Male–female conflict and genitalia: failure to confirm predictions in insects and spiders

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ABSTRACT

Some recent models suggest a new role for evolutionary arms races between males and females in sexual selection. Female resistance to males is proposed to be driven by the direct advantage to the female of avoiding male-imposed reductions in the number of offspring she can produce, rather than by the indirect advantage of selecting among possible sires for her offspring, as in some traditional models of sexual selection by female choice. This article uses the massive but hitherto under-utilized taxonomic literature on genitalic evolution to test, in a two-step process, whether such new models of arms races between males and females have been responsible for rapid divergent evolution of male genitalia. The test revolves around the prediction that 'new arms races' are less likely to occur in species in which females are largely or completely protected from unwanted sexual attentions from males (e.g. species which mate in leks or in male swarms, in which males attract females from a distance, or in which females initiate contact by attracting males from a distance).

The multiple possible mechanical functions of male genitalia are summarized, and functions of male genitalic structures in 43 species in 21 families of Diptera are compiled. Functions associated with intromission and insemination (e.g. seizing and positioning the female appropriately, pushing past possible barriers within the female, orienting within the female to achieve sperm transfer), which are unlikely to be involved in new arms races when females are protected, are shown to be common ($>50\%$ of documented cases). This information is then used to generate the new arms race prediction: differences in genitalic form among congeneric species in which females are protected should be less common than differences among congeneric species in which females are vulnerable to harassment by males. This prediction was tested using a sample of 361 genera of insects and spiders. The prediction clearly failed, even when the data were adjusted to take into account several possible biases. Comparative analyses within particular taxonomic groups also failed to show the predicted trends, as did less extensive data on other non-genitalic male display traits. Arms races, as defined in some recent models, seem to have been less important in male–female coevolution of genitalic structures than has been suggested. By elimination, alternative interpretations, such as traditional female choice, which do not predict associations between female protection from harassment and rapid divergent evolution, are strengthened.

Key words: genitalic evolution, sexual selection, cryptic female choice, male–female conflict.

CONTENTS

I. INTRODUCTION

Recent empirical and theoretical developments have suggested new interpretations of sexual selection. Some evolutionary phenomena that were previously explained by mate choice may be better explained by coevolution of males and females resulting from conflicts of interest between the sexes over control of copulation and fertilization (Parker, 1979; Chapman *et al.*, 1995, 2003; Rice, 1996; Alexander, Marshall & Cooley, 1997; Holland & Rice, 1998, 1999; Rice & Holland, 1999; Johnstone & Keller, 2000; Michiels, 1998; Gavrilets, Arnqvist & Friberg, 2001; Pitnick, Brown & Miller, 2001*a*; Pitnick, Reagan & Holland, 2001*b*; Stutt & Siva-Jothy, 2001; Moore *et al.*, 2001). These recent discussions emphasize one particular class of direct benefits that a female could derive from resisting male sexual behaviour: avoidance of male-inflicted reductions in her ability to produce offspring. Evolutionary interactions between males and females are thought to be driven by selection on females to avoid these costs that are imposed by the male, resulting in subsequent male countermeasures.

For instance, in their 'chase away' model, Holland and Rice (1998) listed the possible costs of mating for females as mating 'too often, [or at a] less-than-ideal time or place'. Gavrilets *et al.* (2001) contrasted the proposed benefits to females from rejecting males under their sexual conflict model as a 'side-effect of females evolving to reduce the direct costs of mating' instead of 'traditional explanations of costly female mate choice, which rely on indirect genetic benefits' (p. 531). Alexander *et al.* (1997) were less explicit about female costs in their discussion of genitalic evolution, but argued specifically against indirect Fisherian payoffs to females. They mention that conflicts 'are always mediated by ecological factors' (p. 8), and the examples they used of benefits to females from resisting males were avoidance of direct costs such as loss of foraging or oviposition opportunities, and loss of benefits from additional matings that would result from unduly long copulations. Other possible direct female costs include increased exposure during copulation to predation and venereal diseases, and interference of copulation with the ability to carry out vital

activities such as feeding, sheltering, or resting. Costs could also be imposed on females after copulation ends, as a result of male effects on her reproductive physiology, such as causing her to make disadvantageously large or premature investments in oviposition due to male induction of egg maturation or oviposition, or to lose the benefits (direct or indirect) that she might obtain from other males due to male-imposed suppression of her receptivity (Chen, 1984). Males and females are envisioned as being engaged in co-evolutionary arms races for control of the events that are associated with copulation, insemination, and ultimately fertilization of the female's eggs. Explicit models of this sort have been proposed for both classic, pre-copulatory female rejections (the 'chase-away' model of Holland & Rice, 1998; Gavrilets *et al.*, 2001), and female rejection during or following coupling (the male–female conflict model of Alexander *et al.*, 1997). These ideas will be referred to here as 'new arms race' models. As noted by Gavrilets *et al.* (2001) they contrast with 'traditional' ideas that emphasize other possible types of benefits that a female could derive from rejecting some types of conspecific males (reviewed by Andersson, 1994). Setting aside the probably small subset of species in which females gain direct benefits (Andersson, 1994), the distinction between the new arms race models and the traditional female choice models involves selection on the female that favours fecundity (new arms races) and selection on the female that favours offspring quality (traditional female choice).

It is important to clarify that the distinction being made here does not imply that male–female conflict *per se* is limited to the new arms race contexts. Any female that exercises classic female choice and does not accede to the attempts of a particular male to fertilize her eggs will be acting against the best interests of that male. The new arms race models thus do not differ from traditional ideas in supposing that male–female conflicts occur (Rosenthal & Servedio, 1999; Getty, 1999; Rice & Holland, 1999; Soulier-Perkins, 2001 on genitalia). In fact, males under traditional sexual selection by female choice are also engaged in 'arms races' with females: males are selected to win in competition with other males by evolving ever more effective ways of stimulating

females to permit them to fertilize their eggs; and females are under selection to filter males ever more effectively in favour of those with the most potent stimulating mechanisms, by denying less well-equipped males access to their eggs. What is different, and potentially important in the new arms race models, is the proposed direct payoff to the female from making such a rejection. New arms race models emphasize the direct benefits just mentioned, and specifically exclude indirect payoffs *via* superior offspring (Alexander *et al.*, 1997; Rice & Holland, 1999; Gavrilets *et al.*, 2001). This distinction leads to differences in both the expected designs of female structures employed in sexual interactions with males (Eberhard, 1997), and in the ecological contexts in which male–female struggles are expected to occur (Alexander *et al.*, 1997). This review exploits these predicted ecological differences to test the new arms race models against traditional ideas.

Data on male genitalia from the immense but hitherto under-utilized taxonomic literature can be used to test the new arms race hypotheses for a wide range of taxonomic groups. In groups in which male genitalic traits have been especially useful in distinguishing closely related species, male genitalia can be characterized as having undergone especially rapid divergent evolution. Both new arms race models and the traditional sexual selection ideas predict frequent rapid divergent evolution of male genitalia. But they differ with respect to both the ecological contexts in which such evolution is expected, and the genitalic functions that are expected to evolve. These differences involve differences in the degree of possible male coercion in initiating male–female interactions, as noted by Alexander *et al.* (1997).

In some animals (for instance, grasshoppers and water striders), females are subject to sexual attacks by males (the 'coercive' male acts of Alexander *et al.*, 1997) while they feed, oviposit, or perform other reproductively important activities. Females of such species may sometimes benefit, under natural selection, from traits that enable them to elude or otherwise defend themselves against copulations resulting from male harassment. At the genitalic level, selection in such species is likely to favour female traits that make it more difficult for male genitalic structures to seize the tip of her abdomen and position his intromittent genitalia for penetration. Under such circumstances, the new arms race models predict that coevolutionary arms races will arise between males and females to control the initiation of copulation. In other species, male–female encounters only occur when the female has actively sought out the male (for instance, by approaching a male that is calling with a song or a pheromone – the 'luring' male acts of Alexander *et al.*, 1997), or by initiating the entire interaction herself (for instance, by emitting her own long-distance attractant pheromone). In many of these species there are no resources associated with the male which would make it otherwise advantageous for the female to approach him. In such species, male–female conflict involving naturally selected costs of copulation is less likely, because females are relatively 'protected' from unwanted male attentions (hereafter, 'protected females'). A protected female would presumably seldom if ever encounter a male except when circumstances

such as depletion or lack of sperm make copulation advantageous for her. Females of such species would be able to more readily avoid unwanted interactions, including both forceful male mating attempts as well as antagonistic seduction (e.g. Holland & Rice, 1998), and thus be less likely to engage in coevolutionary morphological arms races with males to avoid unwanted copulations. Any female resistance to males that might be observed in such a species would be more likely to occur because of the benefit that the female derives indirectly through improved quality in sires, rather than because of direct payoffs from avoiding copulation, such as avoiding predation or disruption of feeding and oviposition, as envisaged in new arms race models.

Luring versus coercion is a continuum (Alexander *et al.*, 1997), however, and these predictions are not always black and white. For instance, a female might sometimes arrive at an aggregation of males and mate with one of them, but then be unable to escape before being accosted and mating additional, unwanted times. Similarly (and more importantly for this review), male genitalia can have multiple functions. Copulation and insemination are often multi-stage processes, and male–female cooperation at one stage could be followed by conflict at a later stage (or *vice versa*). A male cricket, after luring a female with his song, might forcefully hold on to her longer than is convenient for her. It is necessary to analyse different functions separately, because the expectations regarding male–female conflict vary. More specifically, conflicts over holding and positioning the female genitalia so that intromission can occur (a probable function of male genitalic claspers in many species – see Table 1 and below), over prying open or penetrating deeper to reach optimal sperm deposition sites after initial intromission (e.g. Eberhard, 1993*a*; Eberhard & Kariko, 1996; Tallamy *et al.*, in press), or over preventing or inhibiting the female from subsequently discarding the male's sperm, are not expected to occur in groups in which females are protected from male harassment. This is because a protected female will presumably not come into contact with a male except in order to receive sperm. Reduction in new arms race conflict in protected females is also expected for genitalic functions involving removal of sperm or sperm plugs. This is because the payoffs to the female from resisting the male (e.g. resist male attempts to remove sperm deposited by previous males) seem likely to be indirect (screening potential sires), rather than the direct non-selective avoidance payoffs proposed in the new arms race models.

By contrast, new arms race models predict that other possible genitalic functions might nevertheless be subject to conflict in protected females. There could be conflict, for instance, over whether the female oviposits without mating with additional males; over whether the male damages the female's reproductive tract so as to make it less likely that she will remate or that rematings will result in sperm transfer (Wing, 1982; Eberhard, 1993*a*; Crudgington & Siva-Jothy, 2001; Blanckenhorn *et al.*, 2002); over whether the male uses his genitalia to grasp the female for longer than necessary for sperm transfer so as to guard her from other males (Alcock, 1994), and thus interferes with other female activities such as feeding or predator defence; over whether

Table 1. Mechanical functions attributed to male genitalic structures in published studies of Diptera. In the many cases in which multiple functions are probable (for example, pushing past internal structures is facilitated and probably often dependent on a firm external grip), the most immediate function mentioned by the authors is given. Reasons to expect (or not expect) that male-female conflict would occur if the female were protected are given in the Section II. Further hints regarding possible conflict are given by copulation duration, which gives an indication of the likelihood of male-female conflict costs to the female if the male extends the duration longer than is in the best interests of the female (a possible function of clasping male genitalia). Male-female conflict over copulation duration is less probable in shorter copulations. ('sec' indicates <1 min; 'min' indicates <1 hour; 'hr' indicates <1 day). Similarly, contact with soft female structures may be less likely to result in coevolutionary races with males that would select for rapid morphological divergence in male genitalia, because female morphological defences against the male, such as hard processes that fend him off or otherwise impede effective contact, are missing

Function	Family	Species	Type of data[1]	Duration of copulation	Structure	Female structure soft or hard?[2]	Reference
1. Clasp the female							
a. On the outside	Tipulidae	*Dolichopeza* spp.	dir	hr	Outer distyles	Hard	Byers (1961)
			dir	hr	Inner distyles	Hard[3]	Byers (1961)
	Trichoceridae	*Trichocera annulata*	dir	sec	Gonostylus[4]	Hard	Neumann (1958)
	Culicidae	*Aedes aegyptii*	dir	sec	Gonostylus (telomere)	Soft?[5]	Spielman (1964), Jones & Wheeler (1965)
		Anopheles stephensi	dir	?	Gonostylus	Soft	Rao & Russell (1938)
		Culiseta inornata	dir	hr	Gonostylus	Soft	Rees & Onishi (1951)
			dir	hr	Teeth lobes tergite 9	Hard	Rees & Onishi (1951)
			indir	hr	Teeth sternite 10[6]	Hard	Rees & Onishi (1951)
		Deinocerites sp.	?	?	Lobes tergite 9	?	Komp (1956) in Spielman (1964)
	Ceratopogonidae	*Culicoides* spp.	dir	min	Claspers	?	Downes (1955)
		Palpomyia sp.	dir	?	Claspers	Soft[7]	Downes (1978)
		Johannsenomyia annulicornis	dir	?	Claspers	Soft	Downes (1978)
		Clinohelea bimaculata	indir	?	Claspers	Soft?	Downes (1978)
	Psychodidae	*Phlebotomus* spp.	dir?	?	Distylus	Hard	Ortiz & Hernández-Marquez (1963)
	Sciaridae	*Hybosciara gigantea*	dir	min	Gonostylus	Soft	Eberhard (2001 *a*)
	Bibionidae	*Plecia nearctica*	dir	day	Hypogynal valves	?	Leppla *et al.* (1975)
					Lateral claspers	?	Leppla *et al.* (1975)
					Harpogones	?	Leppla *et al.* (1975)
	Asilidae	*Machimus atricapilus*	dir	min	Forceps	Hard?	Reichardt (1929)
		Asilus trifarius	dir	?	Forceps	Hard?	Reichardt (1929)
	Asiloidea	(many)	indir	?	Epandrium	?	Sinclair *et al.* (1994)
	Sphaeroceridae	*Coproica* spp.	dir	min	Comb on sternite 5[8]	Soft	Lachmann (1996, 1997)
	Tephritidae	11 genera, 15 spp.	dir	min/hr	Prensisetae surstyli	Hard	Headrick & Goeden (1994)
		Ceratitis capitata	dir	hr	Prensisetae surstyli	Hard	Eberhard & Pereira (1994)
		Rhagoletis juglandis	dir	?	Prensisetae surstyli	Hard	A. Lachmann, H. Alonso-Pimentel & D. Papaj, (unpublished data)
	Drosophilidae	*Drosophila* spp.	dir	min	Surstyli	Soft	W. G. Eberhard & N. Ramirez (in preparation)
					Genital arch	Hard	W. G. Eberhard & N. Ramirez (in preparation)
	Glossinidae	*Glossina palpalis*	dir	hr	Superior clasper[9]	Soft	Squire (1951)
		Glossina austeni	dir	hr	Superior clasper	Hard	Pollock (1974)

	Family	Species			Structure		Reference
			dir	hr	Sternite 5	Hard	Pollock (1974)
	Muscidae	*Musca domestica*	dir	hr	Lateral process Sternite 5	Soft?	Graham-Smith (1939)
			dir	hr[10]	Arch segment 7 (2nd forceps)	?	Graham-Smith (1939), Degrugillier & Leopold (1973)
			dir	hr	Cerci	Soft	Graham-Smith (1939)
	Scathophagidae	*Scathophaga stercoraria*	dir	min	Sternal forceps	Soft?	Hosken *et al.* (1999)
			dir	min	Claspers	Soft?	Hosken *et al.* (1999)
	Calliphoridae	*Calliphora erythrocephala*	dir	?	Lateral process of Sternite 5	Soft?	Graham-Smith (1939)
			indir	?	Appendage of anal tergum	Soft?	Graham-Smith (1939)
		Lucilia sericata	dir	?	Sternite 5, inferior and superior forceps	Soft	Lewis & Pollock (1975)
b. On the inside	Sepsidae	*Archisepsis* spp.	dir	min	'Spiny Arch'	Soft	Eberhard & Huber (1998)
			dir	min	'Paddle'	Soft	Eberhard & Huber (1998)
2. Interact with internal structures to facilitate sperm deposition							
a. Pry open, straighten, push past female structures (to facilitate deeper penetration)	Tipulidae	*Dolichopeza* spp.	dir	hr	Gonapophyses	Soft	Byers (1961)
	Trichoceridae	*Trichocera annulata*	dir	sec	Paramere	Soft	Neumann (1958)
	Culicidae	*Aedes aegyptii*	dir	sec	Gonocoxa	Soft	Spielman (1964)
			dir	sec	Paraprocts	Hard	Spielman (1964), Jones & Wheeler (1965)
			dir	sec	9th Tergal lobes	Hard?	Jones & Wheeler (1965)
			dir	sec	Teeth aedeagus	Hard	Jones & Wheeler (1965)
	Psychodidae	*Phlebotomus* spp.	dir?	?	Aedeagus	Soft?	Ortiz & Hernández-Marquez (1963), Ilango & Lane (2000)
	Tephritidae	*Ceratitis capitata*	dir	hr	Basal sac glans	Soft	Eberhard & Pereira (1995)
	Glossinidae	*Glossina palpalis*	dir	hr	Inferior clasper	Hard	Squire (1951)
		Glossina austeni	dir	hr	Inferior clasper[11]	Hard	Pollock (1974)
	Sphaeroceridae	*Coproica* spp.	dir	min	Postgonite	Soft	Lachmann (1996, 1997)
			dir	min	Telomere	Hard	Lachmann (1996, 1997)
	Scathophagidae	*Scathophaga stercoraria*	dir	min	Paramere	Soft?	Hosken *et al.* (1999)
					Gonopod	Soft?	Hosken *et al.* (1999)
	Muscidae	*Musca domestica*	dir	hr	Endophallus	Soft	Graham-Smith (1939), Degrugillier & Leopold (1973)
b. Seal (presumably promote sperm transfer)	Culicidae	*Aedes aegyptii*	dir	sec	Lobes aedeagus	Soft	Spielman (1964)
				sec	Anal cone	Soft	Spielman (1964)
				sec	Paraprocts	Hard	Spielman (1964)
	Sphaeroceridae	*Coproica* spp.	dir	min	Phallotreme	Hard	Lachmann (1996, 1997)
	Calliphoridae	*Chrysomya bezziana*	dir	?	Prepuce aedeagus	Soft?	Spradbery & Sands (1976)
	Glossinidae	*Glossina austeni*	dir	hr	Flaps aedeagus	Soft?	Pollock (1974)
c. Engage to anchor	Tipulidae	*Tipula paludosa*	dir	hr	Parts gonostylus	Hard?	Neumann (1958)
	Otitidae	*Tetanops myopaeformis*	dir	?	Aedeagal setae	Soft	Klostermeyer & Anderson (1976)
	Glossinidae	*Glossina palpalis*	indir	hr	Appendices aedeagus	Soft	Squire (1951)
		Glossina austeni	dir	hr	Median apophysis	Soft	Pollock (1974)

