

MINI REVIEW

Sexually antagonistic coevolution in insects is associated with only limited morphological diversity

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Abstract

Morphological traits involved in male–female sexual interactions, such as male genitalia, often show rapid divergent evolution. This widespread evolutionary pattern could result from sustained sexually antagonistic coevolution, or from other types of selection such as female choice or selection for species isolation. I reviewed the extensive but under-utilized taxonomic literature on a selected subset of insects, in which male–female conflict has apparently resulted in antagonistic coevolution in males and females. I checked the sexual morphology of groups comprising 500–1000 species in six orders for three evolutionary trends predicted by the sexually antagonistic coevolution hypothesis: males with species-specific differences and elaborate morphology in structures that grasp or perforate females in sexual contexts; corresponding female structures with apparently coevolved species-specific morphology; and potentially defensive designs of female morphology. The expectation was that the predictions were especially likely to be fulfilled in these groups. A largely qualitative overview revealed several surprising patterns: sexually antagonistic coevolution is associated with frequent, relatively weak species-specific differences in males, but male designs are usually relatively simple and conservative (in contrast to the diverse and elaborate designs common in male structures specialized to contact and hold females in other species, and also in weapons such as horns and pincers used in intra-specific battles); coevolutionary divergence of females is not common; and defensive female divergence is very uncommon. No cases were found of female defensive devices that can be facultatively deployed. Coevolutionary morphological races may have occurred between males and females of some bugs with traumatic insemination, but apparently as a result of female attempts to control fertilization, rather than to reduce the physical damage and infections resulting from insertion of the male's hypodermic genitalia. In sum, the sexually antagonistic coevolution that probably occurs in these groups has generally not resulted in rapid, sustained evolutionary divergence in male and female external sexual morphology. Several limitations of this study, and directions for further analyses are discussed.

Introduction

Traits specialized for male–female interactions have long been known to commonly show rapid and divergent evolution, and thus to differ even among closely

related species (West-Eberhard, 1983; Eberhard, 1985; Andersson, 1994). Traits such as courtship songs and male genitalia are often key traits for distinguishing species (e.g. Mayr, 1963) (Fig. 1). This rapid divergence has enabled taxonomists to use these structures as key traits for distinguishing species, and there is an immense, but under-utilized taxonomic literature, which allows surveys of the evolutionary patterns in these and other traits. Why this particular set of traits should tend to diverge rapidly continues to be debated (e.g. Hosken &

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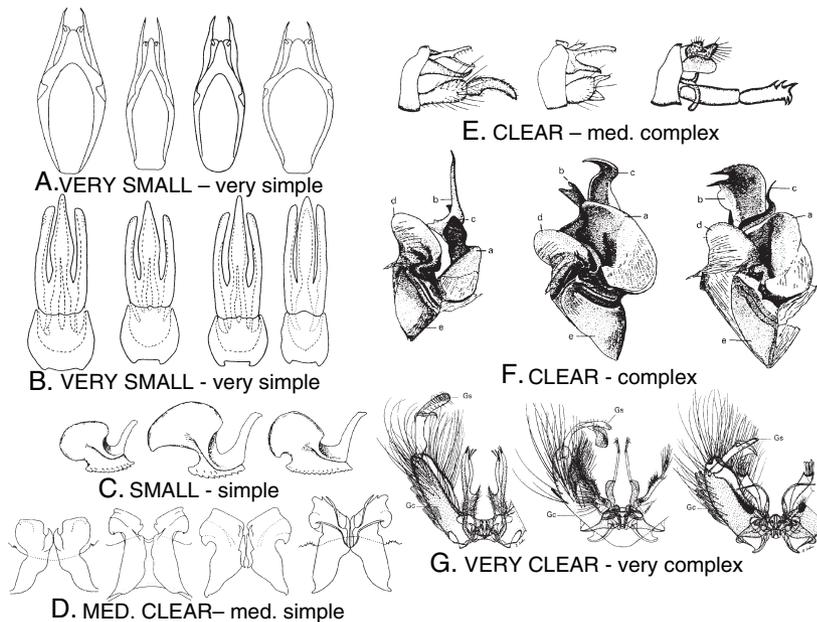


Fig. 1 Different degrees of intra-generic differences (upper case) and complexity (lower case) of male genitalia. Each set of three or four consists of different congeneric species (after Eberhard, 2004a): (a) *Selenodon* (Coleoptera: Cebriionidae) (from Galley, 1999); (b) *Trichogramma* (Hymenoptera: Trichogrammatidae) (from Pinto, 1998); (c) *Pheidole* (Hymenoptera: Formicidae) (from Ogata, 1982); (d) *Hexagenia* (Ephemeroptera: Ephemeridae) (from Burks, 1953); (e) *Apantania* (Trichoptera: Limmephilidae) (from Malicky, 1983); (f) *Periplaneta* (Blattaria, Blattidae) (from Walker, 1922); (g) *Aedes* (sub. gen. *Paraedes*) (Diptera: Culicidae). These categories were used to classify male structures in Figs A2–6 and A9 (Appendix) with respect to intra-generic differences and complexity.

Stockley, 2004). One currently popular hypothesis, sexually antagonistic coevolution, is based on the fact that the reproductive interests of a female are seldom completely congruent with those of the males that attempt to mate with her. In general, mating is less advantageous for females than for males. In some cases selection has led to males that manipulate (or attempt to manipulate) females in ways that reduce the female's direct fitness (i.e. the number of surviving offspring) (Chapman *et al.*, 2003). When such a male trait arises, selection is expected to favour female abilities to reduce the damaging male effects. This can result in a coevolutionary arms race between the sexes, leading to the 'cyclical chases' of Parker (1984), the 'evolutionary chases' of Alexander *et al.* (1997), and the 'chase away' of Holland & Rice (1998). If in such coevolutionary chases neither male nor female traits result in a stable solution to the problems posed by the other sex, extended coevolution could thus explain the rapid divergent evolution that is so common in morphological and behavioural traits involved in male–female interactions. In addition, frequent divergence among closely related species is expected, because the particular male or female traits favoured in a given evolutionary lineage depends on the traits of the other sex in the same lineage. Inasmuch as there are differences in either sex among lineages, this selection is likely emphasize the differences.

These theoretical predictions have been discussed repeatedly (Alexander *et al.*, 1997; Holland & Rice, 1998; Arnqvist & Rowe, 2002a,b; Chapman *et al.*, 2003; Rowe & Arnqvist, 2002), and are supported by some experimental evidence (Martin & Hosken, 2003). On the other hand, some theoretical discussions (Parker, 1979; Moore & Pizzari, 2005; Rowe *et al.*, 2005) have

emphasized that one sex may often win out in such coevolutionary battles: 'the zone of positive payoffs of the sex' with the higher cost function '...could be a relatively small one' (Parker, 1979 p. 157). Male–female antagonistic coevolution is only likely when there are certain balances in the relative power of each sex to control the outcome of conflicts (e.g. asymmetries in the cost functions of Parker, 1979). Sustained rapid divergent evolution in male and female morphology when sexually antagonistic coevolution occurs has been documented in a few cases (Arnqvist & Rowe, 2002a,b; Rowe & Arnqvist, 2002).

There are other possible explanations for the trend toward rapid evolutionary divergence of sexual traits, including sexual selection by female choice and selection for reproductive isolation, and there is currently sharp disagreement over the relative importance of the different hypotheses for explaining patterns of rapid divergent evolution (Alexander *et al.*, 1997; Eberhard, 1997, 2004a, b; Arnqvist & Rowe, 2002a,b; Chapman *et al.*, 2003; Cordero & Eberhard, 2003,2005; Pizzari & Snook, 2003; Arnqvist, 2004; Hosken & Snook, 2005; Crudginton *et al.*, 2005). Empirical tests are thus of interest.

Previously I attempted to test sexually antagonistic coevolution and female choice ideas empirically by surveying groups with rapid divergent morphological evolution. I checked to see if such groups tend to have traits that increase the chances for male–female conflict (Eberhard, 2004a), and have the predicted antagonistic designs (Eberhard, 2004b). Both these types of evidence suggested that sustained sexually antagonistic coevolution of morphology is uncommon. The approach in this review is the inverse. I review groups in which there are

especially good reasons to suppose a history of sexually antagonistic coevolution in morphology associated with males grasping and perforating females, and ask whether their male and female external morphology shows three characteristics predicted by such coevolution: rapid divergent evolution and morphological elaboration of male structures that are specialized to interact with the female in ways that may reduce her reproductive potential (grasp or perforate her); rapid divergent evolution of the corresponding female structures that are contacted by the male; and species-specific 'defensive' designs of female structures that can reduce the cost imposed on the female by the male species-specific structures. Female designs allowing facultative female defence against males (e.g. spines that can be erected, moveable hoods), and thus allow the female to avoid excluding all males (also surely disadvantageous) were considered especially likely. The expectation was that the predictions would be particularly likely to be fulfilled in these groups.

The review thus does not question whether or not sexually antagonistic coevolution ever occurs (this seems quite likely in some groups); rather, it asks what happens to male and female morphology when it does occur. If these species with sexually antagonistic coevolution are associated with the expected patterns in males and females, the argument that sustained antagonistic coevolution has been of general importance in generating observed cases of rapid divergence will be strengthened. Conversely, lack of such association would strengthen alternative hypotheses such as female choice, which predict frequent (though not necessarily complete) lack of species-specific female structures, and frequent selectively cooperative rather than defensive female designs (Eberhard, 1985, 2004b).

Materials and methods

Taxonomic literature was checked in groups for which I found data suggesting antagonistic coevolution of males and females. Several of these groups (*Gerris* waterstriders, dytiscid beetles and bed bugs) have been mentioned by others as possible examples of sexually antagonistic coevolution; others were discovered during reading for other projects. In order to be included in this study, a taxon had to fulfil three criteria: there was some reason to believe that females typically suffer direct costs in their reproductive output due to mating (e.g. reduced survivorship or fecundity); males possess structures that are specialized for interactions with females and whose apparent function could be contrary to the female's interests (either grasping her, or penetrating her body in nongenitalic areas); and some aspect of female morphology (e.g. the area where the specialized male structures seized her) or her behaviour is modified in a way that indicates that females have evolved to adjust to the male structures. I attempted to

include all the groups with the strongest evidence of morphological sexually antagonistic coevolution. I excluded a number of other groups (other beetles, flies, bees and spiders) in which specialized male structures may be damaging to females but in which there is no evidence that female morphology has responded evolutionarily to the male structures (see 'Other groups' in the Appendix).

The results for most groups are illustrated with drawings from taxonomic papers and are also intended to function as data documenting different degrees of complexity of design, using the scale ('very simple' to 'very complex') employed in a previous publication (Eberhard, 2004a) (Fig. 1). Similarly, the degree of difference between congeneric species was rated from 'very small' to 'very clear' (Eberhard, 2004a) (Fig. 1). The figures thus allow the reader the opportunity to see first hand both the degree of differences between congeneric species and higher taxonomic categories, and the overall complexity of the male structures. It should be kept in mind that some drawings are 'sketches' to illustrate salient details that are important for distinguishing species, rather than complete detailed portraits (compare Figs A6 and A7). Both design complexity and species differences were estimated qualitatively; I did not attempt to quantify these aspects of form, to avoid the illusion of precise quantification. Differences in the degrees of morphological detail that different taxonomists include in their drawings (again see Figs S6 and S7) preclude simple, straightforward analyses of drawings from different sources. In addition, there is no guarantee that such quantification, and the statistical tests derived from it, reflects the aspects of the structures that are biologically most important (Eberhard, 2004a) (see 'Limitations and future directions' below).

Results

The evidence regarding the three predictions for rapid divergence in 13 different groups under sexually antagonistic coevolution is summarized in Table 1. Detailed presentations of the evidence for sexually antagonistic coevolution and figures that document much of the evidence are given in the Appendix. Several additional groups not included in Table 1 are also discussed there ('groups not included').

Discussion

General trends

The most important trends in Table 1 are the following: (1) the male morphological traits involved in antagonistic sexual interactions tend to be species-specific, as predicted by the hypothesis that they are the result of sustained sexually antagonistic coevolution (there are, however, some exceptions); (2) the male traits tend to have

Table 1 Summary of information on male structures that may reduce female reproductive potential, and the parts of the female with which these male structures interact. All data refer only to these male and female structures.

Taxon	Male structure, mechanical functions	Male-imposed cost for female	Male species-specific?	Female species-specific?	Degree diff. between congeneric males	Degree male complexity	Female design coevolved with male?	Female design defensive?	Male stimulating function?
Diptera									
<i>Lucilia</i> (20 species)	Genitalia, perforate	Perforate reproductive tract	Yes	?	Clear	Complex	Probably†	Yes	?‡
<i>Glossina</i> (20 species)	Genitalia, grasp	Scrape, perforate abdomen	Yes	No	Clear	Mod. complex	No	Yes/No\$	Yes
Hemiptera									
<i>Gerris</i> (20 species)	Several, grasp	Mortality (predation)	Yes¶	Yes	Weak	Simple	Yes	Yes	?‡
Cimicidae (30 species, 5 genera)	Genitalia, perforate	Hole in cuticle, infections	Yes	Some	Weak	Simple (secondarily reduced)	Some external also internal	No (external), ** Yes? (internal)	?‡†
Anthocoridae (400 species, 54 genera)	Genitalia, perforate	Hole in cuticle, infections?‡‡	Yes	Some	Weak in most	Simple (secondarily reduced)	Some external some internal	No? (external) Yes? (internal)\$\$?‡
Polycitenidae	Genitalia, perforate	Hole in cuticle, infections?‡‡	No	No	None	Simple (secondarily reduced)	None	No	?‡
Plokiophilidae (<30 species, 4 genera)	Genitalia, perforate	Hole in cuticle, infections?‡‡	Yes	Some	Weak	Simple (secondarily reduced)	Some	No? (external) Yes? (internal)	?‡
Strepsiptera (300 species, 20 genera, families) Orthoptera Tettigoniidae	Genitalia, perforate	Hole in brood canal, infections?‡‡	Yes (many)	No	Weak	Simple (secondarily reduced)	Little or none	No	?‡
<i>Anonconotus</i> (3 species)	Cerci, pinch or grasp	Sometimes perforate	No	No	Weak/none	Simple	No¶¶	No¶¶	?‡
<i>Mecanoma</i> (2 species)	Cerci, grasp	Prevent female feed	Yes***	?	Yes	Simple	No¶¶	No¶¶	?‡
<i>Uromenus</i> (26 species)	Cerci, grasp	Prevent female feed	Yes	Yes	Clear	Simple	Yes†††	No (grooves)	?‡
Haglidae									
<i>Cyphoderris</i> (3 species)	Abd. sclerites, grasp	Restrain when lack food	?	?	?	Simple	No¶¶	No¶¶	?‡
Coleoptera									
Dytiscinae (5 genera)	Tarsi, grasp	Slow female swimming	No	Yes†††	Weak/none	Mod. simple/complex\$\$\$	Yes	Yes	?‡

Numbers of hemipteran taxa from Schuh & Slater (1995).

