ECOLOGICAL PHYLOGENETICS OF MATING SYSTEMS AND SEXUAL DIMORPHISM IN WATER STRIDERS (HETEROPTERA : GERRIDAE)

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MATING SYSTEMS
SEXUAL DIMORPHISM
COEVOLUTIONARY ARMS RACE
ECOLOGICAL PHYLOGENETICS
WATER STRIDERS
GERRIDAE

ABSTRACT. – Water striders of the heteropteran family Gerridae are conspicuously adapted for life on the water surface, especially with respect to locomotion, feeding, and reproductive behavior. Sexual dimorphism is usually pronounced in water striders. A basic, female-biased size dimorphism and a significant allometric relationship between sexual size dimorphism and overall size is well documented in temperate water strider species and is here extended to other species of the subfamily Gerrinae. Water striders are also dimorphic with respect to both primary and secondary sexual traits, especially shape and size of fore legs and structure of terminal abdominal segments and genitalia. In this paper the approach called ecological phylogenetics is used to study patterns of sexual dimorphism and mating systems in the monophyletic subfamily Gerrinae, focusing on the evolution of sexual dimorphism in relation to mating systems and the coevolution of male clasping and female anticlasper devices. There are no obvious, global phylogenetic effects or "constraints" on sexual dimorphism in the group, but phylogeny has played a certain role in shaping patterns of F/M size ratios, male clasping devices, and female anticlasper devices within clades. There is no support for the hypothesis that male and female genitalia and other structures have been involved in a coevolutionary "arms race". Finally, the phylogenetic effects on patterns of mating behavior are negligible as demonstrated by the large amount of interspecific variation in some genera, and by the fact that males of the same species may show alternative mating tactics depending on ecological circumstances.

SYSTÈMES D'ACCOUPLEMENT
DIMORPHISME SEXUEL
« COURSE À L'ARMEMENT »
COÉVOLUTIVE
PHYLOGÉNIE ÉCOLOGIQUE
GERRIS
GERRIDAE

RÉSUMÉ. – Les Hétéroptères de la famille des Gerridae sont manifestement bien adaptés à la vie à la surface de l'eau, particulièrement en ce qui concerne la locomotion, la nutrition et la reproduction. Le dimorphisme sexuel est généralement prononcé. Un dimorphisme de taille qui favorise la femelle et une relation allométrique significative entre le dimorphisme sexuel de taille et la taille totale concernant des espèces de Gerris des eaux tempérées sont bien connus et sont étendus ici aux autres espèces de la sous-famille des Gerrinae. Les Gerris montrent aussi un dimorphisme portant sur les caractères sexuels primaires et secondaires, particulièrement en ce qui concerne la forme et la taille des pattes antérieures, la structure des derniers segments abdominaux et les genitalia. Une approche par la phylogénie écologique, permettant d'étudier les modalités du dimorphisme sexuel et les systèmes d'accouplement dans la sous-famille des Gerrinae, qui est monophylétique, cerne l'évolution du dimorphisme sexuel lié aux systèmes d'accouplement et la coévolution des dispositifs d'appariement chez le mâle et de rejet chez la femelle. Il n'existe ni fardeau ni contraintes d'ordre phylogénétique sur le dimorphisme sexuel dans ce groupe, mais la phylogénie a joué un certain rôle sur la distribution des rapports de taille F/M, les dispositifs d'accrochage des mâles et de refus chez les femelles à l'intérieur des clades. Il n'y a pas lieu de supposer que les genitalia mâles et femelles ou les autres structures interviennent dans une « course à l'armement » coévolutive. Enfin, l'influence phylogénétique sur les modalités du comportement sexuel sont négligeables comme le montrent l'importance de la variation interspécifique chez certains genres ainsi que le fait que les mâles d'une même espèce puissent déployer des tactiques alternatives d'accouplement dépendant des conditions écologiques.

INTRODUCTION

Water striders of the heteropteran family Gerridae are conspicuously adapted for life on the water surface, especially with respect to locomotion, feeding, and reproductive behavior (Andersen, 1982a; Spence & Andersen, 1994). Their two-dimensional habitats make gerrids ideal objects for behavioral studies and recent interest in gerrid sexual behavior and strategies has focused on the three principal, Holarctic genera *Aquarius*, *Gerris*, and *Limnoporus*. Most species mate more frequently than necessary to ensure maximum fertility and males seem to contribute only sperm to offspring (Arnqvist, 1989b; 1995). The extremely long spermathecal tube typical of female gerrids (Andersen, 1982a; 1990; 1993b; Andersen & Spence, 1992), suggests that high rates of sperm displacement will be common, a prediction which has been confirmed experimentally (Arnqvist, 1988; Rubenstein, 1989; J. Spence, unpublished data).

