gerris* species, but all involve male harassment of females and female reluctance to mate (Rowe and Arnqvist 1996, 2002; Arnqvist 1997). Females generally resist matings because superfluous mating carries high costs for females (Arnqvist 1989b, 1992a; Rowe 1992, 1994; Fairbairn 1993; Watson et al. 1998). The effectiveness of female resistance is related to their morphology, and sexual selection on male grasping morphologies is an indirect pleiotropic effect of this female resistance (see Rowe et al. 1994; and a priori predictions above). These facts set the stage for sexually antagonistic coevolution of distinct male and female morphologies.

Nonuniform body shape

The proportion of phenotypic covariance of male and female nonuniform body shape that was recovered by a single covariance dimension was high (77%), considering the complexity of body shape (see Rohlf and Corti 2000), and our analysis of independent contrasts documents correlated evolution along this line. The distinct shape changes that occur in the sexes along this trajectory correspond closely with those predicted from prior experiments on the function of these traits (see a priori predictions): the evolution of abdominal grasping features in males that function in the pre-

mating struggle is correlated with other abdominal antigrasping structures in females. We thus suggest that this covariance is generated by sexually antagonistic coevolution.

At one extreme (lower left corner of Fig. 4) are species in which females have evolved a morphology that we expect to increase their efficiency at rejecting harassing males. Shape changes include markedly prolonged, elevated abdominal spines and a less accessible genital tip. Both of these adaptations aid in obstructing the male posterior grip during premating struggles. In these species, males have simultaneously evolved grasping adaptations, primarily by evolving prolonged genital and pregenital segments in conjunction with a relatively flattened distal part of the abdomen. Both of these adaptations assist males in securing the posterior grip. Males and females of *G. incognitus* exemplify species with this type of morphology (Fig. 6A, B). At the other extreme (top right corner of Fig. 4), are species in which sexual dimorphism is much less pronounced and neither sex possess exaggerated forms of these distinct mate rejection/mate grasping adaptations, such as *G. thoracicus* (Fig. 6C, D).

It could still be argued that other coevolutionary processes, such as indirect genetic benefits to females, might at least contribute to the observed covariance between male and female abdominal structures. The results of prior experimental studies, however, give no support for this possibility. Experimental manipulation of the opportunity for female choice, in one of the species included here, had no effect on offspring survival or growth (Arnqvist 1989b). Instead, a series of experimental studies of several water strider species, using a variety of approaches, collectively show that females resist males simply because matings are superfluous and carry direct costs. It is this resistance that, as a side-effect, favors male grasping traits (for reviews and discussions, see Rowe et al. 1994; Arnqvist 1997). Moreover, direct experimental manipulation of female traits in one of the species included here (prolongation and shortening of the abdominal spines in *G. incognitus*; see Arnqvist and Rowe 1995) strongly affected both female ability to resist harassing males and the degree of costly and superfluous mating among females, but had no significant effect on female mate selectivity.

An important and independent test of our suggestion was recently provided by a comparative study of behavior in the species studied here. Theory suggest that sexually antagonistic coevolution should tend to be hidden by balanced adaptation and counteradaptation (see Parker 1979; Chapman and Partridge 1996; Rice 1996). Sexual interactions should therefore change little with absolute coevolutionary escalation, whereas any changes in the relative armament of the sexes should be associated with a relative advantage to one sex. Arnqvist and Rowe (2002) were able to demonstrate that evolutionary change in the outcome of sexually antagonistic interactions across these species (e.g., premating struggle duration, male struggle success, level of costly and superfluous mating among females) was closely related to deviations from, but not location along, the morphological trajectory visualized in Figure 4. The study of Arnqvist and Rowe (2002) showed that as species evolve off this coevolutionary trajectory (Fig. 5) to points where one sex should gain a relative advantage over the other, associated evolutionary changes occur in the outcome of antagonistic sexual inter-