*Data are available for only one species.

†Clear female fit with male in one species suggests probable fit in others.

‡This function is feasible (female receives stimulation from male), but there are no data for or against.

\$Only occurs in 1 of 20 species.

¶One species has male hooks, and two have elongate female spines.

**Female structures do not defend against perforation by the male. They might be damage control devices, but if so, it is unclear why males cooperate by inserting their genitalia here rather than elsewhere.

††Seems unlikely, at least in species in which males stab females at many different sites on her body; it seems unlikely that females would have appropriate sense organs at all these different sites with which to sense male genitalic designs.

‡‡Infections probably occur, on the basis of data from Cimicidae.

\$\$\$On the basis of data Cimicidae, internal female structures may be defensive, but no direct data are available.

¶¶It is possible that defensive female behaviour rather than morphology differs among species, but no data are available.

***K. Vahed (personal communication).

†††'Cooperative' groove in female is lacking in one species in which apparent behavioural conflict between male and female occurs (Vahed, 1997).

‡‡‡There are major differences between females in different genera.

\$\$\$\$Male tarsi are complex, in the sense of having many parts; the parts themselves (adhesive setae or cups) are relatively simple, and are relatively uniform among species.

structurally simple designs, contrary to expectations from sustained sexually antagonistic coevolution and (3) the female morphological traits that interact with these male traits do not tend to be either species-specific in form, or to be defensive in design (again with a few exceptions), contrary to expectations under sustained sexually antagonistic coevolution. These trends and their implications will be discussed in turn (*Glossina* flies are omitted, because there are strong indications that the species-specific aspects of their male genitalia function as stimulators rather than as restraining devices – see Appendix).

Species-specificity of males

Taxonomists have generally used the morphology of specialized male grasping and perforating structures that are involved in possible conflict with females in the groups of this study to distinguish congeneric species. Major exceptions are the genitalia of polyctenid bugs and front tarsi of dytiscine beetles; there are also exceptions in the genitalia of some smaller groups (e.g. the cimicid genus *Cacomus* in Fig. A5, the strepsipteran genera *Acroschismus* and *Pseudoxenos* in Fig. A10). If one calculates totals using families as units (see below), conservatively counting families in which only some genera show species-specificity as showing species-specific male structures, rapid divergent evolution of male genitalia is lacking in only 2 of 17 families (12%). This fraction is, as predicted by sexually antagonistic coevolution, lower than that of 29% of the 328 genera in a general survey of insects (Eberhard, 2004a), although the difference is not statistically significant ($P = 0.12$ with a chi-square test). The lack of species-specificity in the tarsi of male dytiscine beetles is especially puzzling, as the defensive elytral sculpturing of females in this subfamily is diverse, and also more likely to have evolved as a defence against males than the female traits of most other groups (Table 1, Appendix). Perhaps the large intra-specific variation in female sculpturing (Miller, 2003), or inconsistency in the portions of the female's anatomy that the male grasps, are related to this lack of male diversity. Further observations of behaviour might help clear this up.

Complexity of male morphology

With the exception of *Lucilia* flies (below), the groups examined here seem to show relatively simple male structures to manipulate females. This structural simplicity contrasts with the often elaborate, species-specific male morphology that is common in other groups in male structures that are specialized to contact females in sexual contexts (Eberhard, 1985, 2004a,b; Fig. 1). The trend to male simplicity is especially clear in the two large groups with traumatic insemination, cimicoid bugs and Strepsiptera. The male genitalia of both of groups are secondarily reduced and simplified, and have independently lost structures that are present in relatives. In most

cimicoids one paramere has been reduced or lost, and the phallus (which is quite complex in many related groups – see Schuh & Slater, 1995) has been reduced and been incorporated in a highly simplified form in the remaining paramere. There is debate regarding the identity of the closest relatives of strepsipterans (Kithirithamby, 1989), but regardless of whether their closest relatives are Coleoptera or Hymenoptera strepsipteran male genitalia are clearly secondarily simplified, (e.g. Tuxen, 1970). These reductions stand in contrast with the extraordinary diversification in other groups that include new genitalic articulations, processes, muscles, etc. (Tuxen, 1970; Wood, 1991; Sinclair *et al.*, 1994; Cummin *et al.*, 1995).

These impressions can be expressed in terms of the arbitrary scale used to estimate the degree of difference among congeners and the overall complexity of male genitalic structures in a previous study of 304 genera of insects (Fig. 1). Estimates using the same scale (Fig. 1) of the degree of difference among congeners that are illustrated in 24 genera in this study (Figs A1–8, A10) were biased toward smaller differences (Fig. 2a), especially toward 'very small' and 'small'. Similarly, estimates of the complexity of the male structures illustrated in 53 genera in this study (counting those included in Figs A1–8, A10), were strongly biased toward simpler designs (Fig. 2b). In other words, the males of the species of this study, which are especially likely to be undergoing sexually antagonistic coevolution, seem to have smaller rather than larger differences between congeneric species, and simpler rather than more complex male genitalic structures. My categories are admittedly subjective, and some discrimination, such as those between simple and very simple, for example, could surely be contested (the reader is invited to make his or her own classification). But a general trend seems clear: relatively simple designs predominate in the groups in which sexually antagonistic coevolution is likely to be occurring.

This male conservatism is presumably dictated to at least some extent by the invariant laws of mechanics that will determine the abilities of different male designs to grasp or penetrate females. A stabbing function, for instance, can usually best be accomplished by a structure with a dagger-like design. What is striking about the structures discussed here is the contrast they show with other groups of insects in which male damage to the female is improbable or at least less certain. The male structures such as genitalic claspers in many of these groups are confronted with similar mechanical challenges, but are nevertheless more diverse in design. Simple mechanical tasks are not necessarily associated with simple, conservative designs. For instance, throughout the nematoceros Diptera the apparent mechanical function (as opposed to possible stimulating functions) of the male gonostyli is to seize and hold onto structurally simple portions of the female's

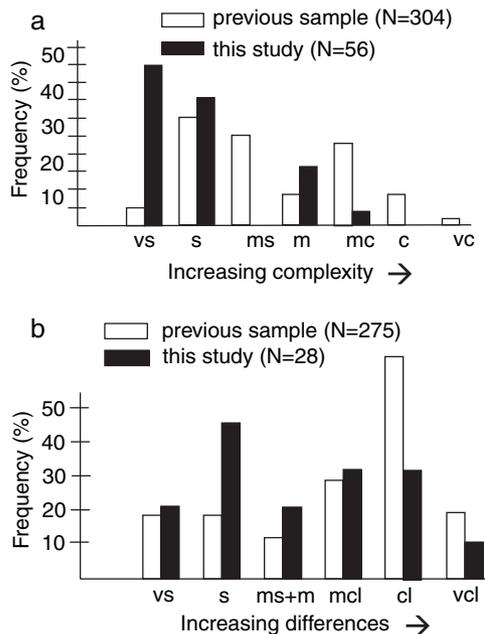


Fig. 2 Distributions of subjective evaluations of the degree of intra-generic differences (a) and the structural complexity (b) arranged in order of increasing differences (a) and complexity (b) in a sample of 304 insect genera compared with the 53 genera illustrated in this study (Figs 2–10) (in a, VS, very small; S, small; MS, medium small; MCL, medium clear; CL, clear and VCL, very clear; in b, vs, very simple; s, simple; ms, medium simple; m, medium; mc, medium complex; c, complex and vc, very complex). Combining VS and S, MS and MCL, and CL and VCL in a, $\chi^2 = 14$, d.f. = 2, $P < 0.001$; combining vs and s, ms, m, and mc, and c and vc in b, $\chi^2 = 44$, d.f. = 2, $P < 0.001$.

abdomen (studies of 10 species in five families – Eberhard, 2004a; see also Wood, 1991); generally the gonostyli grasp intersegmental membranes of the female. Despite this simple mechanical task, the gonostyli of nematocerans are usually species-specific in form, and in some cases extraordinarily elaborate ('Gs' in Fig. 1g). These 'excessively' elaborate designs contrast with the relatively simple, largely utilitarian designs of the male structures in the present study. Other, nongenitalic male grasping structures (e.g. the front legs of male sepsid flies that clasp the female's wings – Eberhard, 2001) also often have apparently 'overly' elaborate or diverse designs for their apparently simple mechanical functions of clasping relatively invariant portions of the female (Eberhard, 2004b). Nor can the conservatism of the male structures in this study be easily attributed to the possibility that the females of these groups put up greater resistance, because it also contrasts with the diversity of weapons that are used for similar mechanical functions (grasping and perforating) in male–male battles (below).

The three predictions of sexually antagonistic coevolution are most clearly met in the blowfly genus *Lucilia*. But the antagonistic nature of male–female coevolution in this group is less convincing than in several others. Losses to the female from mating have not been demonstrated and it is possible that female *Lucilia* gain rather than lose from responding to the ability of the male genitalia to increase the access of male seminal products to the female's body cavity (Eberhard, 1997; Cordero & Eberhard, 2003, 2005). It is also possible that the male genitalia of *Lucilia* have evolved under selection to stimulate the female rather than (or in addition to) opening holes in the lining of her reproductive tract.

Species-specific, defensive female morphology

In most groups, female morphology was neither species-specific nor defensive. In only 4 of 12 groups in Table 1 do females have corresponding species-specific external morphology; and in only two (*Gerris* waterstriders and dytiscine water beetles) is it clear that female traits are defensive in design (I have counted the morphology of cimicids, anthocorids and plokiophilids as nondefensive, because it offers no defence against the types of damage known to result from traumatic insemination such as breaks in the cuticle and infections – see Stutt & Siva-Jothy, 2001; Reinhardt *et al.*, 2003; Morrow & Arnqvist, 2003; and the Appendix). Species-specific female defensive traits may well probably also occur in *Lucilia* blowflies (thickening of the lining of the female reproductive tract where male serrate structures contact it), although species-specificity has yet to be shown, because female defence has been checked in only a single species. The lack of similarly defensive female traits is clear in most other groups, including several genera of orthopterans, and the groups with larger numbers of species (the four families of cimicoid bugs, the eight families of strepsipterans) (Appendix). Paradoxically, from the point of view of avoiding the potential damage from traumatic insemination, females of some Cimicidae, Anthocoridae and Plokiophilidae have apparently 'cooperative' structures such as grooves or copulatory tubes that receive the male's penetrating genitalia, instead of structures such as reinforced cuticle, erectable spines or flaps or other modifications that would shelter sites of possible penetration, and would thus make it more difficult for males to damage the female with their genitalia. Contrary to expectations under sexually antagonistic coevolution, not a single facultative female defensive structure was found in any group.

One untested hypothesis is that females benefit from facilitating male penetration in certain areas because they are better able to deal with the resulting physical damage at these sites. The reason that males would use these female sites rather than other parts of her body is still not clear. The hypothesis (Morrow & Arnqvist, 2003) that cimicid males use female grooves to minimize

damage to their mates, orienting their genitalia toward the portion of the female (the spermalege) best able to resist the damage caused by intromission overlooks the fact that the spermalege also kills a large fraction of the sperm that it receives (Carayon, 1966). In cimicids, and some anthocorids and plokophilids, the diversity of female internal structures, combined with the lack of diversity of external structures (Appendix), suggest that females have evolved to control sperm or seminal products rather than physical damage. These adaptations could be favoured to exercise female choice; or, if seminal products damage the female's reproductive output (Morrow & Arnqvist, 2003), they could be favoured to defend against this damage. There are preliminary hints that the same combination of external uniformity and internal diversity may occur in strepsipterans, but further work is needed to test this. In sum, the females of cimicids and their allies have not been engaged in coevolutionary morphological races to defend against those costs of traumatic intromission that have been clearly demonstrated: physical damage, and perhaps increased risks of associated infections (Reinhardt *et al.*, 2003).

Implications

The trends in Table 1 are compatible with models of male–female conflict that predict only short bursts of antagonistic coevolution (Parker, 1979; Rowe *et al.*, 2005), with one or the other sex often winning out; they do not fit predictions of sustained, long-lasting evolutionary races between males and females (Alexander *et al.*, 1997; Holland & Rice, 1998; Chapman *et al.*, 2003). This conclusion is in accord with the results of previous empirical surveys that tested other sexually antagonistic coevolution predictions using other evidence from morphology (Eberhard, 2004a,b). By elimination, this strengthens other possible explanations for the tendency toward rapid, sustained divergent evolution of traits like male genitalia, such as female choice and selection for species isolation. The conclusion that sexually antagonistic coevolution has not been sustained and common does not imply that it has never had important evolutionary effects (even in groups in which it does not presently occur) (Eberhard, 2004b). Rather it implies that it has not been responsible for the sustained rapid, divergent evolution so typical of these particular types of traits.

The mechanical lock-and-key version of species isolation, already weakened by the results of numerous other studies (summaries in Eberhard, 1985, 2004b; Shapiro & Porter, 1989; Arnqvist, 1998), is further weakened by the lack of complementary female modifications in some of the groups discussed here. The lack of a female 'locks' is particularly clear in tsetse flies (Appendix), and in several groups that were excluded from inclusion in Table 1 ('other groups' in Appendix). It is also suggestive in Strepsiptera, although female morphology has not gen-

erally been described in fine detail in this group (see Appendix).

Other intra-specific weapons

If the male traits examined here are correctly interpreted as male weapons to overcome the female in male–female battles (with the tse-tse flies likely exceptions), then other weapons, such as those used by males in intra-specific battles with other males, offer an interesting comparison. Again the results are a surprise. There is a sharp contrast between the conservatism documented here in these traits, the small numbers of groups in which females avail themselves of external defences, and the simple designs of the female traits (e.g. Fig. A9a), as compared with the frequently species-specific diversity and complexity that characterizes weapons such as the antlers and horns of ungulates and beetles (Arrow, 1951; Geist, 1966; Otte & Stayman, 1979; Enrodi, 1985), and the cerci of earwigs (Brindle, 1971, 1976) (also often used as weapons in male–male battles – Moore & Wilson, 1993; Briceño & Eberhard, 1995). This contrast is especially striking given the fact that both sets of male traits function to solve similar mechanical problems, such as seizing or stabbing another animal (e.g. Geist, 1966; Eberhard, 1979, 1980).