Arnqvist (1995) suggested that matings in water striders can be divided into two distinct types. In Type I matings, males search actively for mates and when females are encountered, males initiate matings by simply lunging at and attempting to grasp females, without prior courtship. A male that is successful in achieving physical contact with a conspecific female will grasp the female's thorax with his forelegs, rapidly extend his genital segments, and attempt to insert his phallic organ into the genital opening of the female. Typically, females struggle vigorously before allowing intromission and are often successful in dislodging males (Arnqvist, 1989a; 1992a; Krupa *et al.*, 1990; Rowe, 1992; Rowe *et al.*, 1994; Weigensberg & Fairbairn, 1994). Males usually exhibit post-copulatory guarding, staying in close contact with the female after intromission is terminated (Andersen, 1982a; Arnqvist, 1995). Type II matings differ from type I matings in that males typically are territorial, defending suitable oviposition sites (Wilcox, 1972; Hayashi, 1985; Vepsäläinen & Nummelin, 1985b; Spence & Wilcox, 1986; Wilcox & Spence, 1986). There are much less apparent conflict and a reduced level of agression between sexes. Males, however, respond aggressively towards other males and engage in fights to defend their territory (Hayashi, 1985 and personal communication; Spence & Wilcox, 1986). Copulation is usually brief and type II matings typically involve post-copulatory noncontact guarding during which the female may oviposit. Using the commonly employed terminology of insect mating systems (Thornhill & Alcock, 1983), Arnqvist's (1995) type I matings can be characterized as "scramble competition polygyny" and type II matings as "resource defence gyny"

polygyny" (Andersen, 1994; Spence & Andersen, 1994).

Sexual dimorphism is usually pronounced in water striders. Males are generally smaller than females except in the largest species. A basic, female-biased size dimorphism (female/male size ratio about 1.1) and a significant allometric relationship between sexual size dimorphism and overall size is well documented in temperate *Aquarius*, *Gerris*, and *Limnoporus* species (Fairbairn, 1990; Erlandsson, 1992; Andersen, 1994). Water striders are also dimorphic with respect to both primary and secondary sexual traits, especially shape and size of fore legs and terminal abdominal segments and genitalia (for examples see Matsuda, 1960 and Andersen, 1982a). Several authors have proposed that, given sexual conflicts over mating, male and female genitalia and other structures may be involved in a coevolutionary arms race (Parker, 1979; 1984; Arnqvist, 1995; Arnqvist & Rowe, 1995). This hypothesis predicts that males should evolve structures to cope with female resistance and that females should evolve structures to resist male harassment and to gain increased control over matings.

So far, studies of insect mating systems have chiefly been focused on single species or on comparisons among species without attention to their phylogenetic relationships. There have been few comparative studies of mating systems and associated structural features within monophyletic insect groups (groups that contain an ancestral species and all of its descendants). However, phylogenetic data can contribute significantly to studies of insect ecology and behavior by permitting inferences about the evolutionary history of traits (Brooks & McLennan, 1991; Harvey & Pagel, 1991; Eggleton & Vane-Wright, 1994; Spence & Andersen, 1994; Miller & Wenzel, 1995). This approach, ecological phylogenetics, is here used to study patterns of sexual dimorphism and mating systems in the monophyletic subfamily Gerrinae (Andersen 1975; 1982a; 1995), focusing on the evolution of sexual dimorphism in relation to mating systems and the coevolution of male clasping devices and female anticlasper devices.

METHODS

Size measurements and records of sexually dimorphic structures were obtained for 45 species (out of c. 160 described species) representing all 14 genera of the Gerrinae (Table 1). Male and female body size were measured (in mm) from the anterior margin of the head to the tip of the genital segments. Three types of data were used: (1) mean values for male and female body lengths

Table 1. – Total length of female (in mm), female/male (F/M) size ratio, male clasping devices (fore legs, genitalia), female anticlasper devices, and mating systems of water striders (Gerridae, Gerrinae). LW = long-winged adults, SW = short-winged or wingless adults. Definition of types of mating systems, see text.