Table 1. (*Cont.*)

Function	Family	Species	Type of data[1]	Duration of copulation	Structure	Female structure soft or hard?[2]	Reference
			dir	hr	Aedeagus[12]	Soft	Pollock (1974)
d. Position self for sperm transfer	Tipulidae	*Tipula paludosa*	dir	hr	Adminiculum	Soft[13]	Neumann (1958)
	Psychodidae	*Phlebotomus perfiliewi*	dir	?	Apex aedeagus	?	Hertig (1949) in Downes (1968)
		Phlebotomus spp.	dir?	?	Parameres	?	Ortiz & Hernández-Marquez (1963)
			dir?	?	Lateral lobes	?	Ortiz & Hernández-Marquez (1963)
	Diopsidae	*Cyrtodiopsis whitei*	dir	sec	Plate epiphallus	Hard	Kotrba (1993)
					Process aedeagus	Soft?	Kotrba (1993)
	Sphaeroceridae	*Coproica* spp.	dir	min	Ridges distiphallus	Hard	Lachmann (1996, 1997)
	Sepsidae	*Archisepsis* spp.	dir	min	Distal body aedeagus	Soft	Eberhard & Huber (1998)
	Scathophagidae	*Scathophaga stercoraria*	dir	min	Gonopod setae	?	Hosken *et al.* (1999)
	Calliphoridae	*Lucilia sericata*	dir	?	Spine	Soft	Lewis & Pollock (1975)
			dir	?	Posterior paramere	Soft	Lewis & Pollock (1975)
e. Lever aedeagus deeper	Culicidae	*Aedes aegypti*	dir	sec	Endomere	na	Jones & Wheeler (1965)
			dir	sec	Paraproct	na	Spielman (1964)
	many nematocerans		dir/indir		Parameres	na	Wood (1991)
f. Pull female duct outside body	Sphaeroceridae	*Coproica* spp.	dir	min	Phallotreme	Hard	Lachmann (1996, 1997)
g. Spermatophore formation[14]	Ceratopogonidae	*Culicoides melleus*	dir	min	Telomeres	Soft	Linley & Adams (1972)
h. Push sperm into female	Tephritidae	*Dacus oleare*	dir	hr	Genital rod	Soft	Solinas & Nuzzaci (1984)
		Rhagoletis juglandis	dir	min	Genital rod	Soft	A. Lachmann, H. alonso-Pimentel & D. Papaj (unpublished data)
i. Introduce sperm deeper[15]	Tipulidae	*Tipula* spp.	indir/dir		Protrusable aedeagus	?	Rees & Ferris (1939) in Downes (1968), Neumann (1958)
	Psychodidae	*Phlebotomus* spp.	dir	?	Aedeagal ducts	?	Sinton (1925) and Hertig (1949) in Downes (1958), Ortiz & Hernández-Marquez (1963)
	Anisopodidae	*Anisopus fuscipennis*	indir	?	Aedeagal filament	?	Edwards (1930) and Abul Nasr (1950) in Downes (1968)
	Dixiidae	(not specified)	indir	?	Aedeagal filament	?	Edwards (1930) in Downes (1968)
k. Sensory	Culicidae	*Culex pipiens*	dir	?	Setae clasper	Hard	Spielman (1966)
	Glossinidae	*Glossina austeni*	dir	hr	Edita	?	Pollock (1974)
3. Damage female (internal or external)	Glossinidae	*Glossina tabaniformis*	indir	hr	Harpes[16]	Hard	Jordan (1963)
		Glossina fusca	indir	?	Harpes	Hard	Machado (1959, 1964) in Pollock (1974)
	Calliphoridae	*Lucilia cuprina*	dir	?	Aedeagus	Soft	Merritt (1989)
		Lucilia sericata[17]	dir	?	Paraphallus tips	Soft	Lewis & Pollock (1975)
		Calliphora erythrocephala	indir	?	Paraphallus[18]	Soft	Graham-Smith (1939)
4. Pump sperm out tip of aedeagus	Tanyderidae	(not specified)	indir	?	Vesica	na	Downes (1968)
	'many'		indir	?	Sperm pump	na	Sinclair *et al.* (1994)

5. Remove sperm of previous males[15]	Scathophagidae	*Scathophaga stercoraria*	dir	min	Scoop on aedeagus[19]	Soft	Hosken *et al.* (1999)
6. Remove sperm plug or spermatophore of previous male	Diopsidae	*Cyrtodiopsis whitei*	indir	sec	Body epiphallus	na	Kotrba (1993)
7. Deposit plug in female	No examples known in Diptera						
8. Mould for part of spermatophore	Sepsidae	*Archisepsis* spp.	indir	min	Distal body aedeagus	na	Eberhard & Huber (1998)
	Diopsidae	*Cyrtodiopsis whitei*	indir	sec	Aedeagus	na	Kotrba (1993)
9. Stimulate female[20]	Tipulidae	*Tipula paludosa*	dir	hr	Two Tufts of setae	Hard	Neumann (1958)
	Sciaridae	*Hybosciara gigantea*	dir	min	Gonostylus	Soft	Eberhard (2001*a*)
	Sepsidae	*Archisepsis, Microsepsis*	dir	min	Surstyli	Soft	Eberhard (2001*b*)
	Sphaeroceridae	*Coproica* spp.	dir	min	Comb sternite 5[10]	Soft	Lachmann (1996, 1997)

1. 'dir' = direct observations by author and statement of possible function; 'indir' = author directly mentioned possible function, but used deductions from shape and size rather than observations of copulating pairs.

2. The structure of the female which the male structure contacts is soft (membrane) or hard (sclerite).

3. Contrary to expectations of new arms race ideas, female 'hypovalves are pocketed on their inner surfaces to receive the tips of the inner distyles of the male, in order to effect a firm attachment in copulation' (Byers, 1961, p. 692).

4. First used to grasp the female, and then to hold her as he pushed the rest of his genitalia against her.

5. The telomere of the clasper seizes female cercus (hard), but its distal claw inserts in the soft membranous region at the base of the cercus (Jones & Wheeler, 1965).

6. The male genital parts work against each other and probably squeeze female sternum 8.

7. Tip of gonostylus presses intersegmental membrane, but slightly more basally the gonostylus presses against the female tergite.

8. Sustained series of rhythmic squeezing movements of the male indicate both clasping and stimulation functions for spine comb on male sternite, which presses on the intersegmental membrane between female tergites 7 and 8.

9. Male superior clasper digs into and damages cushions of tissue on female segment 6. The soft area in the sternite is not indicative of a female resistance structure; on the contrary, the rhythmic squeezing movements during apparent copulatory courtship with the male's middle and hind legs, and the increased squeezing when the female becomes restless, suggest a courtship function. No damage occurs in *G. fusca, G. longipalpis.*

10. Grasp occurs in pouch inside male body, but on the outside surface of the ovipositor.

11. May help align female with male (function 2d).

12. Aedeagus frequently buckles due to force with which it grasps and pulls on the female genital papilla and thus straightens the spermathecal ducts; this may facilitate entry of sperm.

13. Is close to but does not engage the mouth of the female duct.

14. Each telomere is repeatedly withdrawn and then thrust deeply into the intersegmental membrane of the female. They move in strict alternation and each is extended about once every 4 s, usually for 1 s min or more. The authors supposed that the movements 'are connected with' spermatophore, apparently because the spermatophore is formed during this same period. The movements seem more appropriate, however, for stimulating the female than for spermatophore formation.

15. Some of the tubular structures proposed to function in deeper penetration for sperm deposition could function instead to remove sperm by sucking them from the female; removal seems less likely, however, because there are no structures described associated with the tip of the male structure and the associated sperm pumps that could possibly separate sperm to be removed from sperm to be deposited.

16. A tough shield protects the anterior end of the uterus and the entrance of the common oviduct; this is an apparent female defensive structure.

17. The damage, documented by scars in the female reproductive tract, presumably functions to facilitate entrance of male seminal products into female haemocoel; but Lewis & Pollock (1975) argue, because of the absence of muscles associated with the paraphalli, that the female actively participates in producing this 'damage' by contracting circular muscles of her bursa so that it becomes abraded.

18. The female sacs into which barbed extremities of paraphallus fit have very thick walls, so penetration not certain.

19. Description mentions male removing (inefficiently) his own sperm from the bursa; but if sperm from previous males are ejected from the spermatheca by the female, they would also be removed. The authors concluded that '… it is likely that sperm removal is incidental rather than adaptive'.

20. Stimulatory function deduced from rhythmic movements with no mechanical effect other than squeeze or brush against female. For other possible cases, see footnotes 11, 10 and 18.

he is able to plug her genital opening (Boorman & Parker, 1976) and deny her possible naturally selected benefits (e.g. nutrition) from further matings; or over whether he opens holes in her reproductive tract or otherwise facilitates introduction of seminal products into her body cavity, where they can act to induce her to make either larger or more precipitous investment in offspring (Chen, 1984; Eberhard, 1996; Sheldon, 2000), or to suffer reduced survivorship (Chapman *et al.*, 1995; Wolfner, 1997).

On balance, the predicted association of conflict with coercive pre-copulatory interactions made by Alexander *et al.* (1997) is less categorical than they suggested; species in which females are protected from male harassment to initiate copulation will not necessarily lack all types of male–female conflict over genitalic functions. By the same token, my previous discussions of this topic (Eberhard, 1997, 1998*a*) were over-simplified, because I also treated the prediction too categorically. There are various possible functions of male genitalia; some of these functions but not others could result in new arms races even when the female is not coerced by the male in pre-copulatory behavioural interactions.

This means that in order to make the kind of comparison advocated by Alexander *et al.* (1997), it is first necessary to check the relative importance of different types of genitalic functions in general. New arms race ideas predict that the frequency and intensity of conflict over certain genitalic functions (in particular, functions associated with initiation and facilitation of intromission and insemination) should be perceptibly reduced when females are protected from harassment. If such potentially non-conflicting functions are common for genitalia in general, then it is reasonable to expect, if new arms race models are correct, that species with protected females will show reduced tendencies toward rapid divergence in male genitalia. If, on the other hand, such potentially non-conflicting genitalic functions are rare, then the new arms race ideas predict that female protection or lack of protection would have only a minor effect on genitalic evolution.

The first part of this review considers the different possible functions of male genitalia documented in previous studies of male and female genitalic function in a sample of species in the order Diptera. The results confirm that potentially non-conflicting functions are indeed common in Diptera. If one assumes that Diptera is representative of other insects and spiders with respect to the different functions performed by male genitalia, this finding justifies making the 'new arms race' prediction that rapid and divergent genitalic evolution will be more common in these groups when females are unprotected than when they are protected. Traditional female choice hypotheses, by contrast, do not predict a difference in genitalic evolution between species in which females are and are not protected from male harassment. Under female choice, other factors, such as whether and how often females remate (Eberhard, 1985*a*; Arnqvist, 1998) and whether morphologically uniform male genitalia are nevertheless moved in species-specific ways during copulation (Eberhard, 1985*a*, 1998*b*, 2001*a*, *b*) are expected to influence the evolutionary diversification of male genitalia.

The second part of this review then tests this prediction in 343 genera of insects in which behavioural observations have established that females are or are not protected from male harassment. A similar test of new arms race predictions is made in 18 genera of spiders using morphology to infer behaviour. Some spiders have exaggerated sexual size dimorphism (dwarf males and giant females). Tiny males are especially unlikely to be able to coerce giant female spiders, with their genitalia or otherwise, because the female can simply convert harassing suitors into food (see Elgar, 1991; Elgar, Schneider & Herberstein, 2000, and Bukowski, Linn & Christenson, 2001 for cases of such cannibalism, which include such radical female solutions to possible conflict as interrupting copulation to pull the male free and eat him). New arms races are thus less likely in species with especially small males, so species-specific genitalic differences are predicted to be reduced. Again, traditional female choice makes a contrasting prediction: because the intensity of classic female choice is not expected to correlate with differences in the male's physical ability to coerce the female, no correlation is predicted between relative male size and the degree of genitalic divergence.

New arms race models have seldom been tested with respect to genitalic evolution. Huber (1998) argued against new arms race ideas on the basis of a summary of behavioural data from 151 species of spiders. He found that males typically lure rather than coerce females to mate, and that females typically cooperate actively with the male to bring about copulation. He also noted that spider genitalia are generally especially important characters for distinguishing species, and concluded that the male–female conflict hypothesis was thus not supported. Soulier-Perkins (2001) found apparently higher degrees of homoplasy in female genitalic traits than in male genitalic traits, and argued that this supported the idea of sexual conflict rather than classic female choice. The logic of the prediction is not clear, and in any case the difference in homoplasy was not significant ($\chi^2 = 1.3$, d.f. $= 1$, $P = 0.27$). The author's citations indicate that she included classic Fisherian sexual selection by female choice as conflict.

II. METHODS

Data on genitalic functions in Diptera were taken from papers on genitalic mechanics in 43 species in 21 families. Functions were classified as potentially conflicting or not potentially conflicting in species in which females are protected from male harassment as follows.

Facilitation of sperm transfer: this function was taken not to be potentially conflictive, because protected females will have sought out the male in order to receive sperm. While it is true that sperm transfer may often result in dilution or displacement of the sperm of previous males (see footnote 15 in Table 1), this male–male conflict is unlikely to generate male–female conflicts of the types envisioned in the new arms race models. It could bias paternity; but it is unlikely to reduce female production of offspring, which is the cost proposed in the new arms race models (unless females are

sperm-limited and the loss of sperm from previous males results in a reduction in the number of offspring she can produce).

Clasping and anchoring: these functions, which occur both on the outside and within the female, could be both potentially conflictive and potentially non-conflictive. They would not be expected to be conflictive when they serve to facilitate intromission. Potential conflict could occur, however, if clasping or anchoring served to hold the female for longer than necessary for insemination, and if being held this way interfered with other female activities severely enough that female losses in offspring (the costs postulated by the new arms race models) were greater than the indirect benefits that she received from having sons capable of holding females this way (Cordero & Eberhard, 2003).

Damaging the female: this function was taken to be potentially conflictive, although if the female gained more in indirect benefits from having sons capable of producing such damage than she lost from the consequences of the damage, it could be potentially non-conflictive (Cordero & Eberhard, 2003).

Removal of sperm from previous males: this function is unlikely to be potentially conflictive, because in most cases the expected loss to the female from sperm removal would not be a reduction in her ability to produce offspring, but rather a change in paternity. An exception would occur in the seemingly unlikely case that the female lost nutritional benefits from the ejaculatory products of the previous male, or if females were sperm-limited and the loss of stored sperm resulted in reduced reproduction.

Stimulation: this was not expected to be potentially conflictive because stimulation *per se* is unlikely to inflict costs to the female in reduced ability to produce offspring.

Pull part of female reproductive tract inside-out: this would seem potentially damaging to the female, and was thus considered to be potentially conflictive. However, the females of species in which this occurs apparently cooperate actively (Lachmann, 1996, 1997), as the male's phallotreme is not long enough to reach the vaginal plate which it grasps to pull, so the female presumably must move the plate posteriorly to enable him to grasp it.

Further indications regarding possible conflict were available from copulation duration and from female structures. Male–female conflict over copulation duration (and thus male clasping functions) is expected to be less probable in shorter copulations. Soft female genitalic structures that are contacted by the male are less likely to be able to fend off the male genitalia, and are thus unlikely to be involved in coevolutionary races with males that would select for rapid morphological divergence in male genitalia. By contrast, hard processes that could fend him off or otherwise impede effective contact, would be more likely to present effective resistance and to select for male morphology able to overcome this resistance.

Data on genitalic evolution were collected from published taxonomic descriptions and accounts of mating behaviour. I used several strategies to attempt to reconcile the ideal of a large and taxonomically varied sample that was not biased in favour of groups with particular combinations of traits, and the practical impossibility of checking more than a small fraction of the available literature. Several possible sampling pitfalls and their effects on the results are enumerated in Section IV. 2. Since data on mating behaviour are much more scarce than data on genitalia, the first step was to make a list of groups for which data on mating behaviour were available. Fortunately, extensive recent reviews of mating behaviour are available (Thornhill & Alcock, 1983; Tyler, Brown & Wilson, 1994; Choe & Crespi, 1997; Aluja & Norrbom, 2000). I also consulted several general works (Jacobson, 1972; Edmunds, Jensen & Berner, 1976), and John Sivinski kindly loaned me his reprint collection on swarming insects, which was especially extensive for Diptera. I subsequently expanded the list to include additional species whose behaviour I have studied or with which I was otherwise familiar, and a few additional genera encountered as I searched the taxonomic literature (these additions are marked with '$' in Tables 2–4). The overall objective was not to obtain a complete list of species of insects, but rather to assemble an extensive sample including different mating behaviour in a variety of taxonomic groups.

Insect females were classified as protected from harassment if sexual encounters between males and females occur in the following contexts: at leks; in swarms that are not near resources needed by females; at male territories that are not near resources needed by females; after females approach males that use long-range attractant signals (e.g. songs) and males are not near resources needed by females; and after females attract males with long-range signals (e.g. pheromones) of their own. Females were classified as unprotected from male harassment in species in which males occur near female feeding or oviposition sites and attempt to mate with females there, and in which males are associated with sites where adult females emerge from immature stages and mate with them there. In the spiders, females of species with dwarf males or giant females (Hormiga, Scharff & Coddington, 2000) were considered protected, while species with less extreme dimorphism were considered unprotected.