It is not obvious why the weapons used in male–male and male–female contexts should show different patterns of evolution. One possible answer is related to the possibility that females can 'gain by losing' in male–female conflicts over reproduction: the very male traits that reduce a female's immediate reproductive output can increase the reproductive success of her genes in her male descendants (Eberhard, 2005). This effect could limit the intensity of selection on females to resist damage from male weapons, and thus possibly reduce divergence under sexually antagonistic coevolution. A second possibility (D. Hosken, personal communication) is that in a male's battles with females, too much escalation could result in lost fitness for both sexes (a male can 'lose by winning' if he inflicts too much damage on his mate). A male battling with another male, in contrast, does not experience this limitation. Another possible factor is that, if the balance of costs and benefits is appropriate (Cordero & Eberhard, 2005), females could use male weapons to bias female choice decisions. Further work will be needed to resolve these questions.

Conflict and the two-dimensional lives of water striders

The behaviour and morphology of *Gerris* water striders, which have been widely cited in discussions of sexually antagonistic coevolution, contrast with some of the findings reported here. Females in many of the groups examined here lack species-specific, antagonistic

adjustments to male morphology. *Gerris* females, in contrast, show several independent signs of defensive coevolution with male morphology; these have been documented especially thoroughly by the work of Arnqvist & Rowe (2002a,b) and their collaborators (Appendix). Why this difference?

Gerris has been proposed; appropriately I believe, as a model group for male–female conflict. But it may be that *Gerris*, and other insects such as veliid bugs that live on the surfaces of streams and lakes and that also show signs of sexually antagonistic coevolution (Arnqvist, 1997), are a special case and are not representative models for male–female interactions. The reason is that the water surface is a strictly two-dimensional habitat, and thus offers relatively little opportunity for physical escape by the female (Spence & Anderson, 1995). In addition, the sites on the water surface that can be occupied profitably by these insects are often limited (e.g. patches with appropriate current velocities), further reducing the opportunity for females to avoid unwanted male advances. More frequent male harassment could increase the intensity of selection favouring defensive female morphological adjustments to male morphology. The behaviour of some tropical gerrids, which jump off the water surface to sit on overhanging rocks when they have captured food (W. Eberhard, unpublished), and thus avoid harassment and possible robbery, evidences this problem. The possible relation between two-dimensional habitats and male–female conflict could be tested by checking the groups of gerrids and veliids that are not strictly associated with the water surface; they should present fewer signs of sexually antagonistic coevolution than groups limited to the water surface.

Limitations and future directions

The criterion that I used for rapid divergence of a particular structure (whether or not taxonomists utilize the structure to distinguish congeneric species) has the possible drawback that taxonomists may have sometimes ‘over-used’ genitalia. Because male genitalia have proven so important in many insect groups, genitalia may have sometimes been included in species descriptions even though these genitalia have not diverged particularly rapidly compared with other traits (e.g. Hausmann, 1999; Huber, 2003,2005; Eberhard, 2004a). Such a bias could lead to overestimates of the frequency of relatively rapid genitalic divergence. One way to compensate for this possibility is to reclassify those groups in which there are only small or subtle differences, and count them as lacking differences between species (Eberhard, 2004a). This would result in concluding that most of the groups discussed here lack of species-specificity, because the intra-generic differences in most groups are small. This conclusion would constitute another failure to fit with the predictions of sustained sexually antagonistic coevolution. I believe, however, that this adjustment is

inappropriate, because taxonomists specifically singled out male genitalia as useful characters for distinguishing species in several groups with especially small intra-generic differences in male genitalia (cimicids, strepsipterans – see Appendix).

A second problem concerns sample size and phylogenetic inertia. The groups discussed in this paper include approximately 114 genera with between 500 and 1000 species (in 6 orders and 17 families). This seems like a large sample; but the traits of many of these genera are undoubtedly not completely independent of each other because many are closely related. I have distinguished 13 groups in Table 1, on the basis of taxonomic affinities and the amount of information available (combining groups, such as the different families of Strepsiptera, with less complete information). But perhaps, to take one extreme, the four-cimicoid bug families that have traumatic insemination should be taken as single case. Or, in the other direction, perhaps the eight families of strepsipterans should be counted separately. Combining groups can lead to errors of interpretation when the traits involved are prone to evolve rapidly (Losos, 1999). Such a tendency toward rapid evolution is, of course, a hallmark of male genitalia; so large scale lumping seems inappropriate. The recognition of 13 groups probably underestimates rather than overestimates the number of effectively independent groups. I would not claim that the grouping in Table 1 is the only reasonable way to classify the data. But, in the end, I believe this is not crucial, because alternate possible classifications will yield the same qualitative trends: widespread but relatively weak divergence in males; general lack of rapid coevolutionary divergence in females; and even more pronounced lack of defensive female designs. Future studies using methods that adjust for possible phylogenetic inertia could be used to test these conclusions.

Still another potential weakness of the analyses is the supposition that female morphology (rather than, say, female behaviour) is likely to often respond coevolutionarily to changes in male morphology. Perhaps, for instance, females usually respond to changes in male morphology with species-specific changes in their behaviour rather than in their morphology (Eberhard & Pereira, 1996; Eberhard, 2004b). A priori, the possibility of consistent behavioural rather than morphological coevolutionary female responses seems unlikely, because such a trend would leave unexplained why females should fail to use effective and cheap morphological counter-adaptations, such as simple erectile spines, that would fend off the male. Note also that female resistance *per se* is not enough to constitute a sexually antagonistic coevolution explication for species-specific morphology in the male: the female behaviour must vary in species-specific ways that are appropriate as adaptations against the species-specific aspects of the male traits. To my knowledge, the potentially important possibility of species-specific female defensive behaviour patterns that

have evolved in response to species-specific male structures has never been documented. Details of female resistance behaviour have seldom been explored, however, despite the relative ease with which they could be studied. This represents an important direction for future research.

Additional, more quantitative analyses could provide further tests of some of the trends noted here. For instance, there are techniques of morphological analysis that allow one to quantify the overall degree of difference between species (Arnqvist, 1998; Arnqvist & Thornhill, 1998). I was unable to see how to structure such analyses to place appropriate emphases on the biologically important aspects of different structures. But others may be more successful, especially if they build on detailed studies of the behaviour and functional morphology of particular groups.

Nearly all the data used here concern only external morphology; this may be a serious limitation, at least in groups with traumatic insemination. Female internal morphology and perhaps physiological processes are diverse and possibly complex in Cimicidae (Carayon, 1966). There are hints of similar diversity in some other groups with traumatic insemination, such as anthocorid bugs and Strepsiptera (e.g. female cells that engulf sperm in strepsipterans – Beani *et al.*, 2005). Special attention to discriminating female modifications that are appropriate to deal with sperm (a possible result of sexual selection by cryptic female choice) from those designed to deal with the physical damage and infections that can result from traumatic insemination (an expected result of sexually antagonistic coevolution) could help distinguish between the two hypotheses. Detailed studies of female reproductive anatomy and its mesh of the male genitalia during copulation in *Lucilia* and perhaps other blowflies such as *Calliphora* (see Graham-Smith, 1939) would also be of great interest.

Last, but not least, this review calls attention to the huge, largely ignored data bank on morphological evolution that is available in the taxonomic literature. Where else could one ever aspire to review data on literally hundreds of closely related species? These data have limitations and possible biases that need to be taken into account (Huber, 2003; Eberhard, 2004a). But their taxonomic range is unparalleled. This review was limited to insects. Similar reviews of the literature on other groups, such as onychophorans, leeches, and mites (all of which have traumatic insemination in some species), could provide independent tests of the conclusions presented here.

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References

- Aiken, R.B. 1992. The mating behavior of a boreal water beetle, *Dytiscus alaskanus* (Coleoptera Dytiscidae). *Ethol. Ecol. Evol.* **4**: 245–254.
- Aiken, R.B. & Kahn, A. 1992. The adhesive strength of the palettes of males of a boreal water beetle, *Dytiscus alaskanus* J. Balfour Browne (Coleoptera: Dytiscidae). *Can. J. Zool.* **70**: 1321–1324.
- Alexander, R.D., Marshall, D. & Cooley, J. 1997. Evolutionary perspectives on insect mating. In: *The Evolution of Mating Systems in Insects and Arachnids* (J. C. Choe & B. J. Crespi, eds), pp. 4–31. Cambridge University Press, Cambridge, UK.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton NJ.
- Andersson, N.M. 1997. A phylogenetic analysis of the evolution of sexual dimorphism and mating systems in water striders (Hemiptera: Gerridae). *Biol. J. Linn. Soc.* **61**: 345–368.
- Arnqvist, G. 1989. Sexual selection in a water strider: the function, mechanism of selection and heritability of a male grasping apparatus. *Oikos* **56**: 344–350.
- Arnqvist, G. 1997. The evolution of water strider mating systems: causes and consequences of sexual conflicts. In: *The Evolution of Mating Systems in Insects and Arachnids* (J. C. Choe & B. J. Crespi, eds), pp. 146–163. Cambridge University Press, Cambridge, UK.
- Arnqvist, G. 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature* **393**: 784–786.
- Arnqvist, G. 2004. Sexual conflict and sexual selection: lost in the chase. *Evolution* **58**: 1383–1388.
- Arnqvist, G. & Rowe, L. 1995. Sexual conflict and arms races between the sexes: a morphological adaptation for control of mating in a female insect. *Proc. R. Soc. Lond. B* **261**: 123–127.
- Arnqvist, G. & Rowe, L. 2002a. Antagonistic coevolution between the sexes in a group of insects. *Nature* **415**: 787–789.
- Arnqvist, G. & Rowe, L. 2002b. Correlated evolution of male and female morphologies in water striders. *Evolution* **56**: 936–947.
- Arnqvist, G. & Thornhill, R. 1998. Evolution of animal genitalia: patterns of phenotypic and genotypic variation and condition dependence of genital and non-genital morphology in water striders (Heteroptera: Gerridae: Insecta). *Genet. Res. Camb.* **71**: 193–212.
- Arrow, G. 1951. *Horned Beetles*. Dr. Junk, The Hague.
- Aubertin, D. 1933. Revision of the genus *Lucilia* R.-D. (Diptera, Calliphoridae). *Linn. J. Zool.* **38**: 389–436.
- Baer, B. & Schmid-Hempel, P. 1999. Experimental variation in polyandry affects parasite loads and fitness in a bumble-bee. *Nature* **397**: 151–154.
- Beani, L., Giusti, F., Mereati, D., Lupetti, P., Paccagnini, E., Turrilazi, S. & Dallai, R. 2005. Mating of *Xenos vesparum* (Rossi) (Strepsiptera, Insecta) revisited. *J. Morphol.* **265**: 291–303.

- Bergsten, J., Töyrä, A. & Nilsson, A. 2001. Intraspecific variation and intersexual correlation in secondary sexual characters of three diving beetles (Coleoptera: Dytiscidae). *Biol. J. Linn. Soc.* **73**: 221–232.
- Blanckenhorn, W.U., Hosken, D.J., Martin, O.Y., Reim, C., Teuschl, Y., & Ward, P.I. 2002. The costs of copulating in the dung fly *Sepsis cynipsea*. *Behav. Ecol.* **13**: 353–358.
- Bohart, R.M. 1941. A revision of the Strepsiptera with specific reference to the species of North America. *Univ. Calif. Publ. Entomol.* **7**: 91–160.
- Bohart, R.M. 1951. The Myrmecolacidae of the Philippines (Strepsiptera). *Wasmann J. Biol.* **9**: 83–103.
- Briceño, R.D. & Eberhard, W.G. 1995. The functional significance of male cercus morphology in 13 species of tropical earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae). *Smithson. Contrib. Zool.* **555**: 1–63.
- Brindle, A. 1971. A revision of the genus *Doru* Burr (Dermaptera, Forficulidae). *Pap. Avulsos Zool. (São Paulo)* **23**: 173–196.
- Brindle, A. 1976. The Dermaptera of Dominica. *Smiths. Contrib. Zool.* **63**: 1–25.
- Burks, B.D. 1953. The mayflies or Ephemeroptera of Illinois. *Bull. Nat. Hist. Surv. Div. Ill.* **26**: 1–183.
- Buxton, P.A. 1955. *The Natural History of Tsetse Flies*. H. K. Lewis, London.
- Carayon, J. 1966. Traumatic insemination and the paragenital system. In: *Monograph of the Cimicidae* (R. L. Usinger, ed.), pp. 81–167. Entomological Society of America, College Park, MD.
- Carayon, J. 1972. Caractères systématiques et classification des Anthocoridae (Hem.). *Ann. Soc. Entomol. Fr. (N.S.)* **8**: 309–349.
- Carayon, J. 1975. Insemination extra-génitale traumatique. In: *Traité de Zoologie*, Vol. 8 (P. P. Grassé, ed), Paris, Masson.
- Carron, G., Sardet, E. & Wermeille, E. 2002. Revision of the genus *Anonconotus* Cerano, 1878 (Orthoptera: Tettigoniidae) with description of *A. pusillus* sp. n. and *A. baracuensis occidentalis* spp. n. *Rev. Suisse Zool.* **109**: 879–918.
- Chapman, T., Arnqvist, G., Bangham, J. & Rowe, L. 2003. Sexual conflict. *Trends Ecol. Evol.* **18**: 41–47.
- Cordero, C. 2005. The evolutionary origin of *signa* in female Lepidoptera: natural and sexual selection hypotheses. *J. Theor. Biol.* **232**: 443–449.
- Cordero, C. & Eberhard, W.G. 2003. Female choice of sexually antagonistic male adaptations: a critical review of some current research. *J. Evol. Biol.* **16**: 1–6.
- Cordero, C. & Eberhard, W.G. 2005. The interactions between sexually antagonistic coevolution and mate choice in the evolution of female responses to male traits. *Evol. Ecol.*, **19**: 111–122.
- Crudgington, H.S., Beckerman, A.P., Brustle, L., Green, L. & Snook, R.R. 2005. Experimental removal and elevation of sexual selection: does sexual selection generate manipulative males and resistant females?. *Am. Nat.* **165**(Suppl.):S72–S87.
- Crudgington, H.S. & Siva-Jothy, M.J. 2000. Genital damage, kicking and early death. *Nature* **407**: 855–856.
- Cummin, J.M., Sinclair, B.J. & Wood, D.M. 1995. Homology and phylogenetic implications of male genitalia in Diptera – Eremoneura. *Entomol. Scandinav.* **26**: 120–151.
- Damgaard, J. & Sperling, F.A.H. 2001. Phylogeny of the water strider genus *Gerris* Fabricius (Heteropteras: Gerridae) based on COI mtDNA, EF-1 α nuclear DNA and morphology. *Syst. Entomol.* **26**: 241–254.
- Dodson, G.N., Morris, G.K. & Gwynne, D.K. 1983. Mating behavior of the primitive orthopteran genus *Cyphoderris* (Haglidae). In: *Orthopteran Mating Systems Sexual Competition in a Diverse Group of Insects* (D. T. Gwynne & G. K. Morris, eds), pp. 305–318. Westview, Boulder, CO.
- Duvoisin, N., Baer, G. & Schmid-Hempel, P. 1999. Sperm transfer and male competition in a bumblebee. *Anim. Behav.* **58**: 743–749.
- Eberhard, W.G. 1979. The function of horns in *Podischmus agenor* (Dynastinae) and other beetles. In: *Sexual Selection and Reproductive Competition in Insects* (M. Blum & N. Blum, eds), pp. 231–258. Academic Press, New York.
- Eberhard, W.G. 1980. Horned beetles. *Sci. Am.* **242**: 166–182.
- Eberhard, W.G. 1985. *Sexual Selection and Animal Genitalia*. Harvard University Press, Cambridge, MA.
- Eberhard, W.G. 1997. Sexual selection by cryptic female choice in insects and arachnids. In: *The Evolution of Mating Systems in Insects and Arachnids* (J. C. Choe & B. J. Crespi, eds), pp. 32–57. Cambridge University Press, Cambridge, UK.
- Eberhard, W.G. 2001. The functional morphology of species-specific clasping structures on the the front legs of male *Archiseptis* and *Palaeoseptis* flies (Diptera, Sepsidae). *Zool. J. Linn. Soc.* **133**: 335–368.
- Eberhard, W.G. 2004a. Male-female conflict and genitalia: failure to confirm predictions in insects and spiders. *Biol. Rev.* **79**: 121–186.
- Eberhard, W.G. 2004b. Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. *Evolution* **58**: 1947–1970.
- Eberhard, W.G. 2005. Evolutionary conflicts of interest: are female sexual decisions different? *Am. Nat.* **165**(Suppl.): S19–S25.
- Eberhard, W.G. & Pereira, F. 1996. Functional morphology of male genitalia surstyli in the dungflies *Archiseptis diversiformis* and *A. ecalcarata* (Diptera: Sepsidae). *J. Kans. Entomol. Soc.* **69**: 43–60.
- Eberhard, W.G., Platnick, N. & Schuh, R.T. 1993. Natural history and systematics of arthropod symbionts (Araneae: Hemiptera: Diptera) inhabiting webs of the spider *Tengella radiata* (Araneae, Tengellidae). *Am. Mus. Novitat.* **3065**: 1–17.
- Enrodi, S. 1985. *The Dynastinae of the World*. Dr. W. Junk Publ., Boston.
- Fairbairn, D.J., Vermette, R., Kapoor, N.N. & Zahiri, N. 2003. Functional morphology of sexually selected genitalia in the water strider *Aquarius remigis*. *Can. J. Zool.* **81**: 400–413.
- Ferris, G.F. & Usinger, R.L. 1939. The family Polycetenidae (Hemiptera: Heteroptera). *Microentomology* **4**: 1–50.
- Flowers, R.W., & Eberhard, W.G. 2006. Fitting together: copulatory linking in some Neotropical Chrysomelidae. *Rev. Biol. Trop.*, in press.
- Galley, K.E.M. 1999. Revision of the genus *Selenodon* Latrielle (Coleoptera: Cebrionidae). *Occ. Pap. Fla. State Coll. Arthrop.* **10**: 1–49.
- Geist, V. 1966. The evolution of horn-like organs. *Behaviour* **27**: 175–214.
- Gillot, C. and Langley, P.A. 1981. The control of receptivity and ovulation in the tsetse fly, *Glossina morsitans*. *Physiol. Entomol.* **6**: 269–281.
- Graham-Smith, G.S. 1939. The generative organs of the blow-fly, *Calliphora erythrocephala* L., with special reference to their musculature and movements. *Parasitology* **30**: 441–476.