Species	Wing morph	Female length	F/M ratio	Male clasping devices		Female anticlasper devices	Mating system	Source#
				Fore legs	Genitalia			
Limnoporus esakii	LW	10.0	1.25	no	no	yes	I	a
Limnoporus canaliculatus	SW	10.2	1.21	no	no	yes	I	b, c, l
Limnoporus notabilis	LW	18.1	1.04	no	no	yes	I, II	b, c, m
Limnoporus dissortis	LW	14.1	1.06	no	no	yes	I, II	b, c, m
Limnoporus rufoscutellatus	LW	15.5	1.09	no	yes	yes	I, II	d, n, o
Limnoporus genitalis	LW	13.8	1.10	yes	yes	yes	I	a, p
Aquarius najas	SW	16.5	1.28	yes	no	yes	I+	d, n, q
Aquarius cinereus	SW	12.7	1.32	yes	no	yes	I+	e, q
Aquarius remigis	SW	15.2	1.08	yes	yes	no	I+	f, r
Aquarius antigone	SW	13.4	1.17	yes	yes	yes	I	g, l
Aquarius paludum	SW	15.2	1.20	yes	yes	yes	I	d
Aquarius conformis	LW	16.5	1.09	yes	yes	yes	I+	f
Aquarius elongatus	LW	24.4	1.03	no	no	yes	I, II	h
Gerris incognitus	SW	9.5	1.12	yes	no	yes	I	f, s
Gerris nepalensis	SW	8.8	1.22	yes	no	yes	I	a, t
Gerris thoracicus	LW	13.5	1.13	yes	no	no	I	d
Gerris lacustris	SW	9.1	1.10	yes	no	no	I	d
Gerris latiabdominis	LW	10.9	1.16	yes	no	no	I	a, t
Gerris marginatus	LW	10.4	1.11	yes	no	no	I	i, u
Gerris comatus	SW	10.5	1.13	yes	no	no	I	f
Gerris odontogaster	SW	8.7	1.10	yes	yes	no	I	d
Gerris buenoi	SW	8.2	1.11	yes	no	no	I	f, v
Gerris argentatus	SW	7.3	1.19	yes	no	no	I	d
Gerris swakopensis	SW	7.1	1.15	yes	yes	yes	II	c, w
G. (Macrogerris) gracilicornis	LW	13.3	1.15	yes	no	no	I	a, t
G. (Gerriselloides) lateralis	SW	10.2	1.12	yes	no	no	I	d, x
Gigantometra gigas	LW	33.2	1.00	no	no	yes	?	c
Limnogonus fossarum	SW	8.7	1.23	yes	no	yes	I	c, g
Limnogonus buxtoni	SW	7.9	1.57	yes	no	no	?	j
Limnogonus windi	SW	6.5	1.18	yes	no	no	?	g
Limnogonus nitidus	SW	7.8	1.36	yes	no	yes	I+	c, j
L. (Limnogonoides) hypoleucus	SW	10.6	1.17	yes	no	yes	?	j
Tenagometrella grandiuscula	LW	13.3	0.85	no	no	yes	?	c
Tenagometra lanuginea	SW	7.5	1.14	yes	no	no	?	c
Tenagogonus albovittatus	SW	7.5	1.06	no	yes	no	I	c, x
Tenagogonus n.sp.	SW	8.8	1.18	no	no	no	?	g
Limnometra femorata	LW	16.6	0.80	no	no	yes	?	g
Limnometra cursitans	LW	13.4	0.86	no	no	yes	?	g
Limnometra anadyomene	LW	11.3	0.91	no	no	yes	?	c
Limnometra lipovskyi	SW	10.6	1.12	no	no	yes	?	g
Tenagogerris euphrosyne	SW	9.1	1.30	yes	no	yes	I+	c, g
Gerrisella settembrinoi	LW	5.8	1.10	yes	yes	no	?	c
Neogerris parvulus	SW	5.0	1.22	yes	no	yes	I	c, j
Tachygerris surinamensis	LW	6.8	1.15	no	no	yes	?	k
Eurygerris cariniventris	SW	7.1	1.05	yes	no	yes	?	k
Eurygerris flavolineatus	SW	8.5	1.60	yes	no	no	?	c

Source : a, Miyamoto, 1958; b, Andersen & Spence, 1992; c, N.M. Andersen, unpublished; d, Erlandsson, 1992; e, Andersen, 1990; f, Fairbairn, 1990; g, Andersen & Weir, in press; h, Hayashi, 1985; i, Bennett & Cook, 1981; j, Andersen, 1975; k, Nieser, 1970; l, C. Klingenberg, unpublished; m, Spence & Wilcox, 1986; n,Vepsäläinen, 1985; o, Vepsäläinen & Nummelin, 1985b; p, J. Spence, unpublished; q, Vepsäläinen & Nummelin, 1985a; r, Rubenstein, 1984; s, Arnqvist & Rowe, 1995; t, Hayashi, 1992; u, Arnqvist, 1989a; v, Rowe, 1992; w, Nummelin, 1988; x, Arnqvist, 1988.

obtained from the literature (sources listed in Table 1); (2) median values for ranges of body lengths obtained from the literature, and (3) mean values of actual measurements of specimens present in the Zoological Museum, University of Copenhagen. Size distributions usually approach normality in gerrids and the potential error introduced by using median rather than mean values for body lengths are therefore believed to be negligible. In order to simplify the analyses, measurements of adults representing different

populations were pooled to yield estimates for each species. A potential source of error is therefore the relatively large between-population variation in F/M ratios recorded for some gerrids (Fairbairn, 1990; Erlandsson, 1992). Gerrids are usually polymorphic for wing development, with long-winged (LW), short-winged and/or wingless adults (collectively termed SW) in the same population (Andersen, 1982a; 1993a). For the purpose of interspecific comparisons, only measurements of SW individuals were considered (except

in some species of *Aquarius*, *Gerris*, *Limnoporus*, *Limnometra*, and *Tachygerris* which always are LW).

The phylogenies

Phylogenetic hypotheses are available for the genera of the subfamily Gerrinae (Andersen 1995), and for species or species groups of *Aquarius* (Andersen, 1990), *Gerris* (Andersen, 1993b), and *Limnoporus* (Andersen & Spence, 1992). Other phylogenetic relationships shown in the cladograms (Figs. 2-4) are based on a preliminary study involving all genera of Gerridae (N.M. Andersen, unpublished data). The subfamily Eotrechinae, the putative sister group of the Gerrinae (Andersen, 1982a; 1982b; Polhemus & Andersen, 1984), is used as outgroup in the phylogenetic analyses. The relationships depicted in a cladogram published by Calabrese (1980) are disregarded because they cannot be independently verified (Andersen, 1990; Andersen & Spence, 1992; Spence and Andersen, 1994).