I then attempted to track down information on genitalia from taxonomic descriptions in the genera on the list. Once again it was not possible to be exhaustive, and greater ease of access to taxonomic literature led to more thorough reviews of certain groups. I used electronic searches in the Zoological Record for access to literature on many groups. I attempted to use descriptions of the genitalia of the same species whose behaviour had been observed. This was not always possible, however, because of some missing species names in the original lists, the vagaries of electronic searches and journal subscriptions, early publication dates or obscure journals, the lack of recent taxonomic work on some groups, and time constraints. I read more extensively in Diptera, in which good coverage of the taxonomic literature was facilitated by the large review works of Lindner (1925–1980), Carpenter & LaCasse (1955), and McAlpine *et al.* (1981, 1987). Access to reprints and expert advice on the taxonomy of parasitoid wasps facilitated data collection in this group. I concentrated on New World mayflies because of the books by Edmunds *et al.* (1976) and Berner & Pescador (1988), but on Old World caddisflies because of the book by Malicky (1983). I followed up leads to additional genera in three groups because they promised to give especially

Table 2. Genitalic traits in genera in which females are relatively protected from sexual harassment by males. 'Swarm' refers to groups of flying males concentrated in space, usually at apparently arbitrary markers (above tree tops, over light-coloured objects, etc.); 'lek' refers to groups of sexually active, territorial males at sites lacking resources needed by females; 'lure' refers to species in which sexually active males are not grouped, are not associated with resources needed by females, and which either emit signals that attract males ('chem.' = chemical male signals; 'vis.' = visual male signals; 'song' = auditory male signals) or are at arbitrary sites (such as hilltops). The lines of division betwen swarm, lek, and site were not always clear, but in any case females are protected from male harassment in all three. For those species in which no information on the mating behaviour was included other than that given in a review, reference is made only to the review, rather than the original descriptions of behaviour. Numbers in parentheses are numbers of species for which mating system was observed; ' + ' is used when 'spp.' were mentioned in publications without mentioning specific numbers. 'W.G.E.' refers to own unpublished observations; 'sev.' = several; 'N' = no; 'N?' = probably no, because genitalia were not mentioned or because of other reasons (see associated footnotes); 'med.' = medium. Genera included because I happened to be familiar with their mating behaviour or because of directed reading after the original list was complete are marked with '$', and families without genera with unprotected females (Table 4) are indicated with '*'. When more than one genitalic structure was characterized, they are separated by '/' (e.g. small/medium clear)

	Male site	Male genitalia differ among congeners?	Degree of complexity	References mating	Genitalia
Diptera					
Nematocera					
*Anisopodidae					
Anisopoda (2)	Swarm	Clear	Med. simple	Edwards (1928)	Lindner (1930 b)
*Blephariceridae					
Philorus[1] (1)	Swarm[2]	Clear	Very complex	Hogue (1973)	Lindner (1930 a), Hogue (1973)
*Cecidomyiidae					
Anarete (2)	Swarm[3, 4]	Clear	Med. simple	Chiang (1961), Chiang & Okubo (1977), Chiang *et al.* (1978)	Kim (1968)
Ceratopogonidae					
Ceratopogoninae					
Ceratopogonini					
Ceratopogon[5] (several)	Swarm	Med. clear	Simple	Downes (1955)	Goetghebuer & Lenz (1934)
Culicoidini					
Culicoides[5] (24)	Swarm[3, 6]	Med. clear	Simple	Downes (1955), Linley & Adams (1972), Glukhova & Dubrovskaya (1974), Campbell & Kettle (1979), Zimmerman *et al.* (1982) in Blackwell *et al.* (1992), Neems *et al.* (1992), Blackwell *et al.* (1992)	Blanton & Wirth (1979)
Palpomyiini					
Bezzia[5] (1)	Swarm	Clear	Simple	Downes (1955)	Goetghebuer & Lenz (1934)
Palpomyia[6] (sev.)	Swarm	N? no mention	?	Downes (1955, 1978)	Goetghebuer & Lenz (1934)
Sphaeromiini					
Probezzia (1)	Swarm	N[7]	?	Downes (1955)	Wirth (1994)
Stilobezzini					

Serromyia (1)	Swarm	Med. clear	Med. simple	Downes (1955)	Borkent & Bissett (1990)
Stilobezzia (1)	Swarm	Med. clear	Simple	Downes (1955)	Goetghebuer & Lenz (1934)
Forcipomyinae					
Atrichopogon[5] (1)	Swarm[6]	Clear	Med. simple	Downes (1955)	Goetghebuer & Lenz (1934), Boesel (1973)
Forcipomyia[5] (2)	Swarm	Small, clear	Simple	Downes (1955), Kaufmann (1974)	Utmar & Wirth (1976), Wirth & Spinelli (1993)
Leptoconopinae					
Leptoconops (2)	Swarm	Clear[8]	?(not drawn)	Smith & Lowe (1948), Downes (1955)	Smith & Lowe (1948)
*Chaoboridae					
Chaoborus (2)	Swarm[9]	Med. clear	Med. simple	McGowan (1975)	Martini (1929–1931), Borkent (1979)
Chironomidae[10]					
Ablabesmyia (1)	Swarm	Clear	Med. complex	Knab (1907)	Goetghebuer & Lenz 1936, Pinder (1978), Murray & Fittkau (1989)
Allochironomus (1)	Swarm	Clear	Med. complex	Syrjämäki (1964)	Goetghebuer & Lenz (1936)
Chironomus[5] (6)	Swarm[3]	Small, clear	Med. simple	Gibson (1945), Hilsenhoff (1966), Syrjämäki (1966), Koskinen (1969), Downe & Caspary (1973)	Pinder (1978), Cranston *et al.* (1989*a*)
Cladotanytarsus (sev.)	Swarm	Clear	Med. complex	Lindeberg (1964) in Downes (1969)	Pinder (1978), Cranston *et al.* (1989*b*)
Cricotopus (1)	Swarm	Clear	Rel. simple	Syrjämäki (1963) in Koskinen (1969)	Goetghebuer & Lenz (1936), Pinder (1978)
Diamesa (1)	Swarm[3]	Very clear	Med. complex	Young (1969)	Goetghebuer & Lenz (1936), Pinder (1978)
Limnophyes (1)	Swarm[3]	Clear	Med. simple	Syrjämäki (1968)	Goetghebuer & Lenz (1936), Pinder (1978)
Metriocnemus (2)	Swarm	Clear	Med. simple	Gibson (1945)	Goetghebuer & Lenz (1936), Pinder (1978), Saether (1989)
Propsilocerus[11]	Swarm	Clear	Med. complex	Kon *et al.* (1986)	Saether & Wang (1996)
Smittia (1)	Swarm[12]	Clear	Med. simple	Syrjämäki (1968)	Goetghebuer & Lenz (1936), Pinder (1978)
Spaniotoma[13] (2)	Swarm[3, 14]	Clear	Med. simple	Gibson (1945)	Goetghebuer & Lenz (1936)
Stictochironomus (1)	Swarm	Small	Simple-med. complex	Syrjämäki (1965)	Pinder (1978), Cranston *et al.* (1989*a*)
Tanytarsus (sev.)	Swarm[6]	Med. clear[15]	Med. complex	Gibson (1945), Paasivirta (1972), Lindeberg (1964) in Downes (1969)	Goetghebuer & Lenz (1936), Pinder (1978), Cranston *et al.* (1989*b*), Lindeberg (1967)
Culicidae					
Aedes[5] (26)	Swarm[14–18]	Med. small	Med. simple	Roth (1948), Nielsen & Greve (1950), Frohne & Frohne (1952, 1954), Nielsen & Nielsen (1953),	Carpenter & LaCasse (1955)

Table 2. (*Cont.*)

132

	Male site	Male genitalia differ among congeners?	Degree of complexity	References mating	Genitalia
				Nielsen & Nielsen (1958), Downes (1958, 1969, 1970), Nielsen & Haeger (1959), Corbet (1961), Kliewer *et al.* (1967), McAlpine *et al.* (1968), Reisen *et al.* (1977)	
Anopheles[5] (24)	Swarm[16, 17]	Small[19]	Med. simple	Knab (1907), Rao & Russell (1938), Cambournac & Hill (1940), Russell & Rao (1942), Roth (1948), Belkin *et al.* (1951), Wharton (1953), Nielsen & Haeger (1959), Nielsen & Nielsen (1958), Haddow & Corbet (1960, 1961), Quraishi (1965) Reisen *et al.* (1977, 1981), Reisen & Aslamkhan (1979), Charlwood & Jones (1980), Yuval *et al.* (1993)	Martini (1929–1931), Carpenter & LaCasse (1955)
Culex[5] (10)	Swarm[20, 21]	Clear	Med. simple	Reisen *et al.* (1977), Knab (1906), Shannon (1931), Roth (1948), Wharton (1953), Frohne & Frohne (1954), Nielsen & Nielsen (1958), Downes (1958), Reisen *et al.* (1977)	Mattingly (1951), Carpenter & LaCasse (1955)
Culiseta[5] (1)	Swarm	Med. clear	Med.	Haddow & Corbet (1961), Nielsen & Haeger (1959)	Carpenter & LaCasse (1955)
Mansonia (7 +)	Swarm[22]	Clear	Med.	Shannon (1931), Nielsen & Haeger (1959), Haddow & Corbet (1961), Corbet & Haddow (1962), Thompson (1967)	Carpenter & LaCasse (1955)
Psorophora[5] (3)	Swarm	Very clear	Med.	Downes (1969), Nielsen & Haeger (1959)	Carpenter & LaCasse (1955)
Uranotaenia (3)	Swarm	Clear	Med.	Corbet & Haddow (1962), Haddow & Corbet (1961)	Ramos (1993)
*Dixiidae					
Dixa (1)	Swarm	Very clear	Med. simple	Downes (1970)	Martini (1929–1931), Johannsen (1923)
*Limoniidae					
Erioptera (2)	Swarm[23]	Clear?[24]	Very complex	Savolainen & Syrjämäki (1971), Shelly & Whittier (1997)	Alexander (1978)

*Sciaridae					
$*Hybosciara* (1)	Swarm[25]	Clear?[24, 26]	Med.	Eberhard & Flores (2002)	Eberhard (2001 b)
Simulidae					
Prosimulium (1)	Swarm[27]	Small	Med. simple	Davies & Peterson (1956)	Rubtsov (1989)
Simulium (8)	Swarm[3]	Small-med.	Med. simple	Frohne & Frohne (1954), Downes (1958, 1969), Service (1970), Hunter (1979 a)	Rubtsov (1989)
*Tipulidae					
Tipula[28] (1)	Swarm	Very clear	Complex	Perry (1979)	Mannheims & Theowald (1951–1980)
*Trichoceridae					
Trichocera (4)	Swarm[3, 29]	Clear	Med.	Dahl (1965), Downes (1969), Savolainen & Syrjämäki (1972)	Lindner (1930)
Brachycera					
Bombyliidae					
Ceratolaemus (1)	Lure-site	N?[30]	Med. complex	Thornhill & Alcock (1983)	Hesse (1938)
Lordotus (1)	Lek	N? no mention	?	Shelly & Whittier (1997)	Hall (1954)
Empididae					
Empidinae					
Bicellaria (1)	Swarm	Med. clear	Med. complex	Chvála (1980)	Engel & Frey (1956)
Empis[5]	Swarm[3, 31]	Very clear	Complex	Kessel (1959)	Engel & Frey (1956), Downes (1970), Chvála (1980)
Empimorpha[31]	Swarm[31]	Clear	Complex	Kessel (1959)	Collin (1961)
Hilara[5] (6+)	Swarm[3, 31]	Very clear	Med. complex	Poulton (1913), Kessel (1959), Downes (1970), Forrest (1985)	Engel & Frey (1956)
Ocydromiinae					
Anthalia (1)	Swarm	N?[32]	?	Chvála (1980)	Engel & Frey (1956), Chvála (1984)
Euthyneura (1)	Swarm[3]	N?[33]	?	Chvála (1980)	Engel & Frey (1956), Collin (1961)
Leptopeza (1)	Swarm	Clear?[34]	?	Chvála (1980)	Collin (1961)
Oedalea (3)	Swarm	Clear	Med. complex	Chvála (1980)	Chvála (1981)
Trichina (1)	Swarm	Very clear	Med. complex	Chvála (1980)	Collin (1961)
Microphorinae					
Microphorus (3)	Swarm	Very clear	Med. complex	Chvála (1980)	Engel & Frey (1956)
Atelestinae					
Atelestus (2)	Swarm	Clear	Med. complex	Chvála (1980)	Engel & Frey (1956), Collin (1961)
Meghyperus (1)	Swarm	N? no mention	?	Chvála (1980)	Engel & Frey (1956)
Clinocerinae					
Clinocera (2+)	Swarm	Very clear	Complex	Chvála (1980)	Engel & Frey (1956)
Oreogetoninae					
Anthepiscopus (1)	Swarm	Clear	Med. complex	Chvála (1980)	Engel & Frey (1956)
Gloma (1)	Swarm	Very clear	Complex	Chvála (1980)	Engel & Frey (1956), Collin (1961)
Hormopeza	Swarm	Clear	Med. complex	Chvála (1980)	Engel & Frey (1956), Sinclair (1995)
Iteaphila (1)	Swarm	Clear	Med. complex	Chvála (1980)	Engel & Frey (1956)

Table 2. (*Cont.*)

	Male site	Male genitalia differ among congeners?	Degree of complexity	References mating	Genitalia
Oreogeton (1)	Swarm	Clear?[24]	Very complex	Chvála (1980)	Engel & Frey (1956)
*Mydidae					
Mydas (2)	Lure-site	Clear	Med. complex	Shelly & Whittier (1997)	Welch & Kondratieff (1990)
*Rhagionidae					
Atherix (1)	Swarm	N? no mention	?	Downes (1969)	Lindner (1925)
Rhagio (1)	Swarm	N[35]	?	Downes (1969)	Lindner (1925), James (1964), Chillcott (1965)
Symphoromyia (4+)	Site[3]	Med. clear	Simple	Shermanchuk & Weintraub (1961), Hoy & Anderson (1978)	Turner (1974)
Stratiomyidae					
Hermetia (1)	Lek	Clear?[24]	Med. complex	Shelly &Whittier (1997)	Lindner (1938), James (1935), Rozkošnỳ (1983)
*Syrphidae					
Eristalis (2)	Site	Clear	Med. to comp	Corbet & Haddow (1962), W.G.E.	Thompson (1997)
$*Ocyptamus* (1)	Site	Clear	Med. complex	O. Ureña (personal communication)	Thompson (1981)
Ornidia[36] (2)	Site[37]	Clear	Med. simple	Corbet & Haddow (1962), W.G.E.	Thompson (1991)
Syrphus (1)	Lek	Clear?[24]	Very complex	Shelly & Whittier (1997)	Thompson (1981), Vockeroth (1983), He & Chu (1996)
*Tabanidae					
Chrysops (2)	Site	N[38]	?	Corbet & Haddow (1962), Shelly & Whittier (1997)	Kröber (1925), Chvála *et al.* (1972), Middlekauff & Lane (1980)
Tabanus (9)	Site/swarm[39, 40]	N[38]	?	Haseman (1943), Corbet & Haddow (1962), Downes (1969)	Kröber (1925), Chvála *et al.* (1972), Middlekauff & Lane (1980)
Acalypteratae					
*Chamaemyiidae					
Leucopis (1)	Swarm	Clear	Simple	McAlpine & Munroe (1968)	Raspi (1983, 1984, 1985), McAlpine (1971, 1972), McAlpine & Tanasijtschuk (1972)
Drosophilidae					
Drosophila[5] (24)	Lek-site	Clear	Complex	Thornhill & Alcock (1983), Shelly & Whittier (1997)	Duda (1935), Choyne (1993)
*Lonchaeidae					
Dasiops (2)	Swarm	Clear	Med. simple	McAlpine & Munroe (1968)	McAlpine (1961), Norrbom & McAlpine (1996)
Lonchaea (13)	Swarm[3]	Clear	Med. complex	McAlpine & Munroe (1968)	McAlpine & Munroe (1968)
Silba (1)	Swarm	Clear[41]	?[41]	McAlpine & Munroe (1968)	McAlpine (1964)
*Micropezidae					
$*Ptilosphen* (1)	Lek-chem.?[42]	Small[43]	Med. simple[43]	P. Ortiz 2002	Hennig (1934)
$*Taeniaptera*[44] (2)	Lek-chem.?[45]	Med. clear/med. clear[45]	Med. simple/med. simple[45]	W. G. Eberhard in preparation	Hennig (1934), Steyskal (1986), Paes de Albuquerque (1980)