- Gross, G.F. 1955a. A revision of the flower bugs (Heteroptera Anthocoridae) of the Australian and adjacent Pacific regions. *Part I. Rec. S. Aust. Mus.* **11**: 129–164.
- Gross, G.F. 1955b. A revision of the flower bugs (Heteroptera Anthocoridae) of the Australian and adjacent Pacific regions. *Part II. Rec. S. Aust. Mus.* **11**: 409–427.
- Gwynne, D.T. 2001. *Katydid and Bush Crickets: Reproductive Behavior and Evolution of the Tettigoniidae*. Cornell University Press, Ithaca, NY.
- Halvarsson, K. 2001. A review of secondary sexual characters in the tribe Hydatricini (Coleoptera: Dytiscidae). Masters thesis, Univ. of Umea, Sweden.
- Harz, K. 1957. *Die Geradflügler Mitteleuropas*. Gustav Fischer Verlag, Jena.
- Hausmann, A. 1999. Falsification of an entomological rule: polymorphic genitalia in geometrid moths. *Spixiana* **22**: 83–90.
- Herring, J.L. 1967. Insects of Micronesia Heteroptera: Anthocoridae. *Insects Micronesia* **7**: 388–414.
- Holland, B. & Rice, W.R. 1998. Chase-away selection: antagonistic seduction vs. resistance. *Evolution* **52**: 1–7.
- Hosken, D. & Snook, R. 2005. How important is sexual conflict? *Am. Nat.* **165**(Suppl.): S1–S4.
- Hosken, D. & Stockley, P. 2004. Sexual selection and genital evolution. *Trends Ecol. Evol.* **19**: 87–93.
- Huber, B.A. 1993. Genital mechanics and sexual selection in the spider *Nesticus cellulanus* (Araneae: Nesticidae). *Can. J. Zool.* **71**: 2437–2447.
- Huber, B.A. 2003. Rapid evolution and species-specificity of arthropod genitalia: fact or artifact? *Organ. Divers. Evol.* **3**: 63–71.
- Huber, B.A. 2005. Sexual selection research on spiders. *Biol. Rev.* **80**: 363–385.
- Huber, B.A. & Eberhard, W.G. 1997. Courtship, genitalia, and genital mechanics in *Physocyclus globosus* (Araneae, Pholcidae). *Canad. J. Zool.* **74**: 905–918.
- Hughes-Schrader, S. 1924. Reproduction in *Acroschismus wheeleri* Pierce. *J. Morphol. Physiol.* **39**: 157–205.
- Hungerford, H.B. 1954. The genus *Rheumatobates* Bergroth (Hemiptera-Gerridae). *Univ. Kans. Sci. Bull.* **36**: 529–588.
- Jaensen, T.G.T. 1979. Mating behaviour of males of *Glossina pallidipes* Austen (Diptera: Glossinidae). *Bull. Ent. Res.* **69**: 573–588.
- Kelton, L.A. 1978. *The Anthocoridae of Canada and Alaska. Heteroptera: Anthocoridae*. The Insects and Arachnids of Canada. Part 4. Canada Dept. of Agriculture Publications, Ottawa, Canada.
- Kingsolver, J.M. 1999. A new species of *Callosobruchus* (Coleoptera: Bruchidae) from Thailand and China. *Entomol. News* **110**: 51–60.
- Kithirithamby, J. 1989. Review of the Order Strepsiptera. *Syst. Entomol.* **14**: 41–92.
- Kokko, H., Brooks, D., Jennions, M.D., & Morley, J. 2003. The evolution of mate choice and mating bias. *Proc. R. Soc. Lond. B* **270**: 653–664.
- Larson, D.J., Alaric, Y. & Roughley, R.E. 2000. *Predaceous diving beetles (Coleoptera: Dytiscidae) of the Nearctic region*. NRC Research Press, Ottawa. 1–982.
- Lauer, M.J., Sih, A., & Krupa, J.J. 1996. Male density, female density and inter-sexual conflict in a stream-dwelling insect. *Anim. Behav.* **52**: 929–939.
- Lauterbach, G. 1954. Begattung und Larvengeburt bei den Strepsipteren. Zugleich ein Beitrag zur Anatomie der Stylops-Weibchen. *Z. f. Parasitenkunde* **16**: 255–297.
- Leegwater-van der Linden, M.E. & Tiggelman, E.P.M. 1984. Multiple mating and inseminating potential of *Glossina pallidipes*. *Entomol. Exptl. Appl.* **35**: 283–294.
- Lewis, C.T. & Pollock, J.N. 1975. Engagement of the phallosome in blowflies. *J. Entomol. (A)* **49**: 137–147.
- Lossos, J.B. 1999. Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods. *Anim. Behav.* **58**: 1319–1324.
- Malicky, H. 1983. *Trichoptera Atlas of European Trichoptera*. Dr. Junk Publ., Boston.
- Martin, O.Y. & Hosken, D.J. 2003. The evolution of reproductive isolation through sexual conflict. *Nature* **423**: 979–982.
- Mayr, E. 1963. *Animal Species and Evolution*. Harvard University Press, Cambridge.
- Merrett, D.J. 1989. The morphology of the phallosome and accessory gland material transfer during copulation in the blowfly, *Lucilia cuprina* (Insecta, Diptera). *Zoomorphology* **109**: 359–366.
- Miller, K.B. 2002. The evolution of secondary sexual characters, the phylogeny of diving beetles (Coleoptera: Dytiscidae), and the theory of sexual conflict. *Biol. J. Linn. Soc.* **79**: 359–388.
- Miller, K.B. 2003. The evolution of secondary sexual characters, the phylogeny of diving beetles (Coleoptera: Dytiscidae), and the theory of sexual conflict. *Biol. J. Linn. Soc.* **79**: 359–388.
- Morrow, E.H. & Arnqvist, G. 2003. Costly traumatic insemination and a female counter-adaptation in bed bugs. *Proc. R. Soc. Lond. B* **270**: 2377–2381.
- Moore, A.J. & Pizzari, T. 2005. Quantitative genetic models of sexual conflict based on interacting phenotypes. *Am. Nat.* **165**(Suppl.): S88–S97.
- Moore, A.J. & Wilson, P. 1993. The evolution of sexually dimorphic earwig forceps: social interactions among adults of the toothed earwig *Vostox apicedentatus*. *Behav. Ecol.* **4**: 40–48.
- Nadig, A. 1994. Revision der Gattung *Uromenus* Bolivar, 1878 (Orthoptera: Ephippigeridae). *Rev. Suisse Zool.* **101**: 919–1016.
- Ogata, K. 1982. Taxonomic study of the ant genus *Pheidole* Westwood of Japan, with a description of a new species (Hymenoptera, Formicidae). *Kontyu, Tokyo* **50**: 189–197.
- Otte, D. & Stayman, K. 1979. Beetle horns: some patterns in functional morphology. In: *Sexual Selection and Reproductive Competition in Insects* (M. Blum & N. Blum, eds), pp. 259–292. Academic Press, New York.
- Parker, G.A. 1979. Sexual selection and sexual conflict. In: *Sexual Selection and Reproductive Competition in Insects*. (M. Blum & N. Blum, eds), pp. 123–166. Academic Press, New York.
- Parker, G.A. 1984. Sperm competition and the evolution of animal mating strategies. In: *Sperm Competition and the Evolution of Animal Mating Systems*. (R. L. Smith, ed), pp. 2–60. Academic Press, New York.
- Pericart, J. 1972. *Hémiptères Anthocoridae, Cimicidae et Microphylidae de l'Ouest-Paléarctique. Faune de L'Europe et du Bassin Méditerranéen*. 7. Masson et Cie Éditeurs, Paris.
- Pierce, W.D. 1909. A monographic revision of the twisted winged insects comprising the order Strepsiptera Kirby. *Bull. US Nat. Mus.* **66**: 1–232.
- Pinto, J.D. 1998. Systematics of the North American species of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae). *Mem. Entomol. Soc. Wash.* **22**: 1–287.