The characters

The characters of interest in this paper are : (1) the female/male (F/M) size ratio; (2) male clasping fore legs; (3) male clasping genitalia; (4) female anticlasper devices; and (5) mating systems. The meaning of these characters and their states are explained below. Andersen (1994) used the "continuous variable" option of MacClade 3.0 (Maddison & Maddison, 1992) to map the distribution of residual F/M ratios on a phylogeny. In order to simplify the analyses of the present study, the observed range of F/M ratios was divided into four intervals which were scored as discrete states of one character : F/M ratio $< = 1.04$ (0); 1.05-1.14 (1); 1.15-1.24 (2); and > 1.25 (3). Characters (2)-(4) describing the state of male clasping and female anticlasper devices are simply scored as (0) absent or (1) present. Finally, the following states were recognized in character no. 5, mating systems (following Arnqvist, 1995) : type I (0); type I+ (with extended post-copulatory mate guarding) (1); and type II matings (2). These characters were optimized upon the phylogenetic hypotheses mentioned above. Sexually dimorphic traits, such as shape and size of fore legs and terminal abdominal segments, only constitute a small part of the total array of structural characters used to reconstruct these phylogenies. The basic assumption of independence between phylogenetic hypotheses and the traits of interest is therefore not seriously compromised.
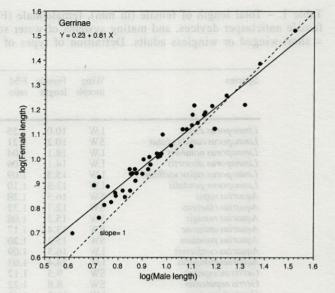

Fig. 1. – Regression plot of male length versus female length (both log-transformed) for selected species belonging to the subfamily Gerrinae (the species listed in Table 1). Regression lines for the actual relationship (slope = 0.81) and for isometric relationship (slope = 1) are also shown. Further discussion in text.

RESULTS

Optimization of sexually dimorphic characters

The variation in female body size and F/M ratio in selected gerrines is summarized in Table 1. Regression plots of male length versus female length (both log-transformed) are shown in Fig. 1 (based on the species listed in Table 1). The pattern of variation in F/M ratios optimized upon the phylogeny of the Gerrinae (Fig. 2A) indicates that a F/M ratio well below 1.25 is the ancestral state in the subfamily as it is in the outgroup Eotrechinae. Transitions to a F/M ratio above 1.25 have occurred in *Eurygerris flavolineatus* (Champion), *Tenagogerris euphrosyne* (Kirkaldy) (and two undescribed species of this Australian genus; Andersen & Weir, in press), *Limnogonus buxtoni* China and *L. nitidus* (Mayr) (Andersen, 1975), and in the *Aquarius najas* group (with four species; Andersen, 1990).

In species belonging to the subfamily Gerrinae, the fore femora are usually more robust in males than in females (Andersen, 1975; 1990; 1993b), curved and ventrally modified in *Eurygerris* and some *Tachygerris* species (Matsuda, 1960). The optimization of male fore leg structure on the gerrine phylogeny (Fig. 2B) suggests that fore legs modified for grasping is the ancestral state. Transitions to a state where the fore femora are slender in both sexes are observed in *Aquarius elongatus*, most *Limnoporus* species, in *Gigantometra gigas* (China) and in species of *Tenagogo-*

nus and *Limnometra*, which include some of the largest water striders (Hungerford & Matsuda, 1958; Matsuda, 1960; Hayashi, 1985; Andersen & Spence, 1992; Andersen & Weir, in press).

The gerrid male abdomen is composed of seven pregenital segments (only six visible on ventral side) and three genital segments which are withdrawn into the pregenital abdomen (Matsuda, 1960; Andersen, 1982a; 1993b). The genital segments are composed of the cylindrical segment 8 and the boat-shaped pygophore (segment 9) upon which lies the lid-shaped proctiger (segment 10). A pair of falciform parameres (genital claspers of Andersen, 1982a) are typically attached laterally to the edge of the pygophore. The phallic organ is hidden inside the pygophore when not inflated for copulation, and is composed of a sclerotized phallotheca and a membranous endosoma (or aedeagus), which again is divided into the conjunctivum and vesica. The latter has various sclerotized structures of great taxonomic importance (Andersen, 1975; 1990; 1993b; Andersen & Spence, 1992). Gerrine water striders lack large, clasping parameres, but many species have enlarged genital segments and various outgrowths or processes on the male terminal abdominal segments which may have a similar, clasping function. The optimization of male genital structure on the gerrine phylogeny (Fig. 3A) indicates that clasping genital structures have evolved in *Gerrisella settembrinoi* Poisson, *Tenagogonus albovittatus* (Stål), *Limnometra lipovskyi* Hungerford & Matsuda, *Limnoporus rufoscutellatus* (Latreille) and *L. genitalis* Miyamoto, in some *Aquarius* species, and in *Gerris odontogaster* (Zetterstedt) and *G. swakopensis* Stål (Hungerford & Matsuda, 1958; Matsuda, 1960; Andersen, 1990; 1993b; Andersen & Spence, 1992).
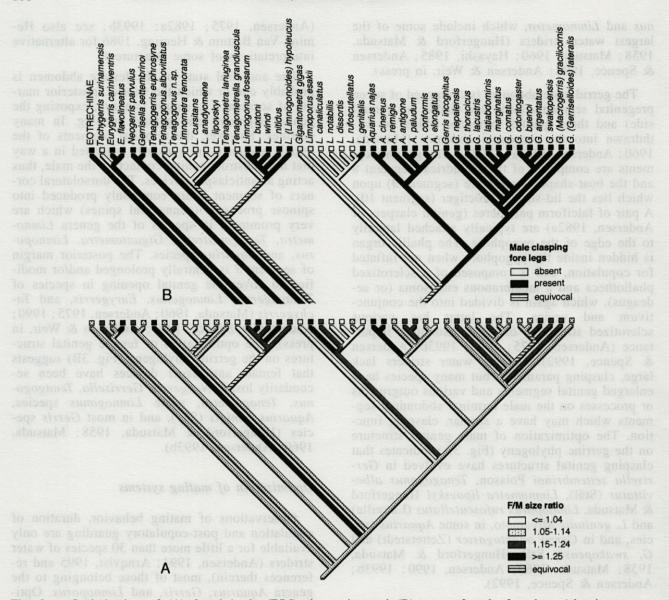
The gerrid female abdomen is composed of seven pregenital segments (only six visible on ventral side) (Matsuda, 1960; Andersen, 1982a; 1993b) and three genital segments which are inserted in the pregenital abdomen facing caudad and slightly ventrad. The large segment 8 is divided along the ventral midline into two, plate-shaped gonocoxae ("valvifers" of Matsuda, 1960); the eighth tergum carries the cone-shaped proctiger on its posterior margin. The ovipositor is normally concealed within segment 8, but is extended during oviposition. It is composed of two pairs of gonapophyses ("valvulae" of Matsuda, 1960) which form a tubular, egg-laying device. Female water striders have a very complicated internal reproductive system, the gynatrial complex, for the acceptance, storage, and distribution of sperm and fertilization of eggs. The gynatrial complex lies on top of the genital chamber and is typically composed of a gynatrial sac, an extremely long, tubular spermatheca, and a fecundation canal provided with a sperm pump