Milichiidae					
Milichiella (1)	Swarm	?[46]	Med. complex	McAlpine & Munroe (1968)	Hennig (1937*a*), Brake (2000)
Otitidae					
Physiphora (1)	Lek[3, 47]	Clear?[48]	Complex[48]	Shelly & Whittier (1997)	Hennig (1940), Hardy & Delfinado (1980)
Platypezidae					
Calotarsa (2)	Swarm	Med. clear	Med.	Kessel & Kessel (1961), Kessel (1963)	Kessel & Maggioncalda (1968)
Platypezina (1)	Swarm[3]	Clear?[24]	Med. complex	Kessel & Kessel (1961)	Kessel & Maggioncalda (1968)
Tephritidae					
Anastrepha[5] (12)	Lek, site-chem.[3, 5]	Small[49]	Simple[49]	Aluja *et al.* (2000), Norrbom *et al.* (2000)	Steyskal (1977), Norrbom (1997)
Blepharoneura (many)	Lek[50]	Small/clear[51]	Med. simple/med. complex[51]	Condon & Norrbom (1994, 2000)	Condon & Norrbom (1994), Condon & Steck (1997)
Ceratitis (1)	Lek-chem.[3, 52]	?/Clear[51]	Simple/complex[51]	Eberhard (2000*a*)	M.deMeyer (personal communication), W.G.E.
Myiolia[53] (1)	Lek	Very small/med. clear	Simple/med. complex	Han & Wang (1997)	Han & Wang (1997)
Procecidochares (1)	Lek	N? no mention	?	Shelly & Whittier (1997)	Aldrich (1929)
Trypeta[5] (1)	Lek	N[54]	?	Han (2000)	Foote (1960)
Cyclorrhapha					
Calliphoridae					
Chrysomyia (2)	Site	Med. clear	Med. complex	Corbet & Haddow (1962)	Zumpt (1956)
Cutebridae					
Cutebra (6)	Site[3, 55]	N?[56]	Complex	Thornhill & Alcock (1983), Shelly & Whittier (1997)	Bau (1930), Bennett (1955), Sabrosky (1986)
Gasterophilus (1)	Site, lek	Med. clear	Med. complex	Thornhill & Alcock (1983), Shelly & Whittier (1997)	Grunin (1969)
Muscidae					
Fannia (3+)	Swarm[57]	Med. clear	Med.	Chillcott (1960), McAlpine & Haddow (1968), Hunter (1979*b*)	Chillcott (1960*b*), Hennig (1964)
Hydrotaea (9)	Swarm	N?[58]	Med. simple	Huckett (1954)	Sabrosky (1949), Huckett (1954), Hennig (1964)
Ophyra (1)	Swarm	N?[58]	Med. simple	Shelly & Whittier (1997)	Hennig (1964)
Oestridae					
Cephenemyia (2)	Lek-site	Med. clear	Med.	Shelly & Whittier (1997), Thornhill & Alcock (1983)	Bennett & Sabroski (1962), Grunin (1966)
Hypoderma (1)	Lek	Med. clear	Med.	Shelly & Whittier (1997)	Grunin (1965)
Ephemeroptera[59]					
Baetidae					
Baetis (4)	Swarm	Very small[60]	Very simple	Cooke (1942), Brodskiy (1973), Edmunds *et al.* (1976), Savolainen (1978)	Edmunds *et al.* (1976), Berner & Pescador (1988)
Callibaetis (1)	Swarm	N[61]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Centroptilum (2)	Swarm	N?[62]	Very simple	Brodskiy (1973), Edmunds *et al.* (1976)	Edmunds *et al.* (1976)

Table 2. (*Cont.*)

	Male site	Male genitalia differ among congeners?	Degree of complexity	References mating	Genitalia
Dactylopaetis (1)	Swarm	Very small	Simple	Edmunds *et al.* (1976)	Traver & Edmunds (1968)
Pseudocloeon (1)	Swarm	N?[62]	Very simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
*Baetiscidae					
Baetisca (1)	Swarm	Very small	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976), Berner & Pescador (1988)
*Caenidae					
Brachycercus	Swarm	N?[62]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Caenis (4)	Swarm,	Very small[60]	Simple	Grandi (1973), Brodskiy (1973), Savolainen (1978)	Burks (1953), Edmunds *et al.* (1976)
*Ephemerellidae					
Ephemerella (3)	Swarm	Clear	Med. simple	Brodskiy (1973), Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
*Ephemeridae					
Ephemera (3)	Swarm	Small	Simple	Brodskiy (1973), Savolainen (1978)	Burks (1953), Edmunds *et al.* (1976)
Hexagenia (7)	Swarm	Med. clear	Med. simple	Lyman (1944), Allan & Flecker (1989)	McDunnough (1927), Edmunds *et al.* (1976)
*Heptageniidae					
Cinygma (1)	Swarm	Clear?[63]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Cinygmula (1)	Swarm	Clear?[63]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Heptagenia (5)	Swarm	N?[62]	Med. simple	Savolainen (1978)	Edmunds *et al.* (1976)
Rithrogena (3)	Swarm	Clear?[63]	Med. simple	Brodskiy (1973)	Edmunds *et al.* (1976)
Stenacron (1)	Swarm	Clear	Med. simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Stenonema (1)	Swarm[64]	Clear	Med. simple	Cooke (1940), Brodskiy (1973), Edmunds *et al.* (1976)	Burks (1953), Edmunds *et al.* (1976), Berner & Pescador (1988)
*Leptophlebiidae					
Habrophlebia	Swarm	?[65]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Habrophlebiodes	Swarm	?[65]	Med. simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Homothraulus	Swarm	?[65]	Med. simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Leptophlebia (3)	Swarm	Clear	Med. simple	Savolainen (1978), Edmunds *et al.* (1976)	Edmunds *et al.* (1976), Berner & Pescador (1988)
Paraleptophlebia (4)	Swarm	Clear	Med. simple	Brodskiy (1973), Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Ulmeritus (1)	Swarm	Small	Simple +	Edmunds *et al.* (1976)	Traver (1956), Edmunds *et al.* (1976)
*Metrepodidae					
Metretopus (1)	Swarm	?[65]	Med. simple	Savolainen (1978)	Edmunds *et al.* (1976)
Siphlopecton (1)	Swarm	Very small	Simple	Edmunds *et al.* (1976)	Burks (1953), Edmunds *et al.* (1976)
*Oligoneuriidae					
Homoeoneuria (1)	Swarm	Very small	Med.	Edmunds *et al.* (1976)	Edmunds *et al.* (1958), Edmunds *et al.* (1976)

Lachlania (2)	Swarm	Small	Simple	Edmunds *et al.* (1976)	Edmunds (1951), Koss & Edmunds (1970)
*Polymitarcyidae					
Campsurus (1)	Swarm	N?[66]	Simple	Morgan (1929)	Edmunds *et al.* (1976)
Ephoron (1)	Swarm	N?[62]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Tortopus (1)	Swarm	Small	Med. complex	Grandi (1973), Edmunds *et al.* (1976)	Traver (1950)
*Potamanthidae					
Potamanthus (1)	Swarm	N?[62]	Simple	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
*Siphloneuridae					
Isonychia (2)	Swarm	Small	Simple	Cooke (1942), Edmunds *et al.* (1976)	Edmunds *et al.* (1976), Berner & Pescador (1988)
Siphlonurus (3)	Swarm	Clear	Med.	Savolainen (1978), Edmunds *et al.* (1976)	Clemens (1915), Burks (1953), Edmunds *et al.* (1976)
Siphlonisca (1)	Swarm	Clear?	Med.	Edmunds *et al.* (1976)	Edmunds *et al.* (1976)
Hymenoptera					
*Anthophoridae					
Centris[5] (1)	Lek	Very clear/med. clear[67]	Complex/simple[67]	Shelly & Whittier (1997)	Snelling (1984)
Xylocopa[5] (7)	Site-chem.[3]	Very clear	Complex	Shelly & Whittier (1997), Thornhill & Alcock (1983)	Hurd & Moure (1963)
Apidae					
Apis[68] (sev.)	Swarm	Clear	Med. complex	Michener (1974)	Simpson (1970)
Bombus[5] (3)	Lek, site	Clear	Complex	Thornhill & Alcock (1983), Shelly & Whittier (1997)	Richards (1927), Laverly *et al.* (1984)
Euglossa (1)	Lek-chem	N/clear[69]	Med. simple	Shelly & Whittier (1997)	Dressler (1978*a*, *b*, 1982*a*,–*c*)
Eulaema (1)	Site-chem	Clear	Med. complex	Shelly & Whittier (1997)	Ospina-Torres (1998)
Braconidae					
Blacus (5)	Swarm[70]	N	?	Stelfox (1944), Southwood (1957), Van Achterberg (1975), Syrjämäki (1976), Van Achterberg (1977)	Van Achterberg (1975)
Formicidae					
Acromyrmex (1)	Lek	N?[71]	?	Shelly & Whittier (1997)	Schultz *et al.* (1998)
Formica (6)	Lek, site	Small	Med. simple	Chapman (1954, 1957), Shelly & Whittier (1997)	Wilson (1976), Tinaut Ranera (1989)
Lasius (2)	Swarm	N?[62]	Med. simple	Collingwood (1958)	Mackay & Mackay (1994)
Leptothorax (3)	Site	Very small	Simple	Collingwood (1957, 1958, 1963)	Tinaut Ranera (1982), Buschinger (1982), Heinze (1989), Heinze & Alloway (1991), Mackay (2000)
Myrmica (6)	Site	N? no mention	?	Wheeler (1919), Chapman (1954, 1957), Hubbard & Nagell (1976), Collingwood (1958)	Radchenko (1994)
Pheidole (1)	Swarm	Small	Med. simple	Thornhill & Alcock (1983)	Ogata (1982)
Stenamma (1)	Site	N[72]	?	Kannowski (1958)	Dubois (1998)

Table 2. (*Cont.*)

	Male site	Male genitalia differ among congeners?	Degree of complexity	References mating	Genitalia
Ichneumonidae					
Colpotrochia (1)	Swarm	N[73]	?	McAlpine & Munroe (1968)	Scaramozzino (1983)
Exochus (2 +)	Swarm	N[73]	?	McAlpine & Munroe (1968)	Tolkanitz (1993, 1999)
Metopius (1)	Swarm	N[73]	?	McAlpine & Munroe (1968)	Tolkanitz (1992)
Masaridae					
Pseudomasaris[5] (1)	Lek	N? no mention	?	Shelly & Whittier (1997)	Richards (1963)
Pompilidae					
Pepsis	Site	Med. small	Med. simple	Alcock & Johnson (1990)	Vardy (2000)
*Siricidae					
Sirex (1)	Site	N?[74]	?	Chapman (1957)	Middlekauff (1960)
Sphecidae					
Bembix[5] (1)	Lek	Clear	Med. simple	Shelly & Whittier (1997)	Bohart & Horning (1971), Evans & Matthews (1973), Evans (1982)
Clypeadon (1)	Site-chem	N? no mention	?	Shelly &Whittier (1997)	Dunning (1898), Bohart (1966)
Eucerceris (8)	Lek, site-chem	N? no mention	?	Evans & O'Neill (1985), Shelly & Whittier (1997)	Bohart & Grissell (1975)
Philanthus[5] (13)	Lek-chem[75]	N? no mention	?	Bohart & Grissell (1975), Shelly & Whittier (1997)	Bohart & Grissell (1975), O'Neill & Evans (1983)
Vespidae					
$*Mischocyttarus* (1)	Site-chem	N	?	W.G.E.	O. Silveira (personal communication)
Polistes[5] (6 +)	Lek, site	Med. small[76]	Med. simple	Shelly & Whittier (1997), Beani (1996)	Richards (1973), Peterson (1990)
Vespula (2 +)	Site	Med. clear	Med. simple	Thornhill & Alcock (1983)	Yamane *et al.* (1980), Archer (1982)
Trichoptera					
*Leptoceridae					
Athripsodes (2)	Swarm[3]	Clear	Complex	Petersson (1989)	Malicky (1983)
Mystacides (3)	Swarm[3, 77]	Clear	Med. complex	Balduf (1939), Petersson (1989)	Malicky (1983)
*Philopotamidae					
Chimarrha (2)	Swarm[3]	Clear	Med. complex	Balduf (1939), Davis (1939)	Malicky (1983)
*Sericostomatidae					
Oecetis (1)	Swarm	Clear	Complex	Davis (1939)	Malicky (1983)
Hemiptera					
*Enicocephalidae					
$*Boreostolus* (1)	Swarm[78]	N?[62]	Simple	Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)
Enicocephalus (1 +)	Swarm	Very small	Very simple	Johannsen (1909), Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)

$Gametostolus (1)	Swarm[78]	N?[62]	Simple	Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)
$Gamostolus (1)	Swarm[78]	N?[62]	Simple	Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)
$Hymenocoris (1)	Swarm[78]	N?[62]	Very simple	Wygodzinski & Schmidt (1991)	Kritsky (1978a), Wygodzinski & Schmidt (1991)
$Lysenicocephalus (2)	Swarm[78]	Very small	Very simple	Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)
$Neoncylocotis (1)	Swarm[78]	N?[62]	Very simple	Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)
$Stenopirates (3)	Swarm[78]	Very small	Simple	Štys (1981)	Ŝtys (1970)
$Systelloderes (2)	Swarm[78]	Med. clear	Simple	Wygodzinski & Schmidt (1991)	Kritsky (1978b), Linnavuori (1984)
$Tornocrusus (5)	Swarm[78]	Med. clear	Simple	Wygodzinski & Schmidt (1991)	Wygodzinski & Schmidt (1991)
Mecoptera					
*Nannochoristidae					
Nannochorista (1)	Swarm[79]	Clear?[24]	Med. complex	Evans (1942)	Evans (1942)
Coleoptera					
Lampyridae					
Luciola[5] (2)	Lek-visual	Clear	Simple	Shelly & Whittier (1997)	Ballantyne & Buck (1979), Ballantyne (1988)
Photinus (1)	Lek-visual	Med. clear	Simple	Shelly &Whittier (1997)	McDermott & Buck (1959)
Pteroptyx (2+)	Lek-visual	Very small/med. clear[80]	Very simple/simple[80]	Shelly & Whittier (1997)	Ballantyne (1987)
*Nitidulidae					
Meligethes (1)	Site[81]	Med. clear	Simple	Cooter (1977)	Spornraft (1992)
Lepidoptera					
Papilionidae					
Battus	Site	Med. clear	Med.	Tyler et al. (1994)	Tyler et al. (1994)
Heraclides (3)	Site	Med. clear	Med. simple	Tyler et al. (1994)	Tyler et al. (1994)
Papilio (2)	Site	Clear	Med. simple	Thornhill & Alcock (1983)	Tyler et al. (1994)
Protesilaus	Site	Clear	Med. complex	Tyler et al. (1994)	Tyler et al. (1994)
Protographium	Site	Clear	Med. complex	Tyler et al. (1994)	Tyler et al. (1994)
Pterourus (Pyrrhosticta)	Site	Med. clear	Med. simple	Tyler et al. (1994)	Tyler et al. (1994)
Homoptera					
*Cicadidae					
Aceropyga (sev.)	Lure-song[82]	Clear	Med. complex	Duffels (1988)	Duffels (1988)
Baeturia	Lure-song[82]	Clear	Simple	Duffels (1988)	Duffels (1988)
Orthoptera					
Acrididae					
Syrbula (1)	Lure-song[83]	N? no mention	?	Thornhill & Alcock (1983)	Otte (1981)
Gryllidae					
$Abmisha (1)	Lure-song[84]	Very small	Simple	Otte (1987)	Otte (1987)
Acheta (5)	Lure-song?	N? no mention	?	Alexander (1957)	Alexander (1957)
$Afrogryllopsis (4)	Lure-song[84]	Clear	Med. complex	Otte (1983)	Otte (1983)
$Agnotecous (1)	Lure-song	Clear[85]	Med. complex	Otte et al. (1987)	Otte et al. (1987)
$Archenopterus (1)	Lure-song[84]	Clear	Simple	Otte et al. (1987)	Otte et al. (1987)
$Astrupia (2)	Lure-song[83]?	Clear	Med. simple	Otte (1987)	Otte (1987)

Table 2. (*Cont.*)

	Male site	Male genitalia differ among congeners?	Degree of complexity	References mating	Genitalia
$Calscirtus (2)	Lure-song[84]	Clear[84]	Med. simple	Otte *et al.* (1987)	Otte *et al.* (1987)
$Cryncus (9)	Lure-song[83]	Very small	Simple	Otte (1985)	Otte (1985)
$Damaracheta (2)	Lure-song[84]	Small	Simple	Otte (1987)	Otte (1987)
Gryllus (8)	Lure-song[84]	Very small	Simple	Zuk & Simmons (1997)	Weissman *et al.* (1980), Otte & Cade (1984*a*)
$Koghiella (4)	Lure-song[84]	Clear	Simple	Otte *et al.* (1987)	Otte *et al.* (1987)
$Modicogryllus (11)	Lure-song[84]	Med. clear	Med. simple	Otte & Cade (1984*b*)	Otte & Cade (1984*b*)
$Neogryllopsis (3)	Lure-song[84]	Very clear	Med. complex	Otte (1983)	Otte (1983)
$Notosciobia (12)	Lure-song[84]	Med. clear	Med. simple	Otte *et al.* (1987)	Otte *et al.* (1987)
Oecanthus (2+)	Lure-song[84]	N? no mention	?	Thornhill & Alcock (1983)	Walker (1967)
$Platygryllus (8)	Lure-song[84]	Very small	Simple	Otte & Cade (1984*c*)	Otte & Cade (1984*c*)
$Scapsipedus (2)	Lure-song[84]	Small	Simple	Otte & Cade (1984*a*)	Otte & Cade (1984*a*)
Teleogryllus (seveal)	Lure-song[84]	Small	Simple	Otte & Cade (1983*a*)	Otte & Cade (1983*a*)
$Tremellia (3+)	Lure-song[84]	Clear	Med. complex	Otte *et al.* (1987)	Otte *et al.* (1987)
$Velarifictorus (5)	Lure-song[84]	Med. clear	Simple	Otte & Cade (1983*b*)	Otte (1987)
*Tettigoniidae					
$Anaulacomera (6)	Lure-song[84, 86]?	Clear	Med. simple	Nickle (1992)	Nickle (1992)
$Cocconotus (6)	Lure-song[84]?	Clear	Simple	Morris & Beier (1982)	Nickle (1992)
$Montezumina (4)	Lure-song[84]	Clear	Simple	Nickle (1984)	Nickle (1992)
$Neoconocephalus (sev.)	Lure-song[84]?	Med. clear	Simple	Walker & Greenfield (1983)	Walker & Greenfield (1983), Nickle (1992)
Orchelimum (1+)	Lure-song[84, 87]	Very small	Simple	Thornhill & Alcock (1983)	Rehn & Hebard (1915), Walker (1971)
$Phylloptera (3)	Lure-song[84]	Small	Simple	Shaw (1968, 1975)	Nickle (1992)
$Scopiorinus (2)	Lure-song[84]	Clear	Simple	Morris & Beier (1982)	Nickle (1992)
$Steirodon (2)	Lure-song[84, 86]	Clear	Simple	Nickle (1992)	Nickle (1992)

1. Hogue (1981) mentions seeing species in other genera (not specified) swarm, and the other genera treated in Hogue (1973) also have very distinct and complex male genitalia.

2. Swarms occur in general area where females emerge, so some harassment could occur.

3. Copulating pairs flew to the ground or away from the pairing site, or males excluded other males from the pairing site; females were thus apparently free of harassing males when copulation ended.

4. One female of *pritchardi* remated, but only after copulating away from swarm and then flying back into it; females often fall from swarm with several males, but extra males may then leave.

5. In some congeneric species females may not be protected, as they mate at resources utilized by the female or where adult females emerge (see Table 4).

6. Intra-specific variation includes alternative male tactic that may involve harassing females.

7. 'structure of the male genitalia is remarkably uniform among species and has not been used taxonomically, contrary to practice … of most other ceratopogonid genera' Wirth (1994, p. 137).