- Pizzari, T. & Snook, R. 2003. Perspective: sexual conflict and sexual selection: chasing away paradigm shifts. *Evolution* **15**, 57: 1223–1236.
- Potts, W.H. 1970. In: *Systematics and identification of Glossina*. The African Trypanosomiasis (H. W. Mulligan, G. Allen & G. Unwin, eds), pp. 243–273. Wiley Interscience, New York.
- Reinhardt, K., Naylor, R. & Siva-Jothy, M. 2003. Reducing a cost of traumatic insemination: female bedbugs evolve a unique organ. *Proc. R. Soc. Lond. B* **270**: 2371–2375.
- Rentz, D.C. 1972. The lock and key as an isolating mechanism in katydids. *Am. Sci.* **60**: 750–755.
- Richards, O.W. 1927. The specific characters of the British bumblebees (Hymenoptera). *Trans. Entomol. Soc. Lond.* **75**: 233–265.
- Riek, E.F. 1973. Strepsiptera. In: *Insects of Australia* (CSIRO, eds), pp. 622–635. Melbourne University Press, Carlton, Victoria, Australia.
- Ronderos, R.A. 1960. Polyctenidae americanos. I. *Actas Trab. Prim. Congr. Sudamer. Zool. (Universidad Nacional de La Plata)* **3**: 175–186.
- Ronkainen, K., Kaitala, A. & Huttenen, R. 2005. The effect of abdominal spines on female mating frequency and fecundity in a water strider. *J. Insect Behav.* **18**: 619–626.
- Roughley, R.E. 1990. A systematic revision of species of *Dysticus* Linnaeus (Coleoptera: Dytiscidae). Part I. Classification based on adult stage. *Quaest. Entomol.* **26**: 383–557.
- Roughley, R.E. & Pengelly, D.H. 1981. Classification, phylogeny, and zoogeography of *Hydaticus* Leach (Coleoptera: Dytiscidae) of North America. *Quaest. Entomol.* **17**: 249–309.
- Rowe, L. 1994. The costs of mating and mate choice in water striders. *Anim. Behav.* **48**: 1049–1056.
- Rowe, L. & Arnqvist, G. 2002. Sexually antagonistic coevolution in a mating system: combining experimental and comparative approaches to address evolutionary processes. *Evolution* **56**: 754–767.
- Rowe, L., Arnqvist, G., Sih, A., & Krupa, J.J. 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol.* **9**: 289–293.
- Rowe, L., Cameron, E. & Day, T. 2005. Escalation, retreat, and female indifference as alternative outcomes of sexually antagonistic coevolution. *Am. Nat.* **165**(Suppl.): S5–S18.
- Sakaluk, S.K., Bangert, P.J., Eggert, A.-K., Gack, C., & Swanson, L.V. 1995. The gin trap as a device facilitating coercive mating in sagebrush crickets. *Proc. R. Soc. Lond. B* **261**: 65–71.
- Saunders, D.S. & Dodd, C.H.W. 1972. Mating, insemination, and ovulation in the tsetse fly, *Glossina morsitans*. *J. Insect Physiol.* **18**: 187–198.
- Schuh, R.T. & Slater, J.A. 1995. *True Bugs of the World*. Cornell University Press, Ithaca, NY.
- Shapiro, A.M. & Porter A.H. 1987. The lock-and-key hypothesis: evolutionary and biosystematic interpretation of insect genitalia. *Ann. Rev. Entomol.* **34**: 231–245.
- Silvey, J.K.G. 1931. Observations on the life-history of *Rheumatobates rileyi* (Berg.) (Hemiptera-Gerridae). *Pap. Mich. Acad. Sci. Arts Lett.* **13**: 433–446.
- Sinclair, B.J., Cumming, J.M. & Wood, D.M. 1994. Homology and phylogenetic implications of male genitalia in Diptera – lower Brachycera. *Entomol. Scandinav.* **24**: 407–432.
- Smith, P.H., Barton Browne, L. & van Gerwen, A.C.M. 1989. Causes and correlates of loss and recovery of refractoriness of *Lucilia cuprina* females after their first mating. *J. Insect Behav.* **2**: 325.
- Smith, P.H., Gillott, C., Barton Browne, L. & van Gerwen, A.C.M. 1990. The mating-induced refractoriness of *Lucilia cuprina* females: manipulating the male contribution. *Physiol. Entomol.* **15**: 469–481.
- Spence, J.R. & Andersen, N.M. 1995. Biology of water striders: interactions between systematics and ecology. *Ann. Rev. Entomol.* **39**: 101–128.
- Squire, F.A. 1951. Observations on mating scars in *Glossina palpalis* (R.-D.). *Bull. Entomol. Res.* **42**: 601–604.
- Stutt, A.D. & Siva-Jothy, M. 2001. Traumatic insemination and sexual conflict in the bed bug *Cimex lectularius*. *Proc. Nat. Acad. Sci. USA* **98**: 5683–5687.
- Tuda, M. 2003. A new species of *Callosobruchus* (Coleoptera: Bruchidae) feeding on seeds of *Dunbaria* (Fabaceae), a closely related species to a stored-bean pest, *C. chinensis*. *Appl. Entomol. Zool.* **38**: 197–201.
- Tuxen, S.L. 1970. *Taxonomist's Glossary of Genitalia of Insects*. S-H Service Agency, Darien, Conn.
- Ueshima, N. 1972. New World Polyctenidae (Hemiptera), with special reference to Venezuelan species. *Brigham Young Univ. Sci. Bull. Biol. Ser.* **17**: 13–21.
- Unger, R.L. 1966. *Monograph of the Cimicidae*. Entomological Society of America, College Park, MD.
- Vahed, K. 1996. Prolonged copulation in oak bushcrickets (Tettigoniidae: Meconematinae: *Meconema thalassinum* and *M. meridionale*). *J. Orthop. Res.* **5**: 199–204.
- Vahed, K. 1997. Copulation and spermatophores in the Ephippigeinae (Orthoptera: Tettigoniidae): prolonged copulation associated with a smaller nuptial gift in *Uromenus rugosicollis* Serville. *J. Orthop. Res.* **6**: 83–89.
- Vahed, K. 2002. Coercive copulation in the alpine bushcricket *Anonconotus alpinus* Yersin (Tettigoniidae: Tettigoniinae: Platycleidini). *Ethology* **108**: 1065–1075.
- VanderPlank, F.L. 1948. Experiments in cross-breeding tsetse flies (*Glossina* species). *Ann. Trop. Med. Parasitol.* **42**: 131–152.
- Walker, E.M. 1922. The terminal structures of orthopteroid insects: a phylogenetic study (Part II). *Ann. Entomol. Soc. Am.* **15**: 1–76.
- Wedell, N. 1998. Sperm protection and mate assessment in the bushcricket *Coptaspis* sp. 2 (Orthoptera Tettigoniidae). *Anim. Behav.* **56**: 357–363.
- Weigensberg, I. & Fairbairn, D.J. 1996. The sexual arms race and phenotypic correlates of mating success in the waterstrider *Aquarius remigis*. *J. Insect Behav.* **9**: 307–319.
- West-Eberhard, M.J. 1983. Sexual selection, social competition, and speciation. *Quart. Rev. Biol.* **58**: 155–183.
- Westlake, K.P., Rowe, L. & Currie, D.C. 2000. Phylogeny of the water strider genus *Rheumatobates* (Heteroptera: Gerridae). *Syst. Entomol.* **25**: 125–145.
- Wood, D.M. 1991. Homology and phylogenetic implications of male genitalia in Diptera. The ground plan. In: *Proceedings of the Second International Congress of Dipterology* (A. Weismann, W. Orszagh & A. Pont, eds) pp. 255–284. The Hague.

Appendix

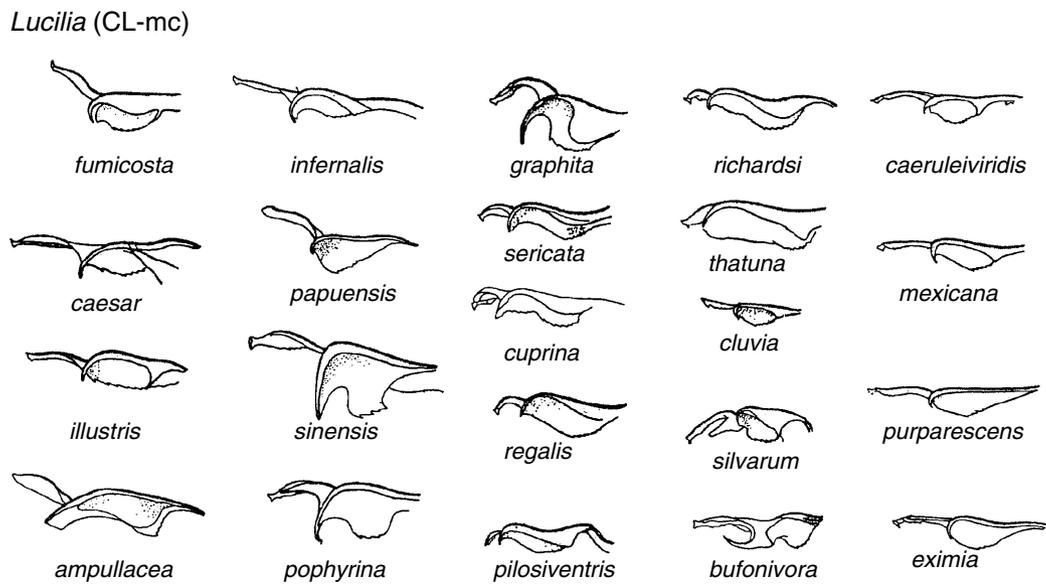


Fig. A1 The male aedeagus in 22 species of *Lucilia* blowflies (Diptera: Calliphoridae). In at least two of these species, *L. sericata* and *L. cuprina* (Lewis & Pollock, 1975; Merrett, 1989), the passage of male accessory gland material through the lining of the female's reproductive tract is facilitated by holes made in the lining of the female's reproductive tract by teeth on the aedeagus (from Aubertin, 1933) (estimates of intra-generic differences in upper case, complexity in lower case).

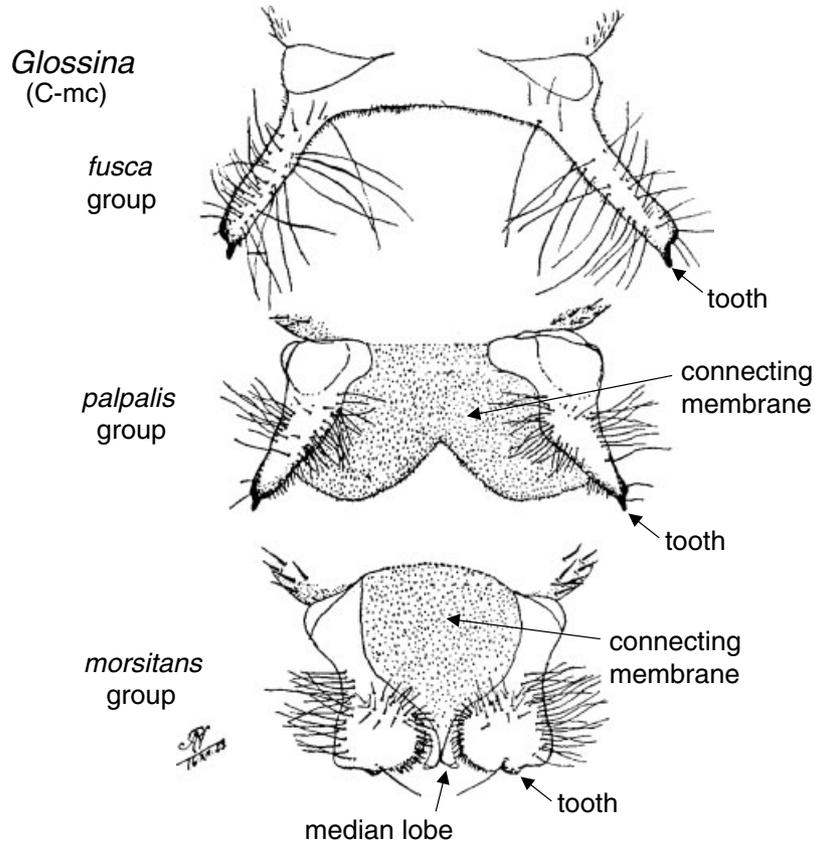


Fig. A2 The male cerci (superior claspers) of one species from each of the three species groups of *Glossina* tsetse flies (Diptera: Muscidae) (from Buxton, 1955). As shown in Fig. S3, the drawings are considerably simplified (estimates of intra-generic differences in upper case, complexity in lower case).

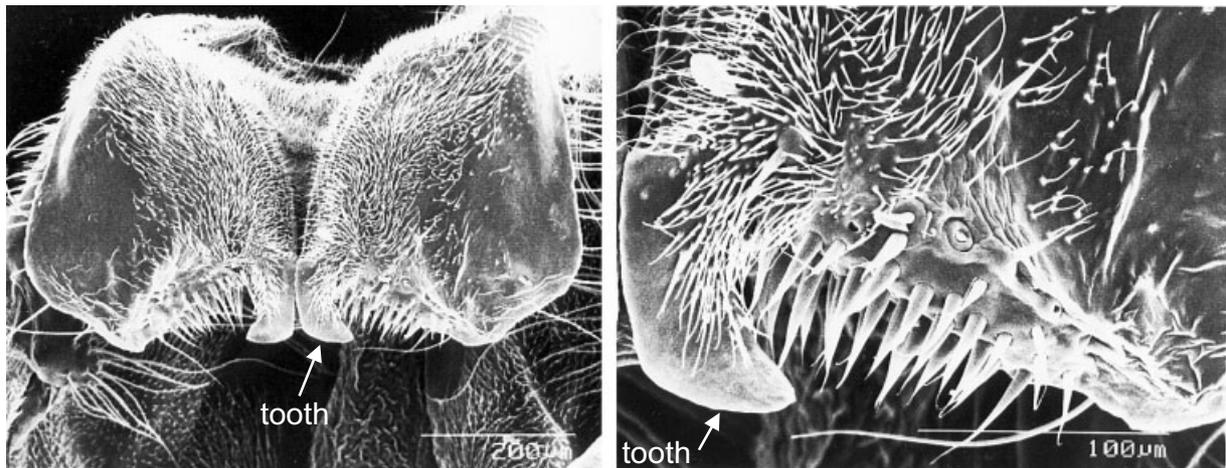


Fig. A3 SEM portraits (two different magnifications) of teeth and setae on the distal margins of the cerci of male *Glossina morsitans* that press against the ventral surface of the female abdomen during copulation.

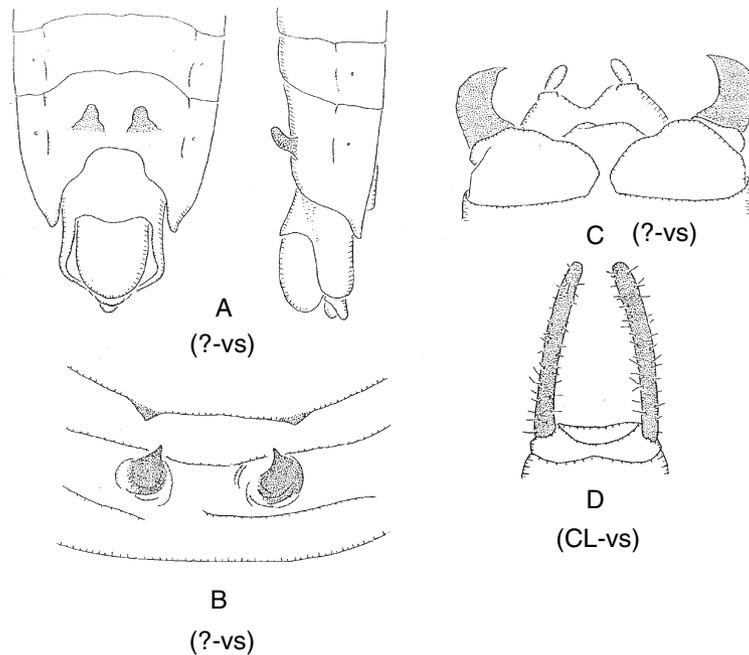


Fig. A4 Coercive male structures (stippled). (a). The abdominal hooks in *Gerris odontogaster* aid the male in remaining mounted when the female struggles to dislodge him (after a photograph by G. Arnqvist). (b) 'Gin trap' of male *Cyphoderris strepitans*, in which the two pairs of teeth pinch the female and enable the male to hold on more firmly (after Sakaluk *et al.*, 1995). (c) Powerful pinching cerci of the male tettigoniid *Anonconotus alpinus* (after Vahed, 2002). (d) Tong-like cerci of the male tettigoniid *Meconema thalassinum* (after Harz, 1957) (estimates of intra-generic differences in upper case, complexity in lower case).

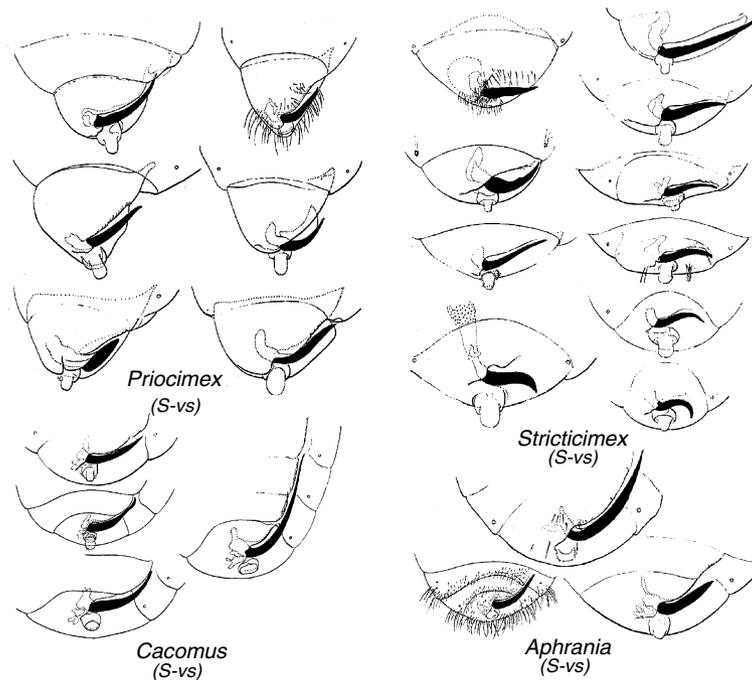


Fig. A5 A sample of male genitalia (the hypodermic left paramere) (black) in four genera of the bedbug family Cimicidae (from Usinger, 1966) (estimates of intra-generic differences in upper case, complexity in lower case).