(Andersen, 1975; 1982a; 1993b; see also Heming-Van Battum & Heming, 1986 for alternative interpretations of some structures).

The ancestral state of the female abdomen is probably one in which the ventral, posterior margin of segment 7 is simply concave, exposing the genital segments and genital opening. In many gerrines, however, the terminal segments of the female abdomen are variously modified in a way that may obstruct genital contact by the male, thus acting as anticlasper devices. The dorsolateral corners of segment 7 are commonly produced into spinose processes (connexival spines) which are very prominent in species of the genera *Limnometra*, *Tenagometrella*, *Gigantometra*, *Limnoporus*, and *Aquarius* species. The posterior margin of segment 7 is ventrally prolonged and/or modified to cover the genital opening in species of *Tenagogerris*, *Limnogonus*, *Eurygerris*, and *Tachygerris* (Matsuda, 1960; Andersen, 1975; 1990; Andersen & Spence, 1992; Andersen & Weir, in press). The optimization of female genital structures on the gerrine phylogeny (Fig. 3B) suggests that female anticlasper devices have been secondarily lost in *Neogerris*, *Gerrisella*, *Tenagogonus*, *Tenagometra*, some *Limnogonus* species, *Aquarius remigis* (Say), and in most *Gerris* species (Hungerford & Matsuda, 1958; Matsuda, 1960; Andersen, 1993b).

Optimization of mating systems

Observations of mating behavior, duration of copulation and post-copulatory guarding are only available for a little more than 30 species of water striders (Andersen, 1994; Arnqvist, 1995 and references therein), most of these belonging to the genera *Aquarius*, *Gerris*, and *Limnoporus*. Optimization of mating systems on the gerrine phylogeny (Fig. 4) indicates that the ancestral type of mating behavior for these genera as well as for the subfamily as a whole probably was "scramble competition polygyny" (type I matings of Arnqvist, 1995). Transitions to "resource defence polygyny" (type II matings of Arnqvist, 1995) have occurred independently in the *Limnoporus rufoscutellatus* group (Vepsäläinen & Nummelin, 1985b; Spence & Wilcox, 1986; Wilcox & Spence, 1986), *Aquarius elongatus* (Uhler) (Hayashi, 1985), and in *Gerris swakopensis* (Nummelin, 1988). Type I+ matings with extended post-copulatory guarding (guarding lasts for several hours or even days) occurs in the *Aquarius najas* group (Sattler, 1957; Vepsäläinen & Nummelin, 1985a; Murray & Giller, 1990) and in *A. conformis* (Uhler) (Fairbairn, 1990; Arnqvist, 1995). In *A. remigis*, pairs remain in copula for a long period of time (Wilcox, 1984; Clark, 1988; Rubenstein, 1989; Sih *et al.*, 1990; Fairbairn, 1990).

Fig. 2. – Optimization of (A) female/male (F/M) size ratios and (B) state of male fore legs (clasping versus non-clasping) on the reconstructed phylogeny of the Gerrinae. Further explanations in text.

The relationships between F/M ratio, male clasping devices, and mating systems

Gerrine water striders typically have male grasping fore legs (Fig. 2B), but the male fore femora of the larger species (*Limnometra* spp., *Tenagometrella grandiuscula*, *Gigantometra gigas*, the *Limnoporus rufoscutellatus* group, and *Aquarius elongatus*) are slender and seemingly not adapted for grasping the female's thorax. This usually coincides with F/M ratios about or below 1, which indicates that the male is as big as or even bigger than the female. Clasping devices of the male terminal abdominal segments (other than parameres) have secondarily evolved in *Gerrisella settembrinoi* and in some species of *Tenagogonus*, *Limnometra*, *Limnoporus*, *Aquarius*, and *Gerris*,

all with a F/M ratio below 1.25 (Fig. 3A). Extended post-copulatory mate guarding is weakly associated with a large F/M ratio (*Tenagogerris euphrosyne*, *Limnogonus nitidus*, and the *Aquarius najas* species group) and with the absence of male clasping genitalia (but not grasping fore legs). Type II matings are weakly associated with non-grasping male fore legs and (in *Aquarius elongatus*) also with relatively unmodified male genitalia.