8. Direct statement in text indicates that male genitalia important to distinguish congeneric species.

9. Neither sex feeds as an adult in *anomalus* so no feeding resource where males can coerce females.

10. All references to genitalia are only to gonocoxae and gonostyles, not to genitalic structures which enter the female. The swarms of some species are at the edges of bodies of water, where females oviposit, but the localized nature of the swarms, the often arbitrary nature of objects used as markers (light stones, trees, etc.) with respect to oviposition, and the special 'offering' flights of females flying into swarms (Downes, 1969), indicate that females are generally protected from male harassment.

11. = *Tokunagayusurika*; males also search for females on the ground.

12. Female induce male swarms by flying low over a marker.

13. = *Psectrocladius*.

14. Captive males of *S. minima* also mate as they fly outside of swarm in at least one species, but this may be an artifact of captivity.

15. Within the *lestagei* group of sibling species, genitalic differences are very small, and identification (on the basis of any trait, genitalic or not) was 'very uncertain or even impossible' (Lindeberg, 1967); differences were clear among other species in the genus, however.

16. A second male was seen interfering in one copulation in *comunis*; in *culifacies* pairs also copulate without swarming; males also attack resting females on walls in the field in *maculipennis*; in *freeborni* some smaller males never swarm, and larger males were more common at peak swarming hours.

17. In five species of *Aedes* and seven of *Anopheles* the copulating pair flies down to ground or away from the swarm and were apparently free of harassing males before copulation ended.

18. In *aegypti* male also attempts to capture females when they come to feed and female sometimes pushes male away from her genitalia with her legs; some mating occurred away from the swarm in *cantans*; in *nigromaculis* few matings were seen in swarms, although males responded to sound of female flight and females released there were rapidly mated; authors speculated that 'most mating … takes place on or near the ground as the females move about …'

19. Differences are clear across entire genus, but closely related species often differ only very slightly.

20. Female *pipiens* fly into the swarm on a straight line, and a pair emerges on other side or falls to ground where they separate.

21. One race of *pipiens* swarms, another (in captivity) does not.

22. Males of *perturbans* also seen around hosts being bitten by females; so some swarms may be resource-based.

23. Mating pairs are accompanied by other males which mate with female after first copulation finished; but the female's original approach to the swarm was clearly performed without harassment.

24. The genitalia of only a single species were described (drawn); judging by their complexity, the genitalia are very likely species-specific.

25. Males were also present at feeding sites, but copulation was seen only at swarms.

26. Male gives the female a complex series of squeezes with his genitalia during copulation.

27. In addition to flying in swarms, males were also seen 'flying over the stream with ovipositing females, but no indication of mating was observed' (Davies & Peterson, 1956, p. 618).

28. In some congeneric species female apparently attracts the male chemically (Table 3).

29. Male can sense female only at very close range within the swarm, and does not respond to newly mated females.

30. Male genitalia 'as for genus', implying a lack of species-specificity.

31. Males of some species of this genus provide females with gifts apparently lacking nutrient value, while those of others apparently feed females; in *Empis opaca* prey is discarded only partially eaten at the end of copulation, while the prey in the balloon of *Empimorpha* sp. is only tiny, arguing against its importance as food as a coercive factor.

32. Genitalia were not mentioned by Engel & Frey (1956) or Chvála (1984).

33. Genitalia were not mentioned by Engel & Frey (1956); Collin (1961) says they are similar in a related genus.

34. Genitalia were not drawn, but said to be 'very distinctive' by Collin (1961).

35. Genitalia were not mentioned by Lindner (1925); James (1964) and Chillcott (1965) concur that 'male genitalia appear to be wholly useless for diagnosis', but these authors were apparently referring to the externally visible male genitalia; the more internal portion (aedeagus) is more complex in one species (Stuckenberg, 1973).

36. = *Volucella*.

37. A copulating pair of *O. obesa* was found far from any male aggregation (W.G.E.), so females are probably not harassed after the first copulation.

38. Male genitalia 'are important for the classification of higher categories but cannot usually be used for separation of genera and species' (Chvála *et al.*, 1972, p. 58); Middlekauf & Lane (1980) (and their citation of Philip, 1957) concur that genitalia do not have the fine, species-specific characters used in other groups.

39. Males of *auropunctatus* flew to females around cattle and mated so females of some species may not be protected; in *bovinus* males widely separated (illustrating a trend towards 'single male swarms').

40. The female of one species apparently must land on the ground below male swarm before the male mounts, and flight of mated female of *bishopi* does not attract males, suggesting that females are protected.

41. Only text descriptions were provided.

42. Mating occurs at sleeping sites in the morning, but behavioural observations indicate that males lure females chemically. Females are free to leave, and courtship is initiated by females, so they are not harassed by males. The liquid which the male feeds to the female during copulation is apparently not nutritious (P. Ortiz, in preparation).

43. Data are only for copulatory fork (abdominal sternite).

44. Includes *Cardiacephala*.

45. Males are territorial and females are free of harassment before and after copulation; the nutritive value (if any) of liquid male feeds to female during copulation not known. The male genitalic structures include the copulatory fork on his subgenital plate, which holds the female's ovipositor during copulation, and his genitalia *per se*.

46. Genitalia were not used by Hennig (1937*b*); genitalia of one species, illustrated by Brake (2000), is moderately complex, and the spermathecal ducts of the female are extremely long (many times the length of the female's body).

47. Thornhill & Alcock (1983) classify this species as territorial, but not as lekking; male territories are not at resources needed by females for food or oviposition, however.

48. The tip of the aedeagus is complex and the aedeagus is very long.

49. Epandrium only.

50. Leks occur on host plant, but females interested in oviposition are apparently not harassed by males.

51. Male genitalia composed of epandrium, which is relatively simple and which differs in detail but not substantially among species, and aedeagus, whose tip, the distiphallus, is moderately complex and which was especially useful in distinguishing otherwise cryptic species. In *Blepharoneura* species differences based on distiphallus form were confirmed by analysis of isoenzymes.

52. Males form leks in the morning, accost females at oviposition sites in the afternoon; most copulations apparently occur at leks (Eberhard, 1999).

53. = *Acidiostigma*.

54. 'male genitalia often exhibit differences of diagnostic value in other fruit fly genera, but in *Trypeta* no such characters could be found….' (Foote, 1960, p. 255).

55. May be leks.

56. Comments by taxonomists give somewhat contradictory impressions: Sabrosky (1986) mentions '… uniformity of the male genitalia …' within the genus (p. 23) and did not use genitalia despite frequent problems in separating species; Bennett (1955) gives importance to genitalic characters in grouping genera.

57. Swarms occurred at protected sites where females also rested, so harassment at a female resource seems possible; but females rested and flew away without harassment.

58. Genitalia of only one species were drawn, and are very similar to those of related genus; no mention was made of genitalia to distinguish species in the text.

59. A general description of mating behaviour for the entire order: 'Mating is preceded by peculiar swarming behavior' (Brodskiy, 1973). The list of genera here is undoubtedly very incomplete.

60. 'adults particularly difficult to identify to species' (Edmunds *et al.*, 1976).

61. 'male genitalia seem to provide only a small range of characters' (Edmunds *et al.*, 1976).

62. Genitalia of only one species were drawn; the great simplicity of their structure suggests that they lack species-specific differences.

63. Genitalia of only one species were drawn, but the text states that species can be distinguished on basis of male genitalia.

64. Solitary males sometimes chased copulating pairs, but none were seen to copulate successfully.

65. Genitalia of only one species were drawn; their intermediate degree of complexity does not allow predictions regarding species-specificity.

66. Genitalia of only one species were drawn, and their great simplicity of structures suggests lack of species-specific differences; but the penes are unusual in being able to revolve in a horizontal plane and point anteriorly, posteriorly or ventrally, so more complex species-specific movements may occur.

67. Genitalia *sensu strictu*/sternites 7 and 8.

68. Female is 'doubly' protected, because males are also attracted to a female-produced pheromone (Jacobson, 1965).

69. Relatively clear genitalic differences were used to distinguish two especially similar species; but in many other species genitalia were not mentioned.

70. 8077 males and 0 females were collected at swarms (Syrjämäki), and he argued that the mating function is uncertain (cited in van Achterberg, 1975); but Van Achterberg (1975) noted that females do occur in some swarms, and argues that mating may occur at night; He also stated that swarming of males '… can be explained by the individual dancing of the males in the neighborhood of emerging females … When a female approaches the dancing males, some males leave the group and try to copulate with her.' Females are probably free to fly away from the male swarm, so females are relatively protected.

71. No mention was made of male genitalia to distinguish species, but 'There are probably useful characters among male genitalia' (Dubois, 1998).

72. There were 'no obvious differences … in male genitalic morphology' (Schultz *et al.*, 1998).

73. No mention was made of male genitalia, and I. Gauld (pers. comm.) states that they are not species-specific.

74. No mention was made of male genitalia, and males were said to be harder to distinguish than females.

75. In one population of *P. zebratus* males 'swarm' over the nesting site; there were no genitalic difference from conspecifics in genitalia that mark territories chemically (Evans & O'Neill, 1985).

76. In many species groups within the genus the male genitalia 'seem to be practically identical,' but genitalia are often useful for distinguishing groups of species.

77. The male may also seize pupae, so some interactions may involve coercion.

78. There are no direct observations of swarming, but Štys (1981) and Wygodzinski & Schmidt (1991) agree 'that all Enicocephalidae capable of flight probably do swarm'.

79. Great numbers were 'flying around shrubs' on a mountain.

80. Aedeagus/tip of abdomen.

81. Although the author termed the behaviour 'swarming' and pairs sometimes fell to ground together, it may be rather long-distance chemical attraction of males or females; in any case, females seem likely to be protected from unwanted sexual attentions from males.

82. Calling songs or male structure to produce them (tympanum) reported; I presume that the male songs attract females. There are differences in male genitalia among subspecies of *Aceropyga* that are allopatric on different islands which could not have arisen as species isolation mechanisms.

83. Receptive female responds to male song with a song of her own that attracts the male.

84. Male song was documented, but it is not certain that no useful resource was associated with male. In some species of these families males transfer either nutritive spermatophores or portions of their own bodies which may represent important resources for females; male song could also function in male–male aggression.

85. Some species can be distinguished only by male genitalia.

86. Male song deduced from his morphology.

87. Female visits several males before copulating.

clear data supporting (Gryllidae and Enicocephalidae) or contradicting (Trichoptera) new arms race model predictions (marked with '$' in Tables 2–4). Of the major insect orders, I concentrated most on Diptera, Hymenoptera, Orthoptera, and Coleoptera, and neglected butterflies, Odonata, Hemiptera and Neuroptera. Although spiders are in general less well studied, the data were less affected by some of these problems, because both relative male size and species differences in genitalia are widely known, and because of the long series of recent revisions of araneoid genera by H. W. Levi. I failed to find taxonomic publications for 93 genera and 27 families of insects and 14 genera but no families of spiders that were on the original expanded list. The final sample included 386 genera in 119 families and 11 orders.

Patterns of genitalic evolution were evaluated by checking the characters used by taxonomists to distinguish congeneric species. Use of male genitalia was taken to imply a relatively rapid divergent pattern of evolution compared with other traits, and the text was checked for statements regarding the relative distinctiveness of genitalic and non-genitalic body parts in closely related species. In a few groups in which male genitalia were not used to distinguish species I was able to check with expert taxonomists to determine whether the omission was due to lack of differences in morphology, or because other traits were sufficient to distinguish closely related species.

No corrections were made for possible phylogenetic inertia (Felsenstein, 1985; Harvey & Pagel, 1991). The relatively rapid rate of change in male genitalia in many groups indicates that such inertia has not been important. Corrections for phylogeny would thus be inappropriate, and could lead to errors (see Losos, 1999). The evolutionary lability of mating behaviour in some groups (see below) also argued in favour of this decision. These topics are examined in further detail in Sections III 2 *a*, and IV 2 *a* ii.

I also did not measure the morphological complexity of genitalia quantitatively (Arnqvist & Thornhill, 1998; Arnqvist, 1998). One problem with such measurements is that there is no guarantee that aspects measured in morphometric analyses will correspond with traits that are under selection. For most groups, there are no data concerning the mechanical mesh between male and female genitalia, locations of female sensory structures, possible stimulating movements of male genitalia during copulation, or female criteria with respect to male genitalic form. Additional problems with attempts to quantify differences are the differing degrees of simplification in the drawings made by different taxonomists, and the fact that taxonomic studies in some groups only include some portions of the male genitalia – usually those portions that are larger, that are external rather than internal, or that are otherwise more easily accessible (see Section IV 2 *a* ii). In analysing data from genera in which several portions of the male genitalia have been studied, I characterized the genus by the most divergent genitalic structures. In order to evaluate the effect of a possible bias among taxonomists to use genitalia in species descriptions even when they are not particularly divergent, I made qualitative judgements regarding the degree of interspecific differences and the general complexity of the genitalia (Figs 1–5) (these judgements are also, of course, not guaranteed to reflect selective importance).

There were 25 genera in which the females of some congeneric species were protected while those of others were not. For instance, the mosquitoes *Mansonia*, *Aedes*, and *Culex* have both swarming (female protected) and non-swarming species (female possibly not protected) (e.g. Shannon, 1931; Haddow & Corbet, 1961); the males of some species of *Culicoides* midges swarm at arbitrary markers (female protected) while others swarm at female feeding sites (female not protected) (Glukhova & Dubrovskaya, 1974). These data demonstrate that mating behaviour can change rapidly with respect to the degree of protection of the female, thus supporting the decision not to use phylogenetic corrections. The prediction of new arms race models is that male genitalia will be more distinctive (diverge more rapidly) among these species within a genus in which females are less protected, while no such difference is predicted by traditional female choice. The new arms race prediction was not supported, as in no case did I find a taxonomist making a direct statement that the degree of divergence in the genitalia was greater in the species with unprotected females in these genera. But given the low frequency of discussions of infrageneric patterns in the degree of difference in genitalia, and the general lack of phylogenies within these genera, this is not convincing evidence against the predictions. As a conservative measure, I omitted all genera in which females were both protected and not protected. Only genera which are known to have a single type of mating behaviour were included in the analyses, and genera rather than species were the units of analysis. Data from ditrysian moths were analysed separately because, due to the relatively uniform mating behaviour and the consistent pattern of genitalic evolution throughout this huge group, data were compiled in a less laborious manner.

III. RESULTS

(1) Functions of male genitalic structures in Diptera

Possible mechanical functions of male genitalia are listed in Table 1, along with predictions discussed above regarding the probability of new arms race types of male–female conflict in groups in which females are protected from male harassment. The probable functions for structures mentioned directly in studies of 43 species in 22 families are listed. Most entries are based on direct statements of the authors, who generally relied on mechanical design, positions during copulation, and associated muscles to infer function. Taking each entry for a structure in Table 1 as a separate case, nearly half (46.7%) of the 105 attributed functions involve interactions with internal female structures that facilitate penetration deeper into the female and sperm transfer to her storage organs. As discussed above, penetration and sperm transfer functions are expected to be potentially 'nonconflictive' in species with protected females.

The next most common function is to clasp the female on the outside of her body (39% of documented functions).

Table 3. Genitalic traits in genera in which the female is protected from male harassment because the male depends on a signal from the female to find her. Numbers in parentheses following genus names refer to number of species for which female attraction has been documented; ' + ' refers to cases that mentioned 'spp.' without specifying precies numbers of species. Genera included because I happened to be familiar with their mating behaviour or because of directed reading after the original list was complete are marked with '$', families without genera with unprotected females (Table 4) are marked with '*'. For those species in which no information on the mating behaviour was included other than that given in a review, reference is made only to the review, rather than the original descriptions. 'W.G.E.' refers to own unpublished observations; 'sev.'=several; 'chem.'=chemical; 'N'=no; 'N?'=probably no, because genitalia were not mentioned or because of other reasons (see associated footnotes); 'med.'=medium. When more than one genitalic structure was characterized, they are separated by '/' (e.g. small/medium clear)

	Attractant female stimulus	Male genitalia differ among congeners?	Degree of complexity	References Mating	Genitalia
Diptera					
Tipulidae					
Dolichopeza (1)	Chem.?[1]	Very clear	Complex	Byers (1961)	Byers (1961)
Hymenoptra					
Braconidae					
Cotesia (2)	Chem.	Clear[2]	?	Kimani & Overholt (1995)	Kimani-Njogu *et al.* (1997)
*Diprionidae					
Diprion	Chem.	?[3]	Med. simple	Hilker *et al.* (2000)	Saini & Thind (1993)
Ichneumonidae					
$*Hymenoepimecis* (1)	Chem.?[4]	N	?	Eberhard (2000*c*)	I. Gauld (pers. comm.)
Itoplectis	Chem.	N	?	Godfray & Cook (1997)	I. Gauld (pers. comm.)
Syndipnus (2)	Chem.	N	?	Godfray & Cook (1997)	I. Gauld (pers. comm.)
*Mutillidae					
Dasymutilla	Chem.?	Clear	Med. simple	Cambra & Quintero Arias (1992)	Manley (1983)
Timulla	Chem.?	Clear	Med. complex	Cambra & Quintero Arias (1993)	Cambra & Quintero Arias (1993)
Coleoptera					
*Cebrionidae					
Selonodon (several)	Chem.?	Very small[5]	Very simple	Galley (1999)	Galley (1999)
Cerambycidae					
Prionus (1)	Chem.?	N? no mention	?	Gwynne & Hostetler (1978)	Chemsak (1979), Hovore (1981), Hovore & Turnbow (1984)
Lampyridae					
Microphotus	Light[4]	Med. clear	Simple	Lloyd (1997)	McDermott & Buck (1959), McDermott (1964)
Photinus (7 +)	Light[6]	Med. clear	Simple	Lloyd (1997)	McDermott & Buck (1959)
Photuris (4 +)	Light[6]	N		Lloyd (1997)	McDermott (1964), Lloyd (1997)
Pleotomodes (2 +)	Light[7]	Very small	Very simple	Lloyd (1997)	Geisthardt (1986)
Pyractomena (6 +)	Light[6]	Clear?[8]	?[8]	Lloyd (1997)	McDermott (1964)
Pyropyga spp.	Chem.[4]	Clear?[8]	?[8]	Lloyd (1997)	McDermott (1964)
Melolonthidae					
Melolontha	Chem.[4]	Clear/clear[9]	Med./complex[9]	Chapman (1957)	Baraud (1992)
Phyllophaga (several)	Chem.[4]	Very clear	Complex	Eberhard (1993*b*), Zhang *et al.* (1997)	Morón (1986), Woodruff & Beck (1989)
Scarabeidae					
Heteronyx (3)	?	Clear[10]	Simple[10]	Morgan (1977)	Britton (2000)
Phyllopertha (1)	Chem.?	Clear	Simple	Thornhill & Alcock (1983)	Li & Yang (1997)
Pleocoma (1)	Chem.?[4]	Clear?[10, 11] (no mention)	Med. complex[10]	Fellin (1981), Sugden & Giblin (1983)	Hovore (1971), W.G.E.
Popillia (1)	Chem.?[12]	Clear/clear[9]	Simple/med. complex[9]	Thornhill & Alcock (1983)	Sabatinelli (1993, 1994)