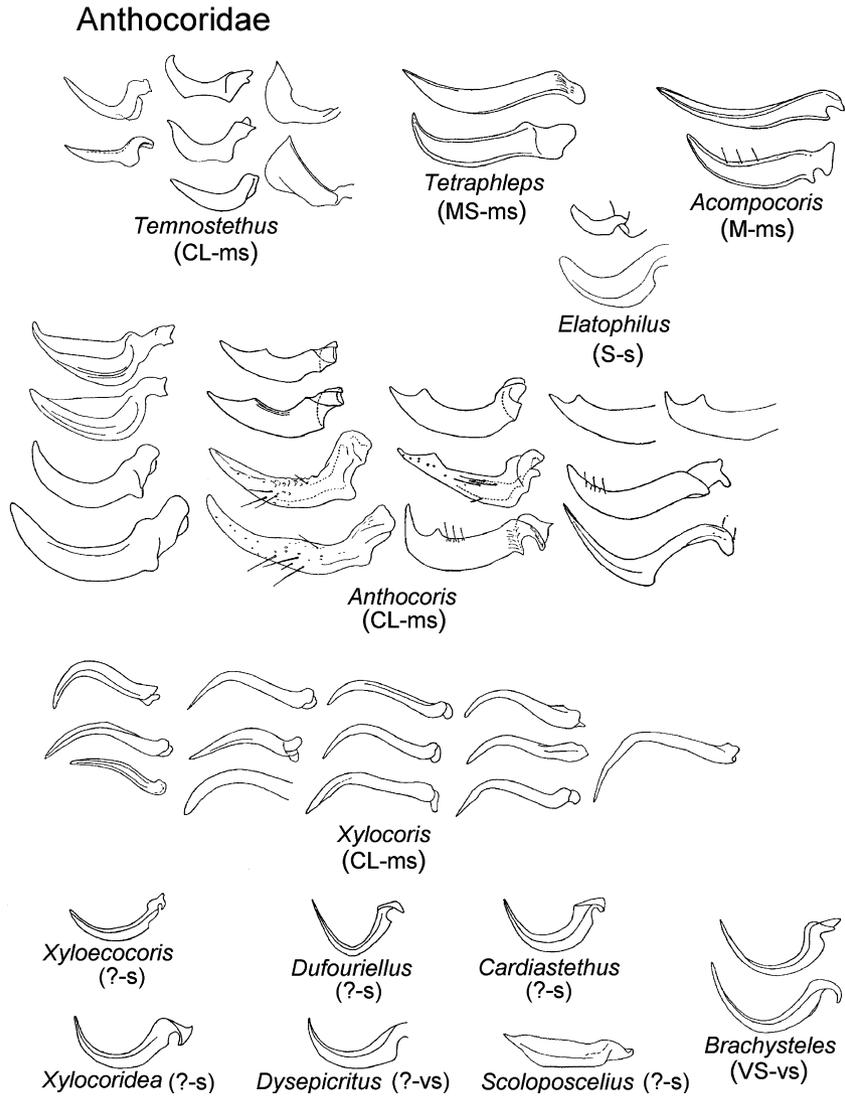


Fig. A6 A sample of male genitalia (the hypodermic left parameres) in the family Anthocoridae (Hemiptera) arranged by taxonomic affinities. There are differences, but the basic design is relatively uniform. Tight groups are genera; less tightly grouped drawings are subfamilies (from Pericart, 1972) (estimates of intra-generic differences in upper case, complexity in lower case).

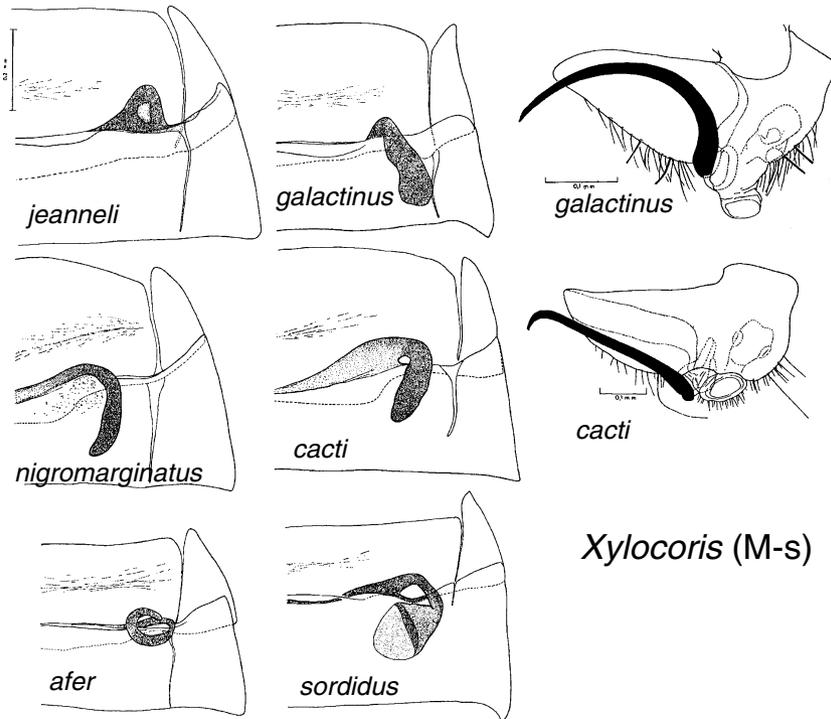


Fig. A7 Internal genitalic morphology of females (left and center columns) and corresponding external male morphology for three species (right column; parameres black) of anthocorid bugs (Hemiptera) in the genus *Xylocoris* (from Carayon, 1972) (estimates of intra-generic differences in upper case, complexity in lower case).

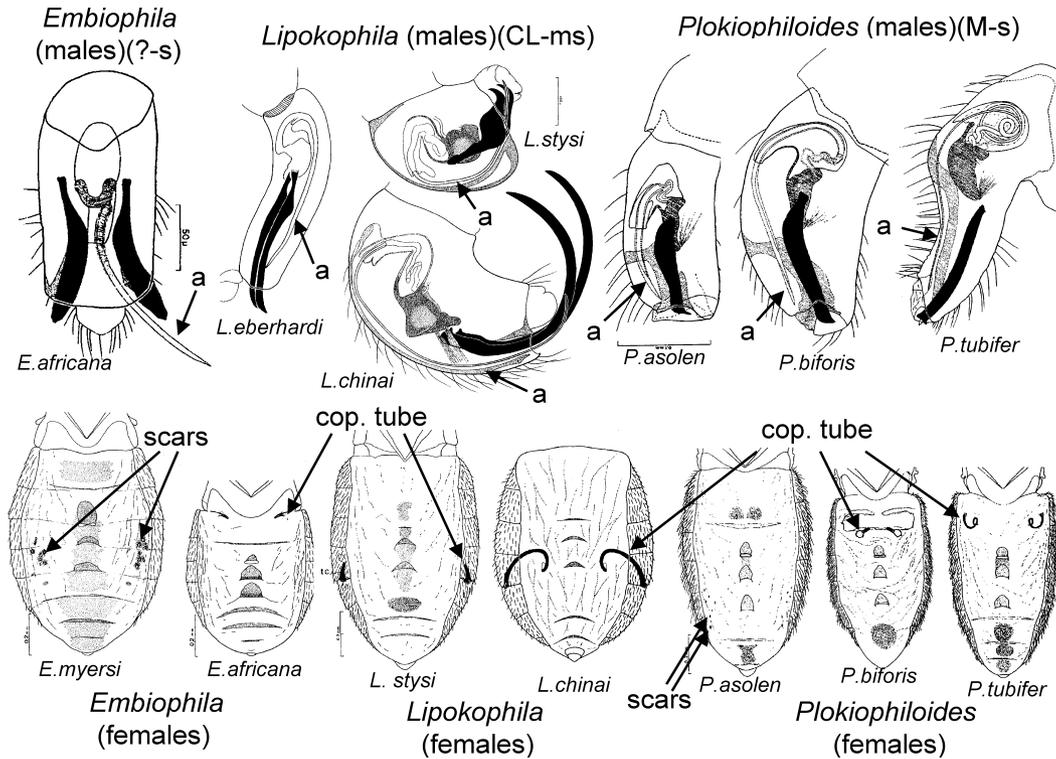


Fig. A8 Male genitalia (above) and female abdomens in dorsal view (below) of three genera of plokiophilid bugs. Male parameres and female copulatory tubes ('cop. Tube') are black; 'scars' are wounds from intromissions by males; a = male aedeagus (estimates of intra-generic differences in upper case, complexity in lower case; these estimates are based on the portions of the male that apparently contact the female – the parameres and the aedeagus).

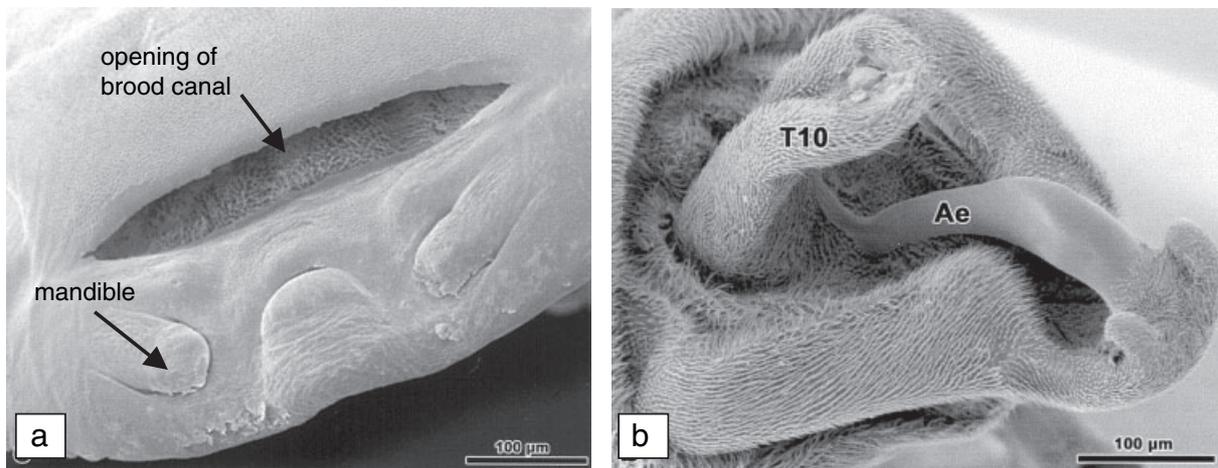


Fig. A9 SEM portraits of the female genital opening (brood canal) (left), and male genitalia (right; 'aed' = aedeagus) in the strepsipteran *X. vesparum* (from Beani *et al.*, 2005), showing the simple morphology of males and females.

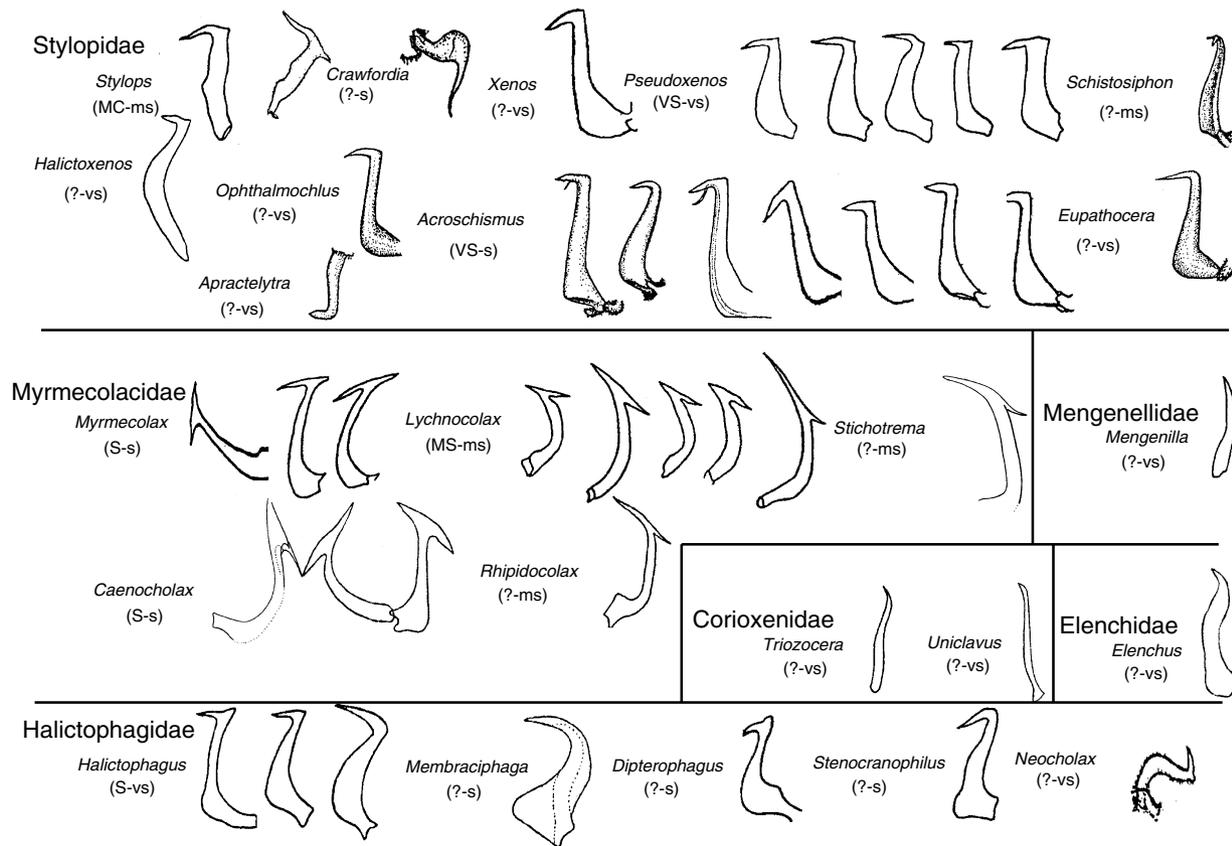


Fig. A10 A sample of male aedeagi in 24 genera of six families of Strepsiptera (solid lines separate families; the drawings in line to the right of each genus name are the aedeagi of different species in that genus (from Pierce, 1909; Bohart, 1941,1951; Kithirithamby, 1989) (to different scales) (estimates of intra-generic differences in upper case, complexity in lower case).