Coevolution of male clasping genitalia and female anticlasper devices

The presence of female anticlasper devices is not the ancestral state in the Gerridae but have
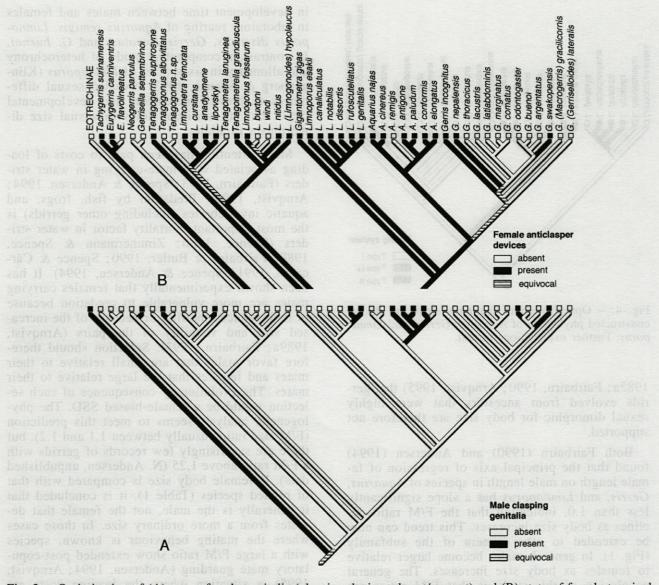
Fig. 3. – Optimization of (A) state of male genitalia (clasping devices absent/present) and (B) state of female terminal abdominal segments (anticlasper devices absent/present) on the reconstructed phylogeny of the Gerrinae. Further explanations in text.

evolved a number of times in the family, with or without the presence of male clasping genitalia (N. Andersen, unpublished data). Structures interpreted as anticlasper devices (connexival spines) have evolved in the absence of male clasping genitalia at the base of the Gerrinae (Figs. 3A and 3B), but have been secondarily lost in species of *Eurygerris, Neogerris + Gerrisella, Tenagogonus, Tenagometra, Limnogonus*, in *Aquarius remigis*, and in most species of *Gerris* s.lat. The presence of connexival spines in *Gerris incognitus* Drake & Harris, *G. nepalensis* (Distant), and *G. swakopensis* is interpreted as secondary. Thus, female anticlasper devices have been lost more often than they have evolved in the species studied and the association between male clasping genitalia and female anticlasper devices is not significant.

DISCUSSION

The largest species of Gerrinae (and of the whole family), *Gigantometra gigas*, is about 7 times as large as the smallest species belonging to the genus *Neogerris* (Table 1). Female/male size ratios varies between 0.8 for some species of *Limnometra* and 1.6 for *Limnogonus buxtoni* and *Eurygerris flavolineatus*. The phylogenetic analysis suggests that males of ancestral gerrines were primitively of about the same size or slightly smaller than conspecific females (F/M ratio between 1.0 and 1.15) and that a more pronounced sexual size dimorphism (F/M ratio above 1.25) has independently evolved several times in the subfamily. Previous suggestions (Andersen,
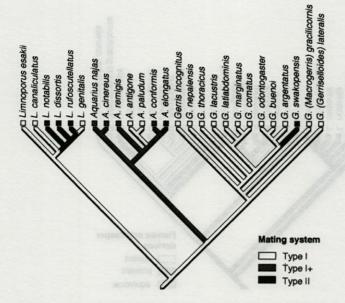
Fig. 4. – Optimization of mating systems on the re-constructed phylogeny of *Aquarius*, *Gerris*, and *Limno-porus*. Further explanations in text.

1982a; Fairbairn, 1990; Arnqvist, 1995) that ger-rids evolved from ancestors that were highly sexual dimorphic for body size are therefore not supported.

Both Fairbairn (1990) and Andersen (1994) found that the principal axis of regression of fe-male length on male length in species of *Aquarius*, *Gerris*, and *Limnoporus* has a slope significantly less than 1.0, indicating that the F/M ratio de-clines as body size increases. This trend can now be extended to other genera of the subfamily (Fig. 1). In general, males become larger relative to females as body size increases. The general conclusion of this study is that F/M ratios are highly variable within and between genera, and that there are no easily recognized, global phylo-genetic effects or "constraints" on sexual size dimorphism in the Gerrinae. This confirms the conclusions by Fairbairn (1990) and Andersen (1994) based on smaller samples of species.

Several factors have been proposed to influence sexual size dimorphism (SSD) in water striders (Fairbairn, 1990; Andersen, 1994; Fairbairn & Preziosi, 1994; Spence & Andersen, 1994; Arnq-vist, 1995; Blanckenhorn et al., 1995). The gene-ral proposition that patterns of SSD are mainly nonadaptive outcomes of allometric growth is not necessarily valid for gerrids (Fairbairn, 1990; An-dersen, 1994) and the correlated increase of leg lengths are of obvious importance since leg length is clearly an adaptive character in water striders (Spence, 1981; Andersen, 1982a; Fairbairn, 1992; Klingenberg & Zimmermann, 1992; Klingenberg & Spence, 1993; Fairbairn & Preziosi, 1994). Fairbairn (1990) found no significant differences

in development time between males and females in laboratory rearing of *Aquarius remigis*, *Limno-porus dissortis*, *Gerris comatus*, and *G. buenoi*. In contrast, a comparative study of heterochrony and allometry in six species of *Limnoporus* (Klin-genberg & Spence, 1993) revealed sexual diffe-rences in growth increments and developmental times, but no consistent links to sexual size di-morphism in adults.