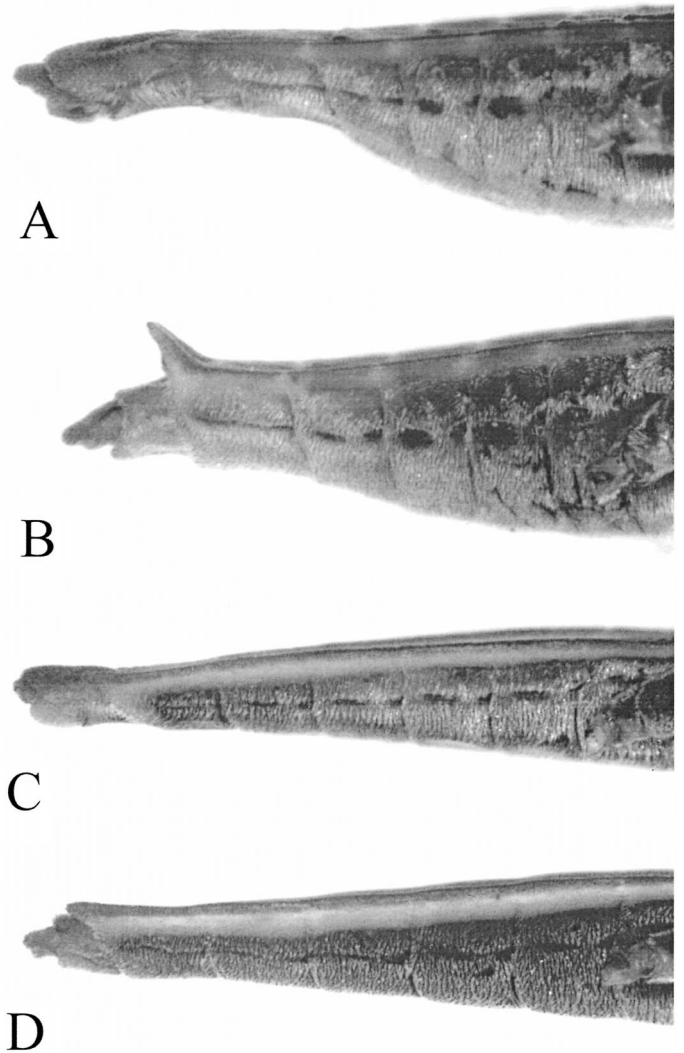


FIG. 6. The degree of sexual dimorphism varies extensively in the genus *Gerris*. At one extreme, we find species such as *G. incognitus* in which males (A) have evolved exaggerated grasping adaptations (e.g., prolonged genital and pregenital segments in conjunction with a relatively flattened distal part of the abdomen), whereas females (B) have simultaneously evolved a morphology that aids in obstructing the male grip during premating struggles (e.g., markedly prolonged, erect abdominal spines and a less accessible genital tip). At the other extreme, we find less dimorphic species such as *G. thoracicus*, where these adaptations are much less pronounced in both males (C) and females (D). See also Figure 4.

actions. For example, it is only when females evolve anti-grasping structures that are exaggerated *relative* to abdominal grasping features in males that evolution of reduced amounts of superfluous mating among females is observed (see Arnqvist and Rowe 2002).

Other traits

We also detected highly correlated evolution across the sexes in both foreleg morphology and body-size elongation. Although we did predict that both of these trait types should coevolve antagonistically in the two sexes, we are currently unable to reject other hypotheses for the pattern detected.

Various components of leg morphology are known to be highly genetically correlated in one of the species studied here (Arnqvist and Thornhill 1998), and it is reasonable to assume that foreleg morphology is genetically correlated to some extent also across the sexes in all species. Similarly, water striders use their forelegs to capture prey and the diets of the two sexes overlap almost entirely (McLean 1989). Natural selection on foreleg morphology imposed by prey availability should therefore be shared between the sexes (Weigensberg and Fairbairn 1996). Thus, there are good reasons to assume that both genetic constraints and a shared environment have contributed to the correlated evolution of foreleg morphology we observe. With regard to body size, genetic constraints per se have been considered an unlikely explanation to the observed correlated evolution of body size in this group of insects (see Fairbairn and Preziosi 1994; Andersen 1997; Fairbairn 1997). However, such correlated evolution may be caused by a similar adaptive responses to a common selective regime in both sexes. Because body size is relevant for virtually every aspect of natural selection, it seems more than likely that both sexes have responded in a similar way to modulations of their environment.

The Dynamics of Sexually Antagonistic Coevolution

Theory on sexually antagonistic coevolution make a few relevant predictions with regard to the coevolutionary dynamics (see a priori predictions above), each of which was supported by our comparative analyses of nonuniform body shape. Species indeed differed greatly in their levels of adaptation and counteradaptation (Fig. 6), and this variation was characterized by correlated evolution between the sexes within species (Fig. 5). We found little correspondence between phenotypic and phylogenetic similarity across species, as indicated by the general lack of phylogenetic effect in our analyses and as verified by a very low and nonsignificant phylogenetic autocorrelation observed at the species level (scaled Moran's I for average score along PLS1 in the two sexes = -0.414 ; $P > 0.1$; see Gittleman and Kot 1990). This fact supports the prediction that sexually antagonistic coevolution lead to rapid character evolution (Losos 1999; see also Arnqvist and Rowe 2002; Rowe and Arnqvist 2002). Unfortunately, however, the prediction of bidirectionality is difficult to test with any degree of confidence, because it is very difficult to document monotonic evolutionary trends over a whole phylogeny. To avoid relying on estimations of ancestral character states, we assessed coevolutionary directionality by simply correlating the number of past speciation events (i.e., nodes) during each species evolutionary history with its location along the coevolutionary trajectory (average score of the two sexes along the first covariance dimension). Assuming that evolution occurs only, or at least primarily, during speciation events, more derived species should be located toward one end of the coevolutionary trajectory if there has been a consistent evolutionary trend. However, the number of estimated past speciation events did not correlate significantly with location along the coevolutionary trajectory (Spearman rank correlation: $r = 0.326$, $P > 0.25$). Although this is not an optimal test of directionality in the coevolution of these traits, it is at least consistent with a scenario of both