Diptera

Lucilia blowflies

These flies fit the predictions of rapid divergence resulting from sustained sexually antagonistic coevolution more clearly than any other group in this study. The aedeagi of male *Lucilia sericata* and *Lucilia cuprina* have arrays of jagged teeth that open holes in the lining of the female's reproductive tract, especially in the area where the male's accessory gland products are deposited (Lewis & Pollock, 1975; Merrett, 1989). These holes probably facilitate movement of male seminal products into the female's body cavity, where they produce inhibition of female remating (Smith *et al.*, 1989,1990). In *L. cuprina*, apparently the only species studied in this respect, females have an apparent defence against the male: the lining of the female's reproductive tract duct is thickened in the area where the male-induced damage occurs (Merrett, 1989). The physical separation of this site from the site where the

male's sperm are deposited makes it clear that the female design is to specifically defend against the male's seminal products, rather than his sperm. As predicted by sexually antagonistic coevolution, the male aedeagus morphology in *Lucilia* is species-specific; the toothed area shows differences in both form and location in different species (Fig. A1; Aubertin, 1933).

There is one major uncertainty regarding the occurrence of sexually antagonistic morphological coevolution in *Lucilia*. It is not known whether the walls of the reproductive tracts of females of different species are thickened at sites that correspond with the sites where the teeth on the male genitalia are brought to bear during copulation (or, possibly in cases in which males are 'ahead' of females, at sites where the teeth of ancestral males caused damage). The precise fit between the thickened wall and the male teeth of *L. cuprina* indicates, however, that such species-specific fits probably also occur in other species.

Glossina tse-tse flies

The well-studied genus *Glossina* has just over 20 species in three species groups (Potts, 1970). Males have powerful genitalic structures, the highly modified cerci ('superior claspers'), that clamp the female's abdomen during the approximately 20 min copulation (VanderPlank, 1949; Jaensen, 1970). The male cerci exert substantial pressure, causing a sharp, deep inward fold in the ventral surface of the female's abdomen (VanderPlank, 1949; Squire, 1951). The powerful and potentially damaging nature of the male cerci is illustrated by the fact that in experimental cross-specific matings of one pair of species, the males drove the tips of their cerci completely through the female's abdomen and out her dorsal surface (the females died, apparently as a result) (VanderPlank, 1948). In some species (but not others) mated females have brown patches of damaged cuticle where the cerci of conspecific males grasped them (Squire, 1951; W. Eberhard, unpublished observation of *Glossina palpalis*, *brevipalpis*, *fuscipes*, *morsitans* and *pallidipes*). In two species groups the male cerci have sharp tips (Fig. S6), and the female in one species (*G. palpalis*) has a pair of cushions on the ventral surface of her abdomen that appear designed to reduce the damage from the male's cerci (Squire, 1951). Thus there is evidence of defensive coevolution in female morphology with that of males.

The morphology of the cerci of male *Glossina*, especially of the distal portion that presses the female abdominal wall inward, is elaborate and quite distinct in different species, especially in the forms and patterns of bristles and setae (Figs A2, A3). To this extent, *Glossina* fits the predictions of sexually antagonistic coevolution. But in most species there are no corresponding female traits that would explain the evolution of species-specific male cercus traits. Traits on the female's ventral abdominal surface, where the male cerci grasp her in apparently all the species in the genus, have not been used to distinguish tse-tse species (Potts, 1970). The mechanics of the male's powerful grip also imply that the species-specific male traits cannot be explained by differences in female resistance behaviour (Eberhard, 2004b). Furthermore, both behavioural and morphological details suggest that rather than being weapons to overcome female resistance, as supposed under the sexual antagonistic coevolution hypothesis, the cerci of male tse-tse flies are instead stimulatory devices. Close observation of copulation in several species (*G. pallidipes*, *G. morsitans*, *G. palpalis*, *G. fuscipes*, and *G. brevipalpis*) revealed that the male's cerci squeeze the female rhythmically, for many minutes at a stretch during copulation (Briceño *et al.*, in preparation). The movements are complex, including at least two different types, and the patterns of squeezing behaviour differ between species (Briceño & Eberhard, in prep.). Several patches on the male genitalia of elongate or dense setae are exactly aligned with and rub against

membranous portions of the female during copulation, giving still further evidence of a stimulatory function (Briceño *et al.*, in preparation). Checks of events inside the female's reproductive tract (where other male genitalic structures are inserted) (Briceño *et al.*, in preparation) showed that the male's external clasp and the squeezing movements do not obviously mechanically facilitate intromission or ejaculation (which occurs only during the last 30 s of the copulation – Jaensen, 1979; Leegwater-van der Linden & Tiggleman, 1984). Mechanical stimulation during copulation increases the likelihood of ovulation (Saunders & Dodd, 1972), and may also inhibit female remating (Gillot & Langley 1981). The exact nature of the stimuli involved is yet to be determined.

In sum, the structurally diverse, and apparently manipulative and potentially damaging male genitalia in *Glossina*, and the female defensive cushions in one species fit sexually antagonistic coevolution predictions. But female counter-adaptations that would be expected under sustained sexually antagonistic coevolution to explain many male traits are lacking in the rest of the genus. In addition, the apparently stimulatory use and design of the male genitalia during copulation suggests that the species-specific male morphology functions to stimulate rather than to simply grasp the female. The overall fit with sexually antagonistic coevolution predictions is poor.

Heteroptera*Gerris water striders*

An especially strong case has been made for antagonistic morphological coevolution in the water strider genus *Gerris* (Arnqvist, 1989; Arnqvist & Rowe, 2002a,b). Dorsally projecting spines near the female's genitalia are elongated to different degrees in different species, and have independently become especially elongate in *Gerris incognitus* and *odontogaster*. Longer female spines impede male attempts to clamp the tip of the female's abdomen with his (Arnqvist & Rowe, 2002a,b). Such clamping helps the male hold onto the female during her energetic struggles after he mounts, and is a necessary prelude to intromission. The possibility of an evolutionary arms race between male and female morphology is directly supported by four types of data: interspecific comparisons; facultative changes in behaviour; experimental phenotypic manipulations; and measurements of costs and benefits. There is a correlation in the relative development of different male and female structures. In the male these include ventral flattening of the abdomen, elongate clasping genitalia, and more powerful front legs; possible defensive traits of the female that enhance her ability to dislodge mounted males include a downward tilt of her abdomen tip, elongate abdominal spines, and more powerful front legs. An independent-contrasts

analysis based on a robust phylogeny (Damgaard & Sperling, 2001) showed that changes in male and female traits probably coevolved as predicted.

Further indications of antagonistic coevolution in *Gerris* come from experiments demonstrating female defensive attributes: male ability to remain mounted decreased when the female traits were experimentally accentuated, and increased when they were reduced (Arnqvist, 1989; Arnqvist & Rowe, 1995). Females benefit from resisting mounts, as predation risk increases sharply when the female is mounted by a male (Rowe, 1994). Females also modulate their resistance in predicted ways (summarized in Rowe *et al.*, 1994; Arnqvist, 1997), and a possible measure of the degree of mismatch between changes in male and female morphology was correlated with several behavioural variables related to male–female conflict (Arnqvist & Rowe, 2002a). Behavioural evidence ruled out the possibility that differences were due to interspecific differences in optimum female remating rate (Rowe & Arnqvist, 2002). In sum these data strongly indicate an important role for antagonistic coevolution in the evolution of some aspects of male and female morphology in *Gerris*, even though possible benefits to the female of morphological and behavioural resistance obtained via superior sons (Cordero & Eberhard, 2003; Kokko *et al.*, 2003; Pizzari & Snook, 2003) have not been taken into account.

With respect to morphological evolution, two of the expectations from sexually antagonistic coevolution are met: male and female morphology has coevolved; and female designs are appropriate to defend against male traits. The third expectation, of morphological diversity, is less clearly fulfilled. The morphological designs of both sexes of *Gerris* are relatively simple and practical (Fig. A4).

Bedbugs and allied groups with hypodermic insemination

Cimicidae

Another heteropteran group in which sexually antagonistic coevolution has been thought to occur is the family *Cimicidae*. This small family of ectoparasites of mammals and birds comprises about 30 species in 5 genera (Usinger, 1966; Pericart, 1972; Schuh & Slater, 1995). Males use their hypodermic-like genitalia to inject semen directly into the female's body cavity, rather than deposit it in her reproductive tract. Knowledge of copulation and subsequent events in the female is largely based on the extraordinary studies of Carayon (summary in Carayon, 1966). Damage to the female that results from copulation can reduce her longevity and her reproductive success (Mellanby in Carayon, 1966; Stutt & Siva-Jothy, 2001; Reinhardt *et al.*, 2003; Morrow & Arnqvist, 2003). Copulation produces external damage (punctured female membranes or

sclerites) and infections; it is not sure whether it also results in other internal damage.

Given this damage, the expectation is that rapid divergence resulting from sexually antagonistic coevolution would produce evolutionary races between female traits that make it difficult for a male to produce damage (insert his genitalia), and male traits that overcome these female defences. Contrary to this expectation, neither sex shows much external diversification, and female external morphology is not defensive. Male genitalia are secondarily reduced, and relatively uniform and simple. The right paramere has been lost, and the vesica, which is elaborate and diverse in related bugs such as Pentatomidea that lack traumatic insemination, is reduced and incorporated in the remaining paramere (Schuh & Slater, 1995). The left paramere is a structurally simple, sharp, and thin (Fig. A5). The parameres of closely related cimicid species differ only in minor details (Fig. A5), and are not used to distinguish species in some genera (Usinger, 1966).

The modifications of female external morphology are also modest, generally in the form of a depression or fissure in the posterior border of the segment covering the membranous site of intromission. Their designs are not obviously defensive (e.g. the slit guides and receives the male's genitalia) (Usinger, 1966). The possibility that the physical damage from intromission (measured as mean cumulative egg production) is minimized when it occurs at this site rather than others on her abdomen was supported by the results of one study with experimental treatments mimicking intromission in *Cimex lectularius* (Morrow & Arnqvist, 2003), but not by another (Reinhardt *et al.*, 2003). Female modifications are divergent enough to place most species to genus; in one genus, *Leptocimax*, the female genitalia are distinctive in each species (Usinger, 1966).

Female bedbugs do have defensive structures, but they consist of internal chambers and ducts (the 'paragenitalia') that receive the sperm after they have entered, and that kill them (Carayon, 1966). The embryonic derivation of the female's paragenitalia from cells that are normally used in fighting off infections (Carayon, 1966), and the high mortality of the sperm that enter them support the hypothesis that they evolved as defensive adaptations. The spermatheca and the associated structures in the paragenital system provide 'the best and most fundamental' characters for cimicids (Usinger, 1966). Females thus seem to have evolved diverse defences against male's semen (or the associated infections?), but, not against the structure that inflicts the external damage – his paramere. Unless these internal female traits somehow reduce the costs of the physical damage and infections that result from traumatic insemination, they fit more readily with cryptic female choice mechanisms to control paternity, than with sexually antagonistic coevolution mecha-

nisms to reduce male-inflicted damage to their reproductive output.

In sum, expectations under sexually antagonistic coevolution are not met in bedbugs. Male–female conflict of interests occurs, but it has resulted in only limited divergence (especially modest in the males), and in female structures that are not apparently designed as expected to prevent damage from being stabbed by the male. It appears that females have evolved to control fertilization and/or internal infections rather than intromission (Reinhardt *et al.*, 2003).

Anthocoridae

Several major aspects of genitalic evolution are similar in the related, larger family Anthocoridae (approximately 450 species), in which traumatic insemination also occurs. Males also have secondarily reduced, asymmetrical hypodermic genitalia (Pericart, 1972; Schuh & Slater, 1995). The right male paramere is greatly reduced or absent, and (except in one subfamily) the aedeagus is simple and resides in a groove in the left paramere, with which the male stabs the female. The females of many groups have derived abdominal ‘copulatory tubes’ into which males introduce their genitalia, while in others the male inserts his genitalia through her abdominal wall. As illustrated in Figs A6 and A7 (see also Carayon, 1972; Kelton, 1978; Gross, 1955a,b), the pattern of evolution of male genitalia resembles that in cimicids in that they are relatively simple in design throughout the family. They appear to have diverged more consistently, as they are often used to distinguish congeneric species (Gross, 1955a,b; Herring, 1967; Carayon, 1972; Pericart, 1972; Kelton, 1978).

Neither the external female genitalia nor the female paragenitalia are illustrated in most taxonomic literature on anthocorids, indicating that at least the external female morphology is relatively uniform (female internal structures are likely to have been checked less often, for practical reasons, so it is not possible to make confident statements about them). Less complete data suggest that, as in cimicids, internal female structures are diverse, in at least some groups (Fig. A7). Also as in cimicids, the external female modifications (grooves or tubes to receive the male genitalia) seem ‘cooperative’ rather than defensive (although they might be damage control devices—see Discussion). No facultatively deployable defences such as erectable setae near intromission sites are known. Still another similarity with cimicids is that in at least some groups, internal female structures are divergent. In *Xylocoris*, spermalege structure is especially useful for phylogeny and classification (Carayon, 1972). In this same genus the left paramere is useful for discriminating species (Carayon, 1972) (Fig. A7), although the differences in the subgenus *Proxylocoris* (not illustrated here) are subtle and require careful examination from different angles (Carayon, 1972). Perhaps further detailed studies of the internal female

morphology of other anthocorid genera will uncover similar internal female diversity.

Polyctenidae

The lack of diversification of male hypodermic genitalia is especially clear in this small family (<30 species) of bat ectoparasites, Polyctenidae. Males have lost their right parameres, and the aedeagus is simple and associated with the left paramere, which is inserted into the female. In a worldwide revision of the family, Ferris & Usinger (1939) found that ‘the genitalia of the males throughout the group seem to offer no aid in generic or specific identification’ (p. 25). Other taxonomists have also failed to use male genitalia to distinguish species (Ronderos, 1960; Ueshima, 1972). Female genitalia have also not been used.

Plokiophilidae

Hypodermic insemination also occurs in the small family Plokiophilidae (in 1975 the total number of species was 10 in four genera). The male genitalia are less derived than in cimicids, as both parameres are present and are only weakly asymmetrical, and the phallus (aedeagus) is symmetrical and free of the parameres (Fig. A8). The females of some species have simple, paired ‘copulatory tubes’ that open on the dorsum of the abdomen to receive the male genitalia. There is no modification of the female’s external surface associated with her copulatory tubes (Fig. A8). Other species lack copulatory tubes, and the male genitalia puncture the soft dorsum of the female’s abdomen, leaving copulatory scars (Fig. A8) (Carayon, 1975; Schuh & Slater, 1995).