Much attention has been paid to costs of loa-ding associated with mate-carrying in water stri-ders (Fairbairn, 1993; Spence & Andersen, 1994; Arnqvist, 1995). Predation by fish, frogs, and aquatic invertebrates (including other gerrids) is the most important mortality factor in water stri-ders (Spence, 1986; Zimmermann & Spence, 1989; Fairbairn & Butler, 1990; Spence & Cár-camo, 1991; Spence & Andersen, 1994). It has been shown experimentally that females carrying males are more vulnerable to predation because of their reduced motility or because of the increa-sed size and visibility of the pairs (Arnqvist, 1989a; Fairbairn, 1993). Selection should there-fore favor males that are small relative to their mates and females that are large relative to their mates. The evolutionary consequence of such se-lection would be a female-biased SSD. The phy-logenetic analysis seems to meet this prediction (F/M size ratios usually between 1.1 and 1.2), but there are surprisingly few records of gerrids with a F/M ratio above 1.25 (N. Andersen, unpublished data). If female body size is compared with that of related species (Table 1), it is concluded that it generally is the male, not the female that de-viates from a more ordinary size. In those cases where the mating behaviour is known, species with a large F/M ratio show extended post-copu-latory mate guarding (Andersen, 1994; Arnqvist, 1995), a situation where the loading costs are assumed to be highest. An alternative explanation of the advantage of small male size has recently been offered by Blanckenhorn et al. (1995) based on the hypothesis that selection favors small males because they use less energy in maintaining activity and therefore may devote more time to search for mates.

The present phylogenetic analysis suggests that males of ancestral water striders had powerful fore legs adapted to grasp the female's thorax during mating, and had clasping genitalic struc-tures suited to grasp or pinch the female poste-riorly. It is also suggested that females of these ancestral gerrids had relatively unspecialized ter-minal abdominal segments. The ancestral and most common mating system in gerrine water striders has been categorized as "scramble compe-tition polygyny" (Thornhill & Alcock, 1983; An-dersen, 1994; Spence & Andersen, 1994; "type I matings" of Arnqvist, 1995) and is characterized by apparent conflicts and dramatic struggles,

where the male tries to gain control over the female which respond with vigorous resistance. It is argued in several recent papers (Rowe *et al*, 1994; Arnqvist, 1995 and references therein) that the predominant mating system in water striders is a direct consequence of sexual conflicts over mating decisions. Matings involve high costs to females (risk of predation and energetic expenditure) but very few, if any, benefits. Relatively few matings are enough for a female to get all of her eggs fertilized. Females are therefore under selection not to mate (Parker, 1979). In contrast, the reproductive success of males is associated with the number of females they mate. Since sperm displacement rates seem to be high in gerrids (Arnqvist, 1988; Rubenstein, 1989, J. Spence, unpublished data), the last male to mate will fertilize most of the female's eggs. Thus, there is a strong selective advantage in males to reduce sperm competition by guarding a female for a certain period of time. Typically, the male rides passively on the female's back during guarding, but in *Limnogonus nitidus* the male is positioned far back on the female and is towed around (Andersen, 1982a and unpublished data). In *Aquarius elongatus* and probably in other species where the male is the larger sex, the male carries the passive female beneath (Hayashi, 1985 and personal communication). Males normally retract their phallic organ during guarding, but *Aquarius remigis* males prolong copulation beyond the time necessary for sperm transfer, thus acting as living mating plugs (Wilcox, 1984; Clark, 1988; Rubenstein, 1989; Sih *et al.*, 1990; Fairbairn, 1990). The prolonged phallic vesica of this species may be an adaptation to that function (Matsuda, 1960).

Direct empirical evidence on sexual selection for body size in water striders is scarce and partly contradictory (Arnqvist, 1995). Females should allow small males to mate longer due to reduced costs of loading (Fairbairn, 1993), but most studies actually show sexual selection for large males (Hayashi, 1985; Fairbairn, 1988; Sih & Krupa, 1992; Krupa & Sih, 1993; Fairbairn & Preziosi, 1994). Large males should be better able to subdue reluctant females and in species where the male is the larger sex, males are known to carry the females during copulation (Andersen, 1982 and unpublished data). A phenomenon which needs further exploration is the extraordinary large variance in male size reported in some water strider species, e.g., *Limnometra anadyomene* (N. Andersen, unpublished data), *L. lipovskyi* (Andersen & Weir, in press), and *Tenagometra lanuginea* (Andersen, 1982a).