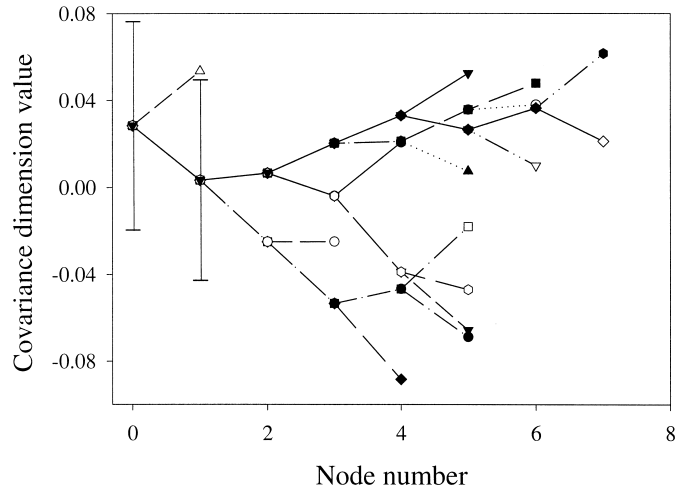


FIG. 7. Representation of the inferred evolutionary trajectories of the 15 species included in the current study. The y-axis represents the average score along the first covariance dimension for males and females of a particular species as either observed (extant species located at the tip of each trajectory) or estimated (ancestral nodes) using the maximum-likelihood approach suggested by Schluter et al. (1997). Correlated evolution downward can be interpreted as mutually increased escalation of armament in the two sexes and vice versa (cf. Fig. 4). The x-axis represents the node number (cf. Fig. 1). The 95% CI of the estimated value for the two most basal ancestors is also indicated (see Schluter et al. 1997), but these should be interpreted with great caution (see Rohlf 2001).

increased and decreased escalation over the evolutionary history of the water strider species studied (see Fig. 7). This implies that benefits to either sex from evolutionary investment in antagonistic adaptations are counterbalanced by natural selection, simply because continuous escalation in antagonistic adaptations is expected if the expression of these are not costly to the bearer (Parker 1979, 1983a; Härdling 1999; Gavrilets 2000; Gavrilets et al. 2001). It has earlier been demonstrated that grasping genitalic adaptations in males of one of the species studied here (*G. odontogaster*) interfere with the molting process and thus result in developmental costs to males (Arnqvist 1994; see also Westlake and Rowe 1999), and it is possible that counteradaptations in females (such as elevated abdominal spines) incur similar costs.

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APPENDIX

<i>Gerris</i> species	Sampling site	Sampling date
<i>argentatus</i>	Sälgsjön, Valbo, Gästrikland, Sweden	May 1997
<i>brasili</i>	Rio Moro, Sierra, Segura, Spain	April 1999
<i>buenoi</i>	Lake Scugog, Port Perry, Ontario, Canada	May 1999
<i>comatus</i>	Lake Scugog, Port Perry, Ontario, Canada	May 1999
<i>gibbifer</i>	Rio Moro, Sierra Segura, Spain	April 1999
<i>gillettei</i>	Fenton Lake, Jemez Mountains, NM, USA	March 1995
<i>incognitus</i>	Bosque del Apache, NM, USA	March 1995
<i>incurvatus</i>	Ditches near Mission, British Columbia, Canada	June 1999
<i>lacustris</i>	Gimonäs pond, Umeå, Sweden	May 1996
<i>lateralis</i>	Tavleå, Umeå, Sweden	May 1996
<i>marginatus</i>	Pond near Lexington, KY, USA	April 1998
<i>odontogaster</i>	Gimonäs pond, Umeå, Sweden	May 1996
<i>pingrensis</i>	George Lake, Alberta, Canada	May 1999
<i>sphagnetorum</i>	Sälgsjön, Valbo, Gästrikland, Sweden	May 1997
<i>thoracicus</i>	Ostnäs fjärden, Umeå, Sweden	June 1997