Lepidoptera					
*Ditrysia[13] (>200 000)	Chem.[4, 14]	Med. to very clear	Med. to very complex	Phelan (1997)	Dominick *et al.* (1971–1998), Amsel *et al.* (1965–2000)
Trichoptera					
*Limnephilidae					
$*Apatania* (1)	Chem.[4]	Clear	Med.	Solem & Solem (1991)	Malicky (1983)
$*Dicosmoecus* (1)	Chem.[4]	Clear?[15]	Med. complex	Resh & Wood (1985)	Malicky (1983)
$*Enoicyla* (1)	Chem.[4]	Clear	Med. complex	Kelner-Pillault (1975)	Malicky (1983)
*Molannidae					
$*Molanna* (1)	Chem.[4]	Clear	Med. complex	Solem & Petersson (1987)	Malicky (1983)
Philopotamidae					
$*Dolophilodes* (1)	Chem.[4]	Clear?[15]	Med. complex	Wood & Resh (1984)	Malicky (1983)
*Rhyacophilidae					
$*Rhyacophila* (2)	Chem.[4]	Clear	Med. complex	Solem (1985), Löfstedt *et al.* (1994), Larsson & Hansson (1998)	Malicky (1983)
Blatteria					
*Blattidae					
Periplaneta	Chem.	Clear	Complex	Bell *et al.* (1977), Jacobson (1965)	Walker (1922), Princis (1951)

1. Mating also occurs at resting sites, but males fail to respond to females at such sites unless they touch them, suggesting that mating there is uncommon.
2. Two of three species (demonstrated by studies of crosses and somewhat overlapping distributions in principal component analysis of 16 non-genitalic morphological traits) that 'are extremely difficult, and sometimes impossible to distinguish using characters related to external morphology' could be discriminated using male genitalia.
3. Genitalia of only one species described; their intermediate complexity does not give clear indication regarding probable species-specificity.
4. The female signal is spontaneous, and not triggered by a male signal (antagonistic seduction not possible).
5. Despite small differences, both species and species groups are generally defined by genitalic differences.
6. The female signal is triggered by a male signal (light).
7. The female lacks functional wings, emphasizing the importance of male searching behaviour.
8. No drawings were provided, but '… for many species [in this genus] determination depends largely on aedeagal differences'.
9. Parameres/sclerites of internal sac.
10. Parameres only.
11. The published account makes no mention of genitalia, but observation of one species (W.G.E) showed parameres to be relatively complex for a scarab; this degree of complexity suggests they are species-specific in form.
12. Mating also occurs at feeding site (plants), but it is not clear whether or not females lure males to these sites.
13. Including approximately 98% of the approximately 250 000 species of Lepidoptera (Phelan, 1997).
14. 'Almost universally, mate finding in ditrysian moths is characterized by a male competitive scramble for females, who 'call' (emit pheromone) …' (Phelan, 1997, p. 241).
15. Genitalia of only one species were drawn; their complexity suggests they are probably species-specific in form.

Table 4. Genitalic traits in genera in which females are not protected from harassment by males, because sexually active males are normally present at sites where females must be to carry out reproductive and feeding activities. 'Food' refers to males that are found at feeding sites for females or in which the male himself provides food to the female; 'ovip.' refers to sexually active males present at sites where females lay eggs; 'nest' refers to sexually active males present at female nesting sites; 'emerge' refers to males present at sites where newly mature females emerge from pupae (when followed by 'M' mating at such sites has been observed, when followed by 'P' only male patrolling behaviour observed); 'med.' = medium. Genera included because I happened to be familiar with their mating behaviour or because of directed reading after the original list was complete are marked with '$', and families without genera with protected females (Tables 2, 3) are marked '*'

	Site controlled by male	Male genitalia differ among congeners?	Degree of complexity	References Mating	Genitalia
Diptera					
Nematocera					
*Bibionidae					
Plecia (1)	Food[1]	Med.	Med. simple	Thornhill (1976, 1980)	Hardy (1945)
Ceratopogonidae					
Ceratopogoninae					
Ceratopogoniini					
Ceratopogon[2] (1)	?[3]	Med. clear	Simple	Downes (1958)	Goetghebuer & Lenz (1934)
Culicoidini					
Culicoides[2] (2)	Food	Med. clear	Simple	Downes (1958, 1969)	Blanton & Wirth (1979)
Culicoides (1)	M	Med. clear	Med. simple	Linley & Adams (1972)	Wirth & Blanton (1969), Blanton & Wirth (1979)
Palpomyiini					
Bezzia[2]	Food[4]	Clear	Simple	Downes (1958, 1969)	Goetghebuer & Lenz (1934)
Palpomyia[2]	Food[4]	N? no mention	?	Downes (1958, 1969)	Goetghebuer & Lenz (1934)
Forcipomyinae					
Atrichopogon[2] (1)	Food	Clear	Med. simple	Downes (1958)	Goetghebuer & Lenz (1934)
Forcipomyia[2] (2)	Food[3]	Small, clear		Downes (1958)	Utmar & Wirth (1976), Wirth & Spinelli (1993)
Chironomidae					
Allochironomus[2] (1)	Resting	Clear	Med. complex	Downes (1969)	Goetghebuer & Lenz (1936)
Chironomus[2] (2+)	Emerge-M	Clear	Med. simple	Downes (1969)	Pinder (1978), Cranston *et al.* (1989a)
Clunio (1)	Emerge-M	Clear(?)[5]	Med. complex	Thornhill & Alcock (1983)	Goetghebuer & Lenz (1936)
Corynocera[6] (1)	Emerge-M	Clear(?)[5]	Enlarged	Downes (1969)	Goetghebuer & Lenz (1936)
Culicidae					
Aedes[2] (8)	Food[7,8] emerge[9]	Med. clear	Med. complex	Shannon (1931), Roth (1948), Nielsen & Haeger (1959), Haddow & Corbet (1961), Gubler & Bhattacharya (1972)	Carpenter & LaCasse (1955)
Anopheles[2] (1)	Ovip. emerge-M	Very small	Med. simple	Nielsen & Haeger (1959)	Carpenter & LaCasse (1955), Belkin (1962)
Culiseta (1)	emerge-M	Med. clear	Med. complex	Kliewer *et al.* (1967)	Carpenter & LaCasse (1955)
Deinocerates (1)	Ovip. emerge-M	Very clear	Med. complex	Nielsen & Haeger (1959), Thornhill & Alcock (1983)	Carpenter & LaCasse (1955)
Eretmapodites (1)	Food	Clear	Complex	Haddow & Corbet (1961)	Haddow (1946)
Haemagogus (1)	Ovip.	Small	Med. complex	Nielsen & Haeger (1959)	Galindo & Trapido (1967)
Psorophora (several)	Food, ovip.	Clear	Med. complex	Nielsen & Haeger (1959)	Carpenter & LaCasse (1955)

$Sabethes (1)	Resting	Very clear	Very complex	Hancock *et al.* (1990)	Harbach & Petersen (1992)
Toxorhynchites (2)	Ovip.	Small[10]	Med.	Haddow & Corbet (1961), Nielsen & Haeger (1959)	Carpenter & LaCasse (1955), Belkin (1962), Ribeiro (1991)
*Mycetophilidae					
$Leptomorphus (2)	Emerge-M	Clear	Med.	Eberhard (1971)	Landrock (1927)
Simuliidae					
Cnephia (2)	Emerge-M[11]	Med. clear	Med.	Davies & Peterson (1956)	Rubzow (1964)
Brachycera					
*Asilidae					
Cerotaina (1)	Food	Clear?[12]	Complex	Thornhill & Alcock (1983)	Theodor (1976)
Empididae					
Empimorpha	Food[13]	Clear	Complex	Kessel (1955)	Collin (1961)
Empis[2] (13)	Food[13]	Very clear	Complex	Kessel (1959), Downes (1970), Chvála (1980)	Engel & Frey (1956)
Hilara[2] (6+)	Food[13]	Very clear	Med. complex	Poulton (1913), Kessel (1959), Downes (1970), Forrest (1985)	Engel & Frey (1956)
Rhamphomyia (10)	Food[14]	Very clear	Complex	Steyskal (1941, 1942, 1950), Crane (1961), Downes (1970), Funk & Tallamy (2000)	Engel & Frey (1956)
Stratiomyidae					
$Himantigera (1)	Ovip.	N?[15]	Med. simple	Eberhard (1988)	James & McFadden (1982)
$Merosargus	Ovip.	N[16]	Med. complex	W.G.E.	James (1967)
Acalyptrata					
Drosophilidae					
$Chymomyza (2+)	Food	Very clear	Complex	Grimaldi (1986), Eberhard (2002c)	Duda (1935), Grimaldi (1986)
Drosophila (2)	Food, ovip. emerge-M	Clear	Complex	Thornhill & Alcock (1983), Markow (2000)	Duda (1935), Coyne (1993)
*Dryomyzidae					
Dryomyza (1)	Ovip.	Clear/small	Med. simple/simple	Otronen (1984)	Kurahashi (1981)
*Ephydridae					
$Ochthera (1)	Food	Clear[17]	Complex	Eberhard (1992)	Clausen (1977)
*Nereidae					
$Glyphidops (1)	Ovip.	N? no mention	Simple[18]	Eberhard (1998b)	Hennig (1937a), Aczél (1961), Eberhard (1998b)
$Nerius (2)	Ovip.	N? no mention	Simple[18]	Wheeler (1924), Eberhard (1998b)	Czerny (1930), Hennig (1937a), Aczél (1961), Eberhard (1998b)
Odontoloxozus (1)	Ovip.	N[19]	?	Mangan (1979)	Mangan & Baldwin (1986)
*Piophilidae					
Centrophlebomyia (1)	Ovip.	N? no mention[20]	?	Sivinski (2000)	McAlpine (1977), Freidberg (1981)
Protopiophila (2)	Ovip.	Clear	Med. complex	Sivinski (2000)	Hennig (1943)
*Platystomatidae					
Euprosopia (3)	Regurgitate to female[21]	N? no mention	?	Sivinski (2000)	Hennig (1945)
Rivellia (2)	Female fed froth[21]	Clear/clear[22]	Med. complex/med-complex[22]	Sivinski (2000)	Namba (1956), Byun *et al.* (1998)
*Sepsidae					
$Archisepsis (6)	Food, ovip.[23]	Clear/clear[24]	Med./complex[24]	Eberhard & Pereira (1996), Eberhard (2001c)	Silva (1993), Ozerov (1993), Eberhard & Huber (1998)
$Microsepsis (3)	Food, ovip.[25]	Clear[26]	Med.[26]	Eberhard (2000a)	Silva (1993)
$Palaeosepsis (2)	Food, ovip.	Clear[26]	Med.[26]	Eberhard (2002b)	Silva (1993)

Table 4. (*Cont.*)

	Site controlled by male	Male genitalia differ among congeners?	Degree of complexity	References Mating	Genitalia
$*Sepsis* (3+)	Food, ovip.[25]	Clear[26]	Med.[26]	Parker (1972), Pont (1987), Eberhard (1999), Ward (1983), Schulz (1999)	Duda (1925, 1926)
$*Themira* (2)	Food	Clear/clear[27]	Med./med.[27]	Schulz (1999), Eberhard (in prep.)	Ozerov (1998)
Tephritidae					
Anastrepha[2] (1)	Food	Small	Simple	Aluja *et al.* (2000)	Norrbom *et al.* (2000)
Bactrocera (4)	Food, ovip.	N? no mention	?	Drew & Romig (2000)	Drew & Hancock (1995)
Dacus (1)	Ovip.	N? no mention	Simple[28]	Drew & Romig (2000)	Drew (1979), Drew & Hancock (1995)
Euaestoides (1)	Food[21]	N? no mention	?	Sivinski *et al.* (2000)	Foote (1958)
Eutreta (1)	Food[21]	N? no mention	?	Sivinski *et al.* (2000)	Hendel (1927)
Neaspilota (1)	Food[21]	Small/clear[29]	Simple/complex[29]	Sivinski *et al.* (2000)	Ibrahim (1982), Freidberg & Mathis (1986)
Paracantha (1)	Food+spittle[21]	Med. clear	Med. simple	Sivinski *et al.* (2000)	Aczél (1952)
Phytalmia	Ovip.[30]	Slight/clear[29]	Med. simple/med. complex[29]	Dodson (2000)	McAlpine & Schneider (1978)
Rhagoletes (7)	Ovip.	Med. clear/clear[31]	Med. simple/complex[31]	Prokopy & Papaj (2000)	Bush (1966)
Strauzia	Ovip.	Very small/clear[32]	Simple/complex[32]	Han (2000)	Stoltzfus (1988)
Trypeta[2] (2)	Ovip.	N	?	Han (2000)	Foote & Blanc (1963)
Calyptrata					
*Glossinidae					
Glossina (1)	Food	Clear	Med. complex	Thornhill & Alcock (1983)	Gouteux (1987)
*Hippoboscidae					
Melophagus (1)	Food	Med. clear	?[33]	Thornhill & Alcock (1983)	Theodor (1964)
*Sarcophagidae					
$*Chrysagria* (1)	Ovip.	Clear	Complex	Eberhard (1990*b*)	Lopes & Achoy (1986)
*Scathophagidae					
Scathophaga (1)	Ovip. (+food?)	Clear	Med. complex	Parker (1970), Borgia (1979)	Hackman (1956)
Hymenoptera					
*Agaonidae					
$*Heterandrium* (1)	Emerge-M	N? no mention	?	W.G.E.	Bouček (1993)
Idarnes (2+)	Emerge-M	N	Simple	Thornhill & Alcock (1983)	Gordh (1975)
*Andrenidae					
Andrena (1)	Emerge-P	Very small	Med. simple	Thornhill & Alcock (1983)	Tadauchi & Hirashima (1987), Gusenleitner (1998), Tadauchi & Xu (2000)
Calliopsis (1)	Emerge-P	Very small	Simple/med. simple	Thornhill & Alcock (1983)	Danforth (1994)
Nomadopsis (13)	Emerge, food	Med. clear	Med. simple	Thornhill & Alcock (1983)	Rozen (1958)
Perdita (2)	Food	Clear/small[34]	Med. simple/simple[34]	Thornhill & Alcock (1983), W.G.E.	Snelling & Danforth (1992)
Nomadopsis (1)	Food, emerge-P	Med. clear	Med. simple	Thornhill & Alcock (1983)	Rozen (1958)

*Anthophoridae					
Centris[2] (2)	Emerge, food	Very clear	Med. complex	Thornhill & Alcock (1983)	Snelling (1984)
Triepeolus sp.	Food	Med. clear/small[35]	Med. complex/simple[35]	Thornhill & Alcock (1983)	Rozen (1989), Genaro (1998, 1999)
Apidae					
Bombus[2] (2+)	Emerge-P	Clear	Med. complex	Thornhill & Alcock (1983)	Richards (1927), Laverly *et al.* (1984)
Xylocopa[2] (2+)	Food, emerge-P	Clear	Med. complex	Thornhill & Alcock (1983)	Hurd & Moure (1963)
Braconidae					
Coeloides (1)	Emerge-M	N? no mention	Very simple	Thornhill & Alcock (1983)	Mason (1978)
*Colletidae					
Colletes (2+)	Emerge	Clear[36]	Med. complex[36]	Thornhill & Alcock (1983)	Rojas & Toro (1993), Michener (1993)
*Eucharitidae					
$*Pseudometagea* (1)	Emerge-M	N?	Med. simple	Ayre (1962)	Burks (1961), Heraty (1985)
*Eulophidae					
Mellitobia	Emerge-M	N? no mention	?	Dahms (1984 *a*)	Dahms (1984 *b*)
Formicidae					
Rhytidoponera (1)	Emerge-P	N? no mention	?	Thornhill & Alcock (1983)	Ward (1985)
*Halictidae					
Nomia (2)	Emerge-P	Clear	Med. complex	Thornhill & Alcock (1983)	Wu (1983)
Ichneumonidae					
Megarhyssa (2+)	Emerge-M	N		Thornhill & Alcock (1983)	I. Gauld (pers. comm.)
Lytrames (1)	Emerge	N	?	Godfray & Cook (1997)	I. Gauld (pers. comm.)
Rhysella (2+)	Emerge	N	?	Godfray & Cook (1997)	I. Gauld (pers. comm.)
Rhyssa (2+)	Emerge-M	N	?	Godfray & Cook (1997)	I. Gauld (pers. comm.)
Masaridae					
Pseudomasaris (2)	Food	N? no mention	?	Longair (1987)	Richards (1963)
*Megachilidae					
Anthidiellum (2+)	Food	N? no mention/ med. clear[37]	?/simple[37]	Thornhill & Alcock (1983)	Grigarick & Stange (1968)
Anthidium (2+)	Food	N? no mention/ med. clear/small[38]	?/simple/simple[38]	Thornhill & Alcock (1983)	Grigarick & Stange (1968), Snelling (1992)
Callanthidium (1)	Food	N? no mention/ clear/slight[38]	?/med. simple/simple[38]	Thornhill & Alcock (1983)	Grigarick & Stange (1968)
*Melittidae					
Meganomia (1)	Food, emerge-P	Small/clear[39]	Med. simple/ med. simple[39]	Thornhill & Alcock (1983)	Michener (1981)
*Oxaeidae					
Protoxaea (1)	Food	Very small	Med. simple	Alcock (1990)	Hurd & Linsley (1976)
Pompilidae					
$*Auplopus* (1)	Emerge-M	Y?[40]	Med. complex	Wcislo *et al.* (1988)	Shimizu (1986)
*Pteromalidae					
Nasonia (1)	Emerge-P	N?[15] no mention	Simple	Whiting (1967), Thornhill & Alcock (1983)	Darling & Werren (1990)
Spalangia (1)	Oviposit	N	?	Godfray & Cook (1997)	Bouček (1965)
*Scelionidae					
$*Phanuropsis* (1)	Emerge-M	N? no mention	?	Eberhard (1975)	Johnson (1987)
$*Trissolcus* (1)	Emerge-M	N? no mention	?	Eberhard (1975)	Johnson (1985, 1991)
Sphecidae					