The male genitalia are generally useful in distinguishing species, but are structurally simple, and the differences are relatively small (e.g. parameres ‘nearly straight’ vs. ‘nearly straight but apically decurved’ in different *Lipokophila*—Eberhard *et al.*, 1993) (also Fig. A8); differences are lacking in some congeneric species. Female copulatory tubes are simple in form, but are located at different sites on the abdomen in different genera; they are also species-specific in some groups (Fig. A8). In *Plokiophiloides* the length of the copulatory tube correlates with the length of the male’s phallus, but not of his parameres; in *Lipokophila* the relationship is reversed, as their length correlates with that of his parameres (Fig. A8).

Coleoptera

Dytiscinae

Another group with apparent sexually antagonistic coevolution (Chapman *et al.*, 2003) is the taxonomically well-studied diving beetle family Dytiscidae. The front tarsi of the males in some groups of the subfamily Dytiscinae have evolved, sucker-like ‘disc’ setae, with which the male adheres to the female’s elytra as she swims (Aiken & Kahn, 1992). Mounting is probably

costly for the otherwise rapidly swimming female, as pairs are probably able to swim less rapidly. Males of the few species whose behaviour has been studied apparently mount passing females without preliminaries, and females resist energetically (Aiken, 1992). Pairing can last up to 10 h (Aiken, 1992).

Following the evolutionary origin of male disc setae, females in five different lineages independently evolved coarse ('rugose') elytral sculpturing, which is probably a defensive trait that reduces the strength of the male's adhesion (Miller, 2003). The type of sculpturing (multiple ridges, grooves and pebbly) differs in different genera; in some genera (*Hydaticus*, *Hyderodes*, *Acilius*, *Dytiscus*) several species have rugose females. Some aspects of sexual interactions need further study (including the force of male adhesion to different types of elytra, the effect of mounted males on female swimming, the significance of dimorphisms in female elytral rugosity, and the possibility that female 'resistance' behaviour serves instead to screen males). Nevertheless, it appears very likely that morphological antagonistic coevolution has occurred between males and female in these dytiscines (Miller, 2003).

Surprisingly, from the point of view of antagonistic male–female coevolution, this male–female conflict and the diversity of female morphology has led to only very limited divergence in male grasping structures. In one species, *Graphoderus zonatus*, the frequency of rugose females in different lakes was positively correlated with the number and size of disc setae in males from the same lakes, as expected if male and female traits are coevolving (Bergsten *et al.*, 2001). There are also some inter-generic differences in male tarsi (Halvarsson, 2001), and the largest differences in male front tarsi are between species with females, which have rugose rather than nonrugose elytra. In general, however, the male front tarsi of dytiscines are not species-specific (Larson *et al.*, 2000; Halvarsson, 2001). Male front tarsi are not useful in distinguishing species in several genera with rugose females, including *Hydaticus* (Roughley & Pengelly, 1981), *Acilius* (K. Miller, 2002), and *Dytiscus* (Roughley, 1990) (species have instead generally been distinguished using male genitalic differences). Consultation with expert dytiscid taxonomists (K. Miller, J. Bergsten, in press) confirmed that the lack of use of male front tarsi to distinguish species is not due to taxonomists having failed to check them for useful characters.

Strepsiptera

In nearly all the species of this small order of insect parasites (about 300 species), the larva-like adult female remains inside the host, with only the nearly featureless anterior end of her puparium (her 'cephalothorax') protruding to the outside (Fig. S9). Copulation is traumatic in the sense that the male introduces his sperm into the female's haemocoel, which contains her eggs. The

male inserts his genitalia through an opening of the 'brood canal' on the female's anterior surface, a structure that is unique to Strepsiptera. This opening may have coevolved with the males' traumatic insemination. However, the offspring also emerge here (Hughes-Schrader, 1924), so the opening could have evolved in the context of birth rather than mating. Males of *Xenos vesparum* sometimes deposit sperm through this opening into the brood canal (Beani *et al.*, 2005). The inner end of each of the several internal branches of the brood canal lead to the haemocoel and is covered by a delicate epithelium that is only one cell thick (Hughes-Schrader, 1924); individual sperm cells presumably pass through this covering. In other cases, the male's aedeagus perforates the wall of the brood canal near the external opening, and introduces his sperm directly into the haemocoel (Lauterbach, 1954). Males generally die within a few minutes after copulating (Kithirithamby, 1989, Beani *et al.*, 2005). In two species (*Coriophagus rieki* and *Stichotremia dallotoreanum*), the male's aedeagus sometimes remains in the female after copulation (Kithirithamby, 1989).

The genitalia of male strepsipterans are reduced, having lost all structures (such as parameres) other than the aedeagus itself (Kithirithamby, 1989) (Fig. A9). The aedeagus is often used to distinguish species, but it is relatively simple and only moderately divergent (Fig. A10). Kithirithamby (1989) qualifies its usefulness: 'the aedeagus can, to a certain extent, be used for taxonomic differentiation of species' (p. 57). While in the family Myrmecolacidae, 'the most constant specific characters are to be found in the aedeagus and the legs' (Bohart, 1951, p.84), in some genera of other families the differences are quite small (e.g. *Acroschismus*, *Pseudoxenos* in Fig. A10).

Female genitalic structures in Strepsiptera are even less diverse. While the outline of the female cephalothorax is relatively constant within a species (Kithirithamby, 1989), the external opening of the brood canal seems not to show any modification (Riek, 1973), and it has not been used as a taxonomic character, contrary to expectations under sexually antagonistic coevolution. There is no sign that female designs are potentially defensive. The number and arrangement of the inner ducts of the brood canal (which are beyond the reach of the male's aedeagus) vary widely among families (Riek, 1973). This diversity may be similar to that of the internal female structures of bedbugs, but I was not able to find data to determine whether these female traits vary among closely related species.

In sum, the strepsipterans are reminiscent in several ways of cimicoid bugs. Male genitalia are secondarily simple and only weakly differentiated; it is possible that internal female structures that handle sperm are diverse. Contrary to the expectations from sexually antagonistic coevolution, the external female morphology is basically unmodified; it is even less diverse than that of the cimicoids.

Orthoptera

Tettigoniidae

Additional cases of likely male–female conflict involving aggressive male structures occur in some orthopterans in which males have strong clasping organs that appear to be used as weapons to overcome female resistance. These include two or three genera of katydids, each in a different subfamily: *Anonconotus*, *Meconema* and possibly *Uromenus* (Vahed, 1996, 2002) (Fig. A4). Male–female conflict is suggested in *Anonconotus* by two facts: males attack females without any preliminary luring (in most katydids the male lures females by singing); and the male seizes (and sometimes injures) the soft cuticle on the side of the female’s abdomen with his short, powerful pointed cerci (Fig. A4b), then gradually works his cerci rearward toward the tip of her abdomen (Vahed, 2002). Conflict over copulation is suggested in *Meconema* by the fact that after the male lures the female from a distance by drumming on the substrate, he fails to give her the nuptial gift (a spermatophylax) that is transferred to the female by the males of most other katydids (the spermatophylax is probably ancestral in katydids, and protects the male’s sperm from being eaten by the female before they enter her reproductive tract – Vahed, 1997; Gwynne, 2001). The duration of genitalic coupling after the male inserts his spermatophore into the female is unusually long in both *Meconema* and *Uromenus rugosicollis*, which also has a reduced spermatophylax (Vahed, 1996, 1997). The male *Meconema* clasps the female unusually strongly, clamping her abdomen and ovipositor with his front legs, his mouthparts, and his unusually long, curved cerci. These males thus appear to delay female ingestion of the sperm-containing portion of the spermatophore by force, rather than with the gift of a spermatophylax. The male cerci of other groups of katydids are typically shorter, and do not encompass the female’s abdomen – Rentz, 1972; Vahed, 1996). Females of both *Anonconotus* and *Meconema* kick, bite, and drag males about in apparent attempts to free themselves during copulation (Vahed, 1996, 2002). A final indication of male–female conflict in *Anonconotus* and *U. rugosicollis* is that the male’s basal cercal tooth is inserted into the female’s abdominal membrane, rather than into the usual pocket near the female’s subgenital plate (the ‘copulatory groove’). In other katydids this groove functions as a ‘selectively cooperative’ structure that receives this tooth and helps lock the pair together (Rentz, 1972). Cercal teeth are not present in *Meconema* (K. Vahed, personal communication), and, at least in *U. rugosicollis*, the copulatory groove is missing in the female (Nadig, 1994; K. Vahed, personal communication).

This morphological conflict with females has apparently not led to rapid divergent evolution in male *Anonconotus*. The male’s clamping cerci have apparently not diverged rapidly, as they are not used to separate

species; instead male genitalic ‘tillators’ (which are moved rhythmically during copulation in some tettigoniids – Vahed, 1997), and the size and shape of the elytra and the body are most important (Carron *et al.*, 2002). On the female side, the cerci seize otherwise featureless membranous areas on her abdomen (Vahed, 2002), so antagonistic coevolution of this portion of the female’s body seems not to have occurred. The genus *Meconema* has only two described species (in both of which males may impose costs on females – Vahed, 1996). The cerci are relatively simple in form (Harz, 1957; Fig. S4), but are longer in one species than the other (Vahed, 1996). The male cerci of *Uromenus* are also simple in design, but are important in distinguishing species (Nadig, 1994). The female’s ‘copulatory groove’ differs between species in a complementary manner (Nadig, 1994). The female designs (grooves) are appropriate to facilitate the male’s grasp on the female (‘selective cooperation’), rather than to defend against male grasps.

Haglidae

A similar male–female conflict occurs in the cricket *Cyphoderris strepitans*. Experimental modification of the male’s abdominal gin trap, two pairs of teeth that close against each other to pinch the female (Fig. S4c), showed that the trap’s ability to hold the female has an important role in preventing her from escaping when the male is unable to feed her a sufficiently large nuptial meal (Sakaluk *et al.*, 1995). Again, the male structure has a mechanically simple utilitarian design. As in *Meconema*, it is difficult to evaluate the relative rate of divergence of gin trap designs compared with other traits, because *Cyphoderris* has only three species (Dodson *et al.*, 1983), and the behaviour of the other two apparently has not been described.

Male pinching structures occur in five orthopteran families (Sakaluk *et al.*, 1995), and prolonged copulation (and thus possible male–female conflict) also occurs in scattered groups in five families (Vahed, 1997; Wedell, 1998); further comparative study of ensiferan clasping structures and associated behaviour would be of interest.

Groups not included in Table 1

There are several other groups that represent independently derived cases of apparent male–female morphological conflicts that were not included, due to their lacking signs of morphological female antagonistic coevolution. Both *Callosobruchus* (bruchid) and *Metricoidea* (chrysomelid) beetles (Crudginton & Siva-Jothy, 2000; Flowers & Eberhard, in press) have male genitalic traits that inflict physical damage on the female (pierce her bursal wall). The available data on divergence in these male genital structures (not completely satisfactory, because the male structures are drawn in their folded rather than their

unfolded, exerted state), suggests that, at least in the bruchids, they have species-specific forms (Kingsolver, 1999; Tuda, 2003). However, the information available on the female morphology of these groups (one species of *Callosobruchus*, two species of *Metrioidea*) gives no sign of female coevolution. The bursal walls of the females show no obvious thickening or other signs of the coevolution expected under sexually antagonistic coevolution to reduce male damage (Crudginton & Siva-Jothy, 2000; Flowers & Eberhard, in press).

Similarly, sharp aedeagal scales and bristles on the genitalia of the sepsid fly *Sepsis cynipsea* may damage the lining of the female's vagina (Blanckenhorn *et al.*, 2002), but again the female lining is apparently unmodified. In addition, judging by the strong general morphological similarity of male and female *S. cynipsea* with the closely related *Archiseptis* (W. Eberhard, unpublished), the site where the male spines mesh with the female during at least most of copulation is probably far from the site where damage was observed (Eberhard & Huber, 1997), so the male spines may not produce this damage. The male chelicerae of the spider *Physocyclus globosus* may rub setae off of the female's genitalia when the male squeezes her with his pedipalps (Peretti & Eberhard, in preparation), but the setae on the female epigynum do not differ dramatically among species (they have not been studied carefully, however – B. Huber, personal communication). In the distantly related spider *Nesticus cellulanus*, a portion of the male genitalia obligatorily penetrates the female epigynal cuticle during copulation (Huber, 1993); the female cuticle at the site of damage is contrary to antagonistic coevolution expectations for female defences *thinner* than in adjacent areas. It is not clear, however, that this penetration causes a reduction in female reproductive potential. Males of *Bombus* bumblebees leave copulatory plugs in females, and it is possible (though not certain) that the plugs reduce female ability to remate (Duvoison *et al.*, 1999), which is advantageous to her (Baer & Schmid-Hempel, 1999). It has long been known, however, that there are no species differences in the relatively featureless area of the female abdomen in *Bombus* where some species-specific male genitalic structures make contact during copulation (Richards, 1927); the possibility that the spermatophore itself is species-specific in form and that the site on the female that is contacted by the spermatophore shows modifications remains untested.

In spite of the strong evidence of antagonistic coevolution in *Gerris*, other groups of water striders were omitted

because support for male–female morphological coevolution is much less clear. As expected, male front legs are stronger than those of the female in several groups (with exceptions – Andersson, 1997), and in *Aquarius remigis* both long male legs and long male genitalia are important in resisting female struggles (Weigensberg & Fairbairn, 1996; Fairbairn *et al.*, 2003). Female resistance in *A. remigis* is also modulated in some ways that are predicted by sexually antagonistic coevolution (Lauer *et al.*, 1996), and female spines in *A. paladum* increase female abilities to reject mating attempts (Ronkainen *et al.*, 2005). But female genitalic morphology has apparently not coevolved with that of the male, and the male genital traits are not counter-adaptations to those of the female in *Aquarius* (Fairbairn *et al.*, 2003). In addition, female reproduction in *A. paladum* was increased rather than reduced by multiple matings (Ronkainen *et al.*, 2005). Males of *Rheumatobates* have very elaborate antennae and legs that they use to grasp the female (Silvey, 1931), but females do not show the expected complementary species-specific modifications; instead, they have very uniform, relatively simple outlines (Hungerford, 1954; Westlake *et al.*, 2000). Male–female morphological coevolution may not have occurred in the family as a whole: 'For the Gerridae as a whole, transitions to female anticlasper devices are not significantly more frequent in lineages with male clasping genitalia ...' (Andersson, 1997; p. 358). This conclusion is somewhat tentative, as it depends on the accuracy of the phylogeny on which the analysis was based, and claspers and anti-clasper devices were analysed as qualitative rather than quantitative traits. No species-specific differences in female resistance behaviour that might explain male morphology have been documented in any water strider, but detailed observations have apparently never been made.

A final group that might offer possible cases are the several groups of Lepidoptera in which the female bursa seems to have coevolved with male genitalic and spermatophore traits. It has not been demonstrated, however, that these male traits damage the female's fecundity or survival. The effect which has been proposed is inhibition of female remating (see Cordero, 2005), which might or might not reduce direct female reproductive output.

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