It is assumed that males with the more powerful fore legs are better able to grasp the female's thorax during copulation and sexual selection for more incrassate femora has been experimentally demonstrated in *Aquarius remigis* males (Rubenstein, 1984). The terminal abdominal segments and genitalia are modified in many water striders, provided with outgrowths and processes of various shape and large, clasping parameres (Matsuda, 1960; Andersen, 1982). It is assumed that such modifications function as claspers during copulation. In *Gerris odontogaster*, males are provided with paired, tooth-like processes on the venter of the seventh abdominal segment (Arnqvist, 1989b; Andersen, 1993b). Through a series of studies, Arnqvist (1989a; 1989b; 1992a; 1992b; 1992c; 1994) has convincingly demonstrated that these structures are critical for males in enduring the pre-copulatory struggle by the female, and hence achieve more matings both in the laboratory and the field. Thus, in *G. odontogaster* there is sexual selection by female choice for long ventral teeth with a clasping function. More casual observations suggest that many, if not all, modifications of the male genitalia in water striders have a similar function (Andersen, 1982a).

Several authors have proposed that, given sexual conflicts over mating decisions, females should evolve counter-adaptations to cope with sexual harassment and to gain increased control over matings (Parker, 1979; 1984; Eberhard, 1985; Arnqvist, 1995). The connexival spines of *Gerris incognitus* females have been found to function in this way. By manipulating the length of these spines Arnqvist & Rowe (1995) showed that the spines increase female ability to dislodge males during the pre-copulatory struggle, and thus gain increased control over mating decisions. As shown in the present study, a number of structures of the terminal abdominal segments of females are potential candidates for a similar function. If such traits represent "counter-adaptations" to enable females to control matings by making it more difficult for males to establish genital contact, one should expect that such anticlasper devices had evolved at the same time or immediately after the evolution of male genital clasping devices. Comparisons between the optimization of female and male traits on the reconstructed phylogeny of the Gerrinae (Figs. 3A and 3B) suggest that female anticlasper devices (especially connexival spines) have evolved in the absence of male clasping genitalia in this subfamily. In this sense, females seemingly have taken the lead in the "arms race" between sexes. However, by making it costly for females to resist matings (e.g., when harassment rates are high), males may be said to have won the "battle of the sexes" (Arnqvist, 1995). Thus, the hypothesis of an evolutionary "arms race" between sexes cannot be unambiguously tested, at least not for the Gerrinae.

Type II matings (Arnqvist, 1995) or "resource defence polygyny" (Thornhill & Alcock, 1983; Andersen, 1994; Spence & Andersen, 1994) see-

mingly evolved from type I matings at least four times during the evolutionary history of the Gerridae : (1) in the genus *Rhagadotarsus* (Wilcox, 1972; Nummelin, 1988; N. Andersen, unpublished data); (2) in *Aquarius elongatus* (Hayashi, 1985); (3) in species of *Limnoporus* (Spence & Wilcox, 1986; Wilcox & Spence, 1986); and in *Gerris swakopensis* (Nummelin, 1988). It should be emphasized, however, that sexual behavior used to categorize mating systems are not at all rigid and that both males and females may use alternative behaviors. For instance, *Aquarius elongatus* shows both type I and type II as well as intermediate mating behavior varying through the season (Hayashi, 1985, and personal communication). Spence & Wilcox (1986) also showed that males of both *Limnoporus dissortis* and *L. notabilis* employ the full range in mating behavior. Finally, observations of *Gerris swakopensis* in the laboratory suggest that males are not necessarily territorial either (J.R. Spence, unpublished).

Arnqvist (1995) suggested that sexual conflicts has played a crucial role in the evolution of type II mating behavior from type I matings. As in other insects, female water striders are particularly sensitive to male harassment during oviposition. In cases where type II matings are involved, males provide females with oviposition sites and protect them from harassment by other males. Female *Limnoporus* were found to lay more eggs if protected by a guarding male (Spence & Wilcox, 1986). If females, in order to achieve such protection, evolve traits (behavioral and/or structural) that increase their control of mating initiation, it may be more profitable for males to be more sedentary and to "court" rather than harass females. In type II matings, males are typically territorial, defending suitable oviposition sites, seeking to attract females by surface ripple signals (Wilcox, 1972; Hayashi, 1985; Wilcox & Spence, 1986; Nummelin, 1988). Males of *Aquarius elongatus* respond aggressively towards other males and engage in fights to defend their territory. The middle legs of the male (which are relatively longer than in the female) are used as weapons during such fights, but I suggest that they also may have an "ornamental" function during the courtship (Hayashi, 1985 and personal communication). Sexual differences in the middle and/or hind legs of *Gigantometra gigas* and some *Limnometra* species (Hungerford & Matsuda, 1958; Andersen, 1982a; Andersen & Weir, in press) may suggest a similar function.

In conclusion, there is a considerable interspecific variation in sexual dimorphism and mating behavior in water striders belonging to the subfamily Gerrinae. There are no obvious, global phylogenetic effects or "constraints" on sexual dimorphism in the group, but phylogeny has played a certain role in shaping patterns of F/M size ratios, male clasping devices, and female anticlasper devices within clades. There is no support for the hypothesis that male and female genitalia and other structures have been involved in a coevolutionary "arms race". Finally, the phylogenetic effects on patterns of mating behavior are negligible as demonstrated by the large amount of interspecific variation in some genera (e.g., *Limnoporus*, *Aquarius*, and *Gerris*), and by the fact that males of the same species may show alternative mating tactics depending on ecological circumstances (Spence & Andersen, 1994). Many aspects of the biology of water striders make them ideal for both comparative and experimental behavioral studies and a growing literature has proven water strider to be well suited to address many general issues about the evolution of mating systems. I hope that this paper will stimulate additional, taxonomically broadly based studies of sexual dimorphism and mating systems in this group of insects.

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