Table 4. (*Cont.*)

	Site controlled by male	Male genitalia differ among congeners?	Degree of complexity	References Mating	Genitalia
Bembecinus (2)	Emerge-P/M[41]	Very small	Very simple	Evans & O'Neill (1986)	Bohart (1997)
Bembix (many)	Nest, emerge-M	Clear	Med. simple	Evans & Matthews (1973), Thornhill & Alcock (1983)	Bohart & Horning (1971), Kimsey & Kimsey (1981), Evans (1982), Griswold (1983)
Oxybelus (2+)	Burrow	N? no mention	?	Thornhill & Alcock (1983)	Bohart & Schlinger (1957)
Philanthus (3)	Nest	N? no mention	?	O'Neill & Evans (1983)	Ferguson (1983 a, b), Gayubo (1991)
Trypoxylon (2+)	Nest	Clear	Med. complex	Bohart & Menke (1976)	Matthews (1983), Amarante (1991), Antropov (1994)
$*Trigonopsis* (1)	Emerge-M[42]	Med. clear	Med. simple	Eberhard (1974)	Vardy (1978)
*Tenthredinidae					
Pristiphora (1)	Emerge-M	Clear	Simple	Thornhill & Alcock (1983)	Togashi (1989), Lacourt (1995)
Vespidae					
Polistes[2] (1)	Nest, hibernate	Med. clear	Med. complex	West Eberhard (1969), O'Donnell (1994)	Bohart & Bechtel (1957), Richards (1978 a, b), Kojima & Kojima (1988)
Lepidoptera					
*Heliconiidae					
Heliconius (several)	Emerge-M	Small	Med. simple	Brown (1981)	Emsley (1965)
Papilionidae					
Papilio (2)	Ovip. puddle	Small	Med. simple	Thornhill & Alcock (1983)	Tyler *et al.* (1994)
Hemiptera					
*Coreidae					
$*Acanthocephala* (2)	Food	N? no mention	?	Mitchell (1980), Eberhard (1998 c)	Gibson & Holdridge (1918), H. Brailovski (pers. comm.)
*Saldidae					
$*Pentacora* (1)	Food	Small	Med. simple	W.G.E.	Polhemus (1985)
Coleoptera					
*Buprestidae					
$*Acmaeodera* (1)	Food[23]	N?[15]	Simple	Eberhard (1990 a)	Nelson (1996)
Hippomelas (1)	Food	Very small	Simple	Thornhill & Alcock (1983)	Verity (1978), Nelson (1988)
Cerambycidae					
Monochamus (1)	Ovip. (?)	N? no mention	?	Thornhill & Alcock (1983)	Harde (1966)
*Chrysomelidae					
$*Macrohaltica* (2)	Food[23]	Small	Simple	Eberhard *et al.* (1993)	Santisteban (1997)
*Cleridae					
Thanasimus (1)	Food	Clear	Simple	Thornhill & Alcock (1983)	Kolibáč (1992)
*Coccinellidae					
Hippodamia (2+)	Hibernate[43]	Med. clear	Med. complex	Thornhill & Alcock (1983)	Capra (1931)
*Curculionidae					
Anthonomus (1)	Ovip.	Clear	Simple	Thornhill & Alcock (1983)	Clark (1987, 1988 a, b)
Lampyridae					
Photuris (1+)	Food[44]	N	Simple	Lloyd (1997)	McDermott & Buck (1959), McDermott (1964)

*Meloidae					
Epicauta (2+)	Food	Med. small/clear	Simple/med. simple	Pinto (1980)	Pinto (1980)
Pyrota (3+)	Food	Clear	Med. simple	Thornhill & Alcock (1983)	Selander (1982)
Melolonthidae					
\$*Golofa* (2)	Food	Clear[45]	Simple[45]	Howden & Campbell (1974), Eberhard (1977a)	Endrödi (1985)
\$*Macrodactylus* (4)	Food[22]	Small/clear[46]	Simple/med. complex[46]	Eberhard (1993a)	Carrillo & Gibson (1960), Eberhard (1992, 1993a)
Oryctes (1)	Food(?)	Clear[45]	Med. simple[45]	Thornhill & Alcock (1983)	Endrödi (1985)
Podischnus (1)	Food	N? no mention	?	Eberhard (1977b)	Endrödi (1985)
Scarabeidae					
Onthophagus (2+)	Food, ovip.	Clear	Med. complex	Halffter & Edmunds (1982)	Génier & Howden (1999)
Phanaeus	Food, ovip.	N? no mention	Simple	Halffter & Edmunds (1982)	Zur Strassen (1980)
Scarabaeus (2+)	Food, ovip.	N[47]	?	Halffter & Edmunds (1982)	Edmunds (1994)
*Scolytidae					
Dendroctonus (several)	Ovip.	N[48]	?	Borden (1982), Thornhill & Alcock (1983)	Bright & Stark (1973), Hopping (1963a, b, 1964, 1965a–c)
Ips (several)	Ovip.	N[48]	?	Borden (1982), Thornhill & Alcock (1983)	Bright & Stark (1973), Hopping (1963a, b, 1964, 1965a–c)
Odonata					
*Calopterygidae					
Hetaerina (3+)	Ovip.[49]	Clear[50]	Med. simple[50]	Thornhill & Alcock (1983), Eberhard (1985b), E. Rojas (unpub.)	Garrison (1990)
Orthoptera					
Acrididae					
Hylopedetes (1)	Food	Clear?[40]	Med. complex	Greenfield (1997)	Descamps & Rowell (1978), Rowell (1995)
Ligurotettix (2)	Food[51]	N? no mention	?	Greenfield (1997)	Rehn (1923)
Gryllidae					
Gryllus (1)	Burrow	N[52]	Very simple	Thornhill & Alcock (1983)	Weissman *et al.* (1980)
\$*Neoxabea* (2+)	Food[3]	Clear	Simple	Walker (1967)	Walker (1967)

1. Males also encounter females near emergence sites.
2. Other species in the same genus have protected females.
3. Female consumes the male.
4. Mating has not been observed, but male antennal morphology suggests that males do not swarm.
5. Text describes differences (only one species drawn).
6. Both male and female are brachypterous.
7. Males also form small swarms.
8. In *albopictus* female contact with swarming males that led to copulation seemed to be random, but it was more common for nulliparous females, suggesting a bias in contact (due to female flight?).
9. Resource defence by males apparently only occasional.
10. Genitalia of conspecific subspecies could not be distinguished (Carpenter & LaCasse, 1955).
11. Ball of males around female on rocks at edge of water often seen (sometimes they roll into the water).
12. Genitalia of only one species were drawn; they are probably species-specific because very complex structure and strong differences with other genera in same tribe.
13. Mating occurs in swarms, but males of many species provide females with gifts of food, although in some species the prey is minute.
14. The male gives a nutritive gift to female in most species (although it is very small compared with size of female in *curvipes*); in some species females appear to depend on such gifts, and have never been seen to hunt prey themselves.
15. Genitalia of only one species were drawn; judging by relative simplicity of male genitalia, they are probably not species-specific in form.

16. It was difficult to distinguish at least one pair of closely related species.
17. Genitalic differences revealed a complex of species in what was formerly thought to be a single species.
18. Surstyli and aedeagus.
19. Author made specific statement that male genitalia did not differ in related species.
20. Genitalia were described as 'similar' to those in another genus (McAlpine, 1977).
21. Nutrient value (if any) of material regurgitated by male and fed on by female is not known; if it is not nutritious (as appears to be the case in *Spathulina sicula*; Sivinski *et al.*, 2000), then these genera should be reclassified as female protected.
22. Tergite 9 and epandrium complex/glans of aedeagus.
23. The male mounts female without courtship.
24. Hypandrium/aedeagus.
25. Mating also occurs at least occasionally elsewhere, where males also assault females without courtship.
26. Epandrium only.
27. Epandrium/sternite 4.
28. Surstyli only.
29. 'external male genitalia … rarely used [to distinguish species] because other more easily accessible taxonomic characters are present' (Foote & Blanc, 1963, p. 4).
30. Males stay on their territories, so their ability to harass females may be limited.
31. Epandrium and surstyli/aedeagus.
32. Epandrium/aedeagus.
33. Page with drawing was missing.
34. Genital capsule/sternite 7/sternites 5, 6, 8.
35. Genitalia/sternites 7 and 8.
36. Both genital capsule and sternite 7.
37. Genitalia/tergite 7; authors used traits that require 'a minimum of effort in preparation', thus presumably discriminating against genitalia.
38. Genitalia/tergite 7/tergite 8 and sternite 8; authors used traits that require 'a minimum of effort in preparation', thus presumably discriminating against genitalia.
39. Genitalia/sterna 5–8.
40. The complexity of drawings of genitalia of a single species suggests that genitalia are probably species-specific.
41. Mating seen did not occur as female emerged.
42. Females also mate away from emergal site, but the context is unknown.
43. Mating occurs at probable hibernating sites for females, perhaps elsewhere also.
44. Males of other species are potential food for the female; the males of this group respond to conspecific females when they emit signals to lure males of other species; '... the aedeagi of all *Photuris* so far examined are practically identical ...' (McDermott, 1964).
45. Parameres only.
46. Parameres/internal sac.
47. Author made direct statement to this effect.
48. '… the male genitalia differ between the species of each group only in minor detail (Hopping, 1963*a*).
49. In some species, but not others, male territory is not in area where oviposition occurs (E. Rojas, unpublished observations, W.G.E.).
50. Superior abdominal appendages.
51. Contrary to statements by Alexander *et al.* (1997) regarding forced copulation in acridids, 'There is no evidence for forced copulation, and if a female does not curve her abdomen downward, the mounting is quickly terminated [without copulation]' (Greenfield, 1997, p. 76).
52. '… genitalia are not species-specific in our taxa …'
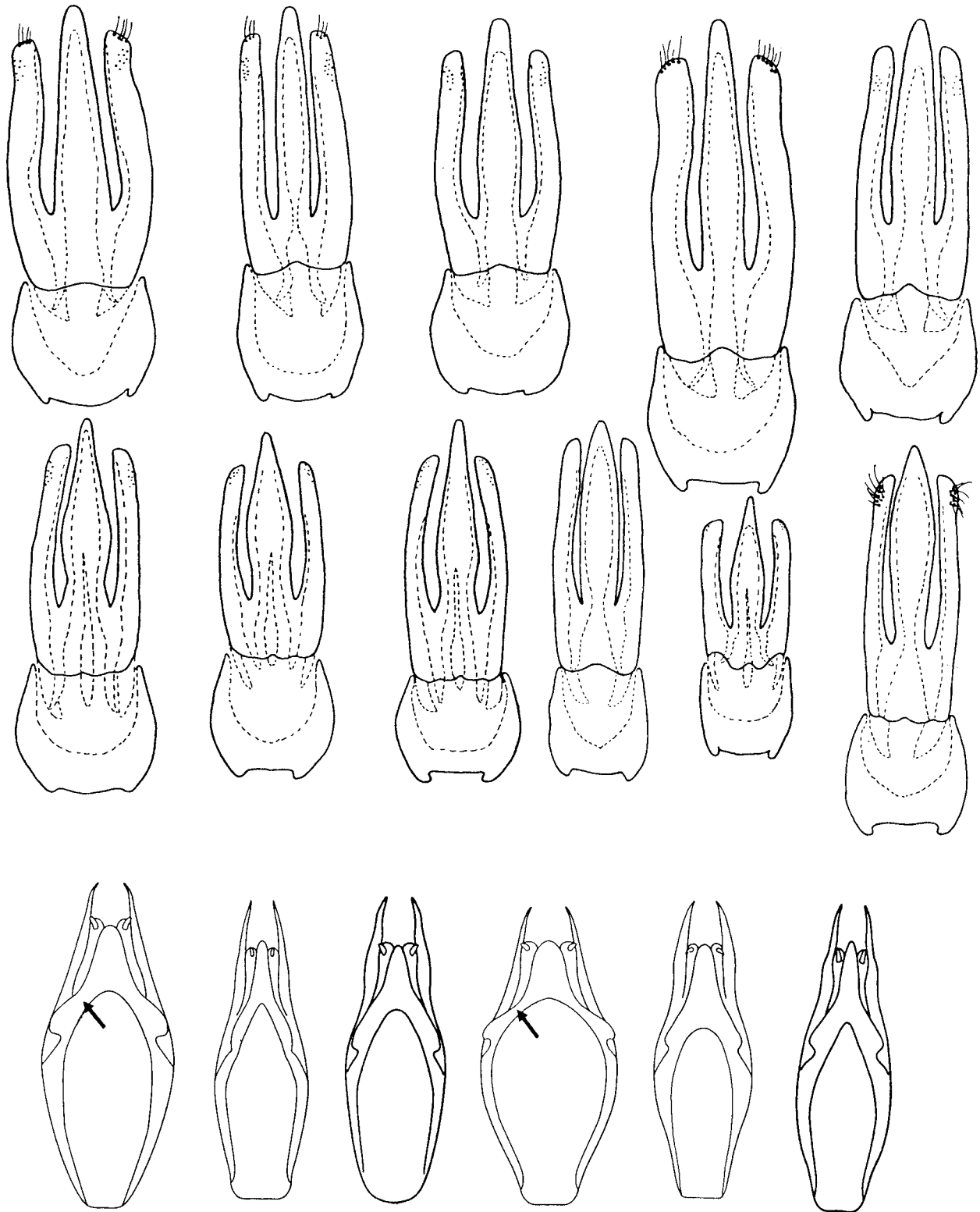
Fig. 1. Very simple male genitalia which show very small differences between species of the beetle genus *Selenodon* (Cebrionidae) (upper two rows), and the parasitoid wasp genus *Trichogramma* (Trichogrammatidae) (lower row). Despite the very small differences, distinctions between species in both of these genera rely heavily on male genitalia (arrows mark a trait used to distinguish two species) (from Pinto, 1998; Galley, 1999) (drawn to different scales).
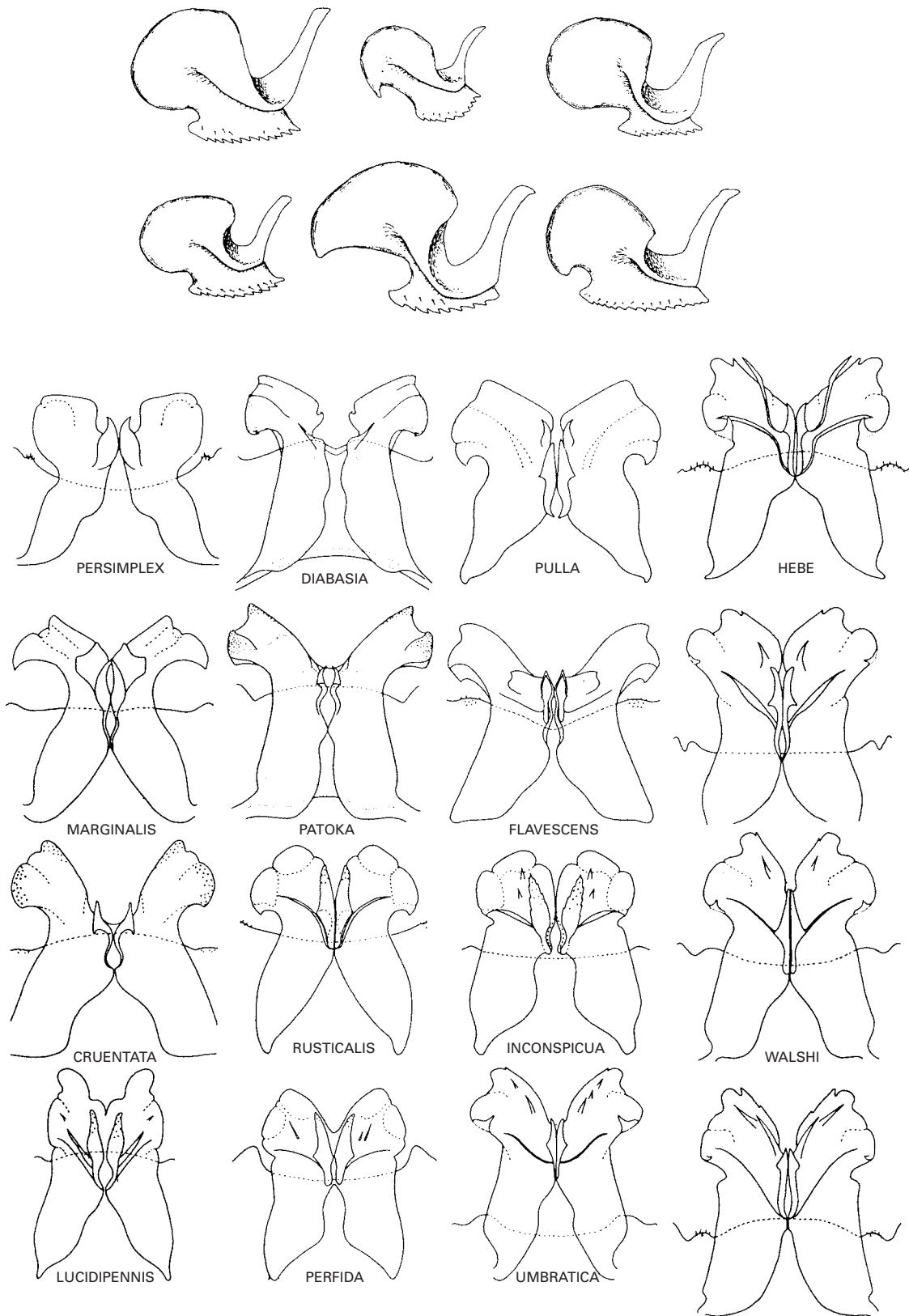
Fig. 2. Simple male genitalia with small interspecific differences in the ant genus *Pheidole* (upper two rows) and the mayfly genus *Hexagenia* (below) (from Burks, 1953; Ogata, 1982) (drawn to different scales).
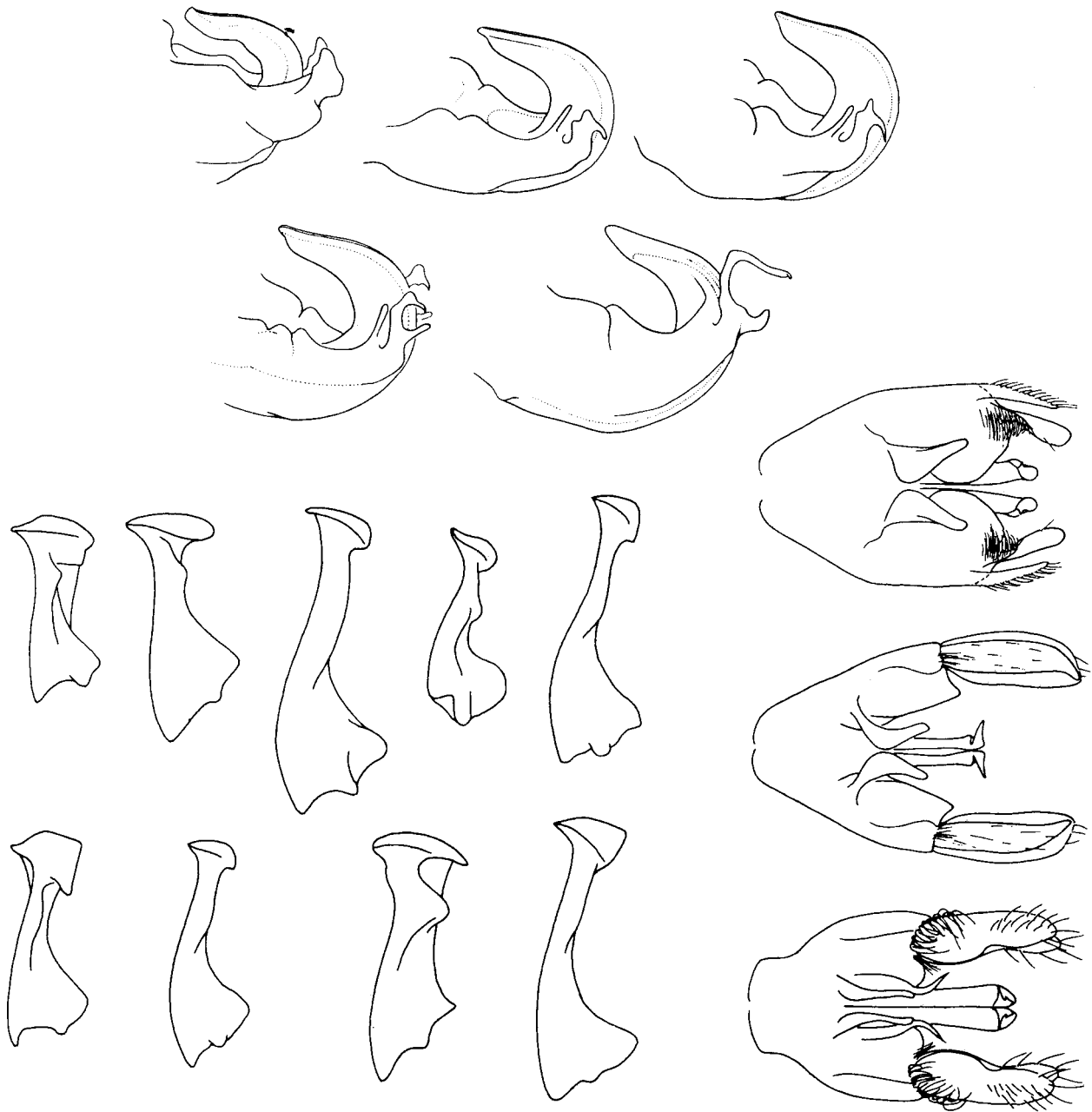
Fig. 3. Moderately complex male genitalia with clear interspecific differences in the cricket genus *Tremellia* (above), the beetle genus *Melolontha* (lower left), and the mud dauber wasp genus *Trypoxylon* (lower right). Females of the cricket and the beetle are protected from male harassment (male crickets attract females with songs; males of the beetles are attracted by female-produced pheromones). Females of the wasp may be subject to harassment by males, which in some species inhabit nests where females provision their young (from, respectively, Matthews, 1983; Otte, Alexander & Cade, 1987; Baraud, 1992) (drawn to different scales).

Clasping is expected to be sometimes potentially non-conflictive in species with protected females, when it serves to position male and female genitalia to facilitate intromission and sperm transfer. It is also expected to be potentially conflictive in some species with protected females, when the cost to the female of being held for longer than is ideal for her is greater than the indirect benefit she obtains from having sons better able to hold females. Conditions in which

male–female conflict over clasping is less likely are common. Of the 40 cases of clasping, copulation lasted only seconds or minutes in 10 (40 % of the species in which copulation duration was determined). Male genitalic structures clasped soft, apparently unresisting female structures in 18 (56 % of the species in which this variable was determined).

These frequencies do not take into account possible inflation of the sample by counting the same structures of
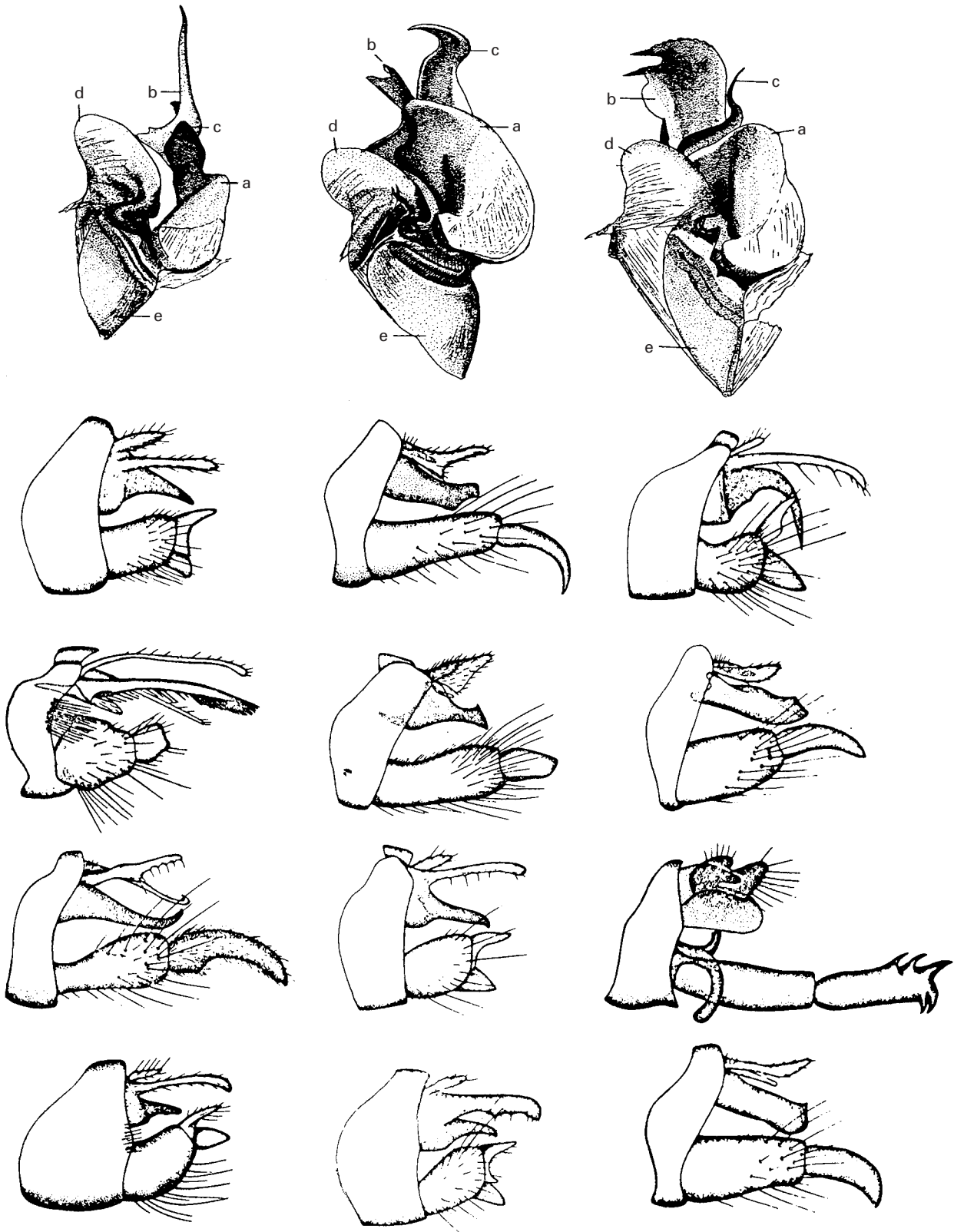
Fig. 4. Complex male genitalia, which show clear differences between species, in the cockroach genus *Periplaneta* (upper row) and the caddisfly genus *Apantania* (below). In both these genera males depend on long-distance attractant pheromones released by the female to encounter females, so females are presumably highly protected from male harassment. Male genitalia of different species are in some cases so different that it is not easy even to recognize homologous structures in different species of the same genus (labelled with the same letters in the cockroaches) (from Malicky, 1983; Walker, 1922).
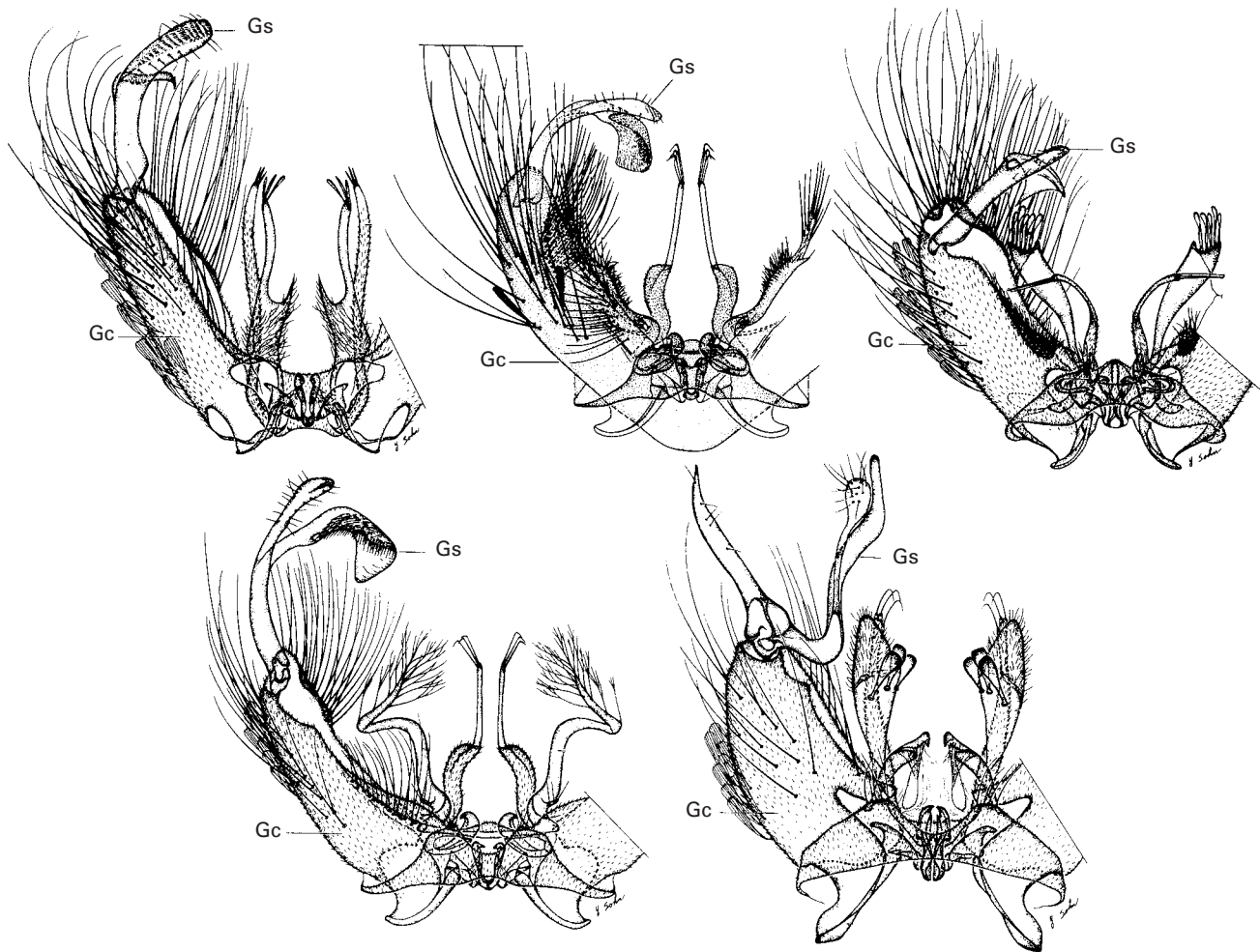
Fig. 5. Very complex male genitalia with clear interspecific differences within the mosquito subgenus *Paraedes* of the genus *Aedes*. Some homologous structures are labeled. The claspers (Gs – gonostyli) are used by male mosquitoes to hold the female abdomen (Rao & Russell, 1938; Spielman, 1964) (from Reinert, 1981).

several closely related species. If the data are re-analysed to reduce this possible effect, by taking families instead of species as the taxonomic units, the frequencies are only slightly affected. There are 85 attributed functions in 22 families, of which 52.9 % facilitate deeper penetration and sperm transfer, and 32.9 % clasping. The evolutionary flexibility of function in dipteran genitalia (Wood, 1991; Sinclair, Cumming & Wood, 1994; Cumming, Sinclair & Wood, 1995; Lachmann, 1996) imply that this correction is conservative. In sum, male genitalic functions that are potentially 'non-conflictive' when females are protected are clearly common in Diptera.

(2) Comparisons of groups with protected and unprotected females

(a) Totals of genus-by-genus counts

Comparisons of genitalic evolution between insect genera in which females are protected from male harassment (Tables 2 and 3) and those in which females are not protected (Table 4) did not conform to the new arms race predictions. The totals for all insects (in 113 families and 10 orders, not counting ditrysian moths) showed a weakly significant trend, but in the direction opposite to that predicted by new arms race models: of the 223 genera in which females are relatively protected from male harassment and in which male genitalic differences could be evaluated, male genitalia differed among congeneric species in 74.9 % (this count includes all genera with 'N' and 'N?' in Tables 2–4); the corresponding number for 105 genera with unprotected females is 62.9 % ($\chi^2 = 4.46$, d.f. $= 1$, $P = 0.03$). Adding the spider data (Table 5) did not change this conclusion (Fig. 6), other than lowering the statistical significance: the grand totals are 75.4 % of 236 genera with protected females, and 68.8 % of 125 genera with unprotected females ($\chi^2 = 1.82$, d.f. $= 1$, $P = 0.17$).

One possible source of bias in these data stems from the likelihood that because of the usefulness of genitalia in other taxa, some taxonomists used genitalia to characterize species even in groups in which they have not diverged particularly rapidly (e.g. Hausmann, 1999; Huber, in press). This could lead to overestimates of the frequency of relatively rapid

genitalic divergence. One way to compensate for this possible bias is to reclassify those groups that had only relatively small or subtle differences (Figs 1 and 2) as lacking differences between species. Because it is not possible to decide on appropriate quantifications of differences (see Section II), I performed two different reclassifications: (A) the 21 genera with 'very small' differences were reclassified as 'no difference'; (B) the 43 genera with either 'very small' or 'small' differences were reclassified as 'no difference'. The results were similar, and neither revealed the trend predicted by new arms race models. Both continued to show insignificant trends in the opposite direction to that predicted – (Fig. 6). In A, 68.2% of 236 genera with protected females showed species-specific genitalic differences while 65.6% of 125 with unprotected females lacked such differences ($\chi^2 = 0.26$, d.f. = 1, $P = 0.61$). Corresponding values using criterion B were 61.4% of the 236 protected genera, and in 60.8% of the 125 unprotected genera ($\chi^2 = 0.01$, d.f. = 1, $P = 0.91$).

These reclassifications of genera are probably overly radical. For instance, in several genera in the beetle families Lampyridae (fireflies) and Cebrionidae (all with protected females), genitalic differences between species are very small (Fig. 1), but taxonomists nevertheless stated clearly that the genitalic differences, small as they were, were the best characters available: '... for many species, determination depends largely on aedeagal differences' (McDermott, 1964; p. 14 on several lampyrid genera); '... in general, the aedeagus defines species groups, as well as diagnosing individual species' (Galley, 1999, p. 6 on the cebrionid genus *Selonodon*).

A second source of uncertainty concerns the 35 genera in which genitalia were not mentioned, and there was no clear statement by the taxonomist regarding their possible value ('no mention' in Tables 2–4). Because genitalia are widely known often to provide useful characters, their omission in some groups could seem to imply that they were checked and found not to vary between species in these groups. It is also possible, however, that failure to use male genitalia in such groups was not due to lack of rapid divergent evolution, but to lack of study. The history of studies in several groups show that this sometimes occurs. Early works on several groups included no mention of male genitalia, but genitalia were nevertheless later found to have complex and highly species-specific structures (contrast Aldrich, 1906 and Kessel, 1963 with Kessel & Maggioncalda, 1968 on the platypezid fly genus *Calotarsa*; Sack, 1935 with Thompson, 1981, 1991, and 1997 on several genera of syrphid flies; Hennig, 1945 with Byun *et al.*, 1998 on several genera of platystomatid flies; Hendel, 1927 with Han & Wang, 1997 on tephritid flies; Howden, 1973 with Gérnier & Howden, 1999 on *Onthophagus* beetles). One way to compensate for this problem is to omit all genera for which there was no mention of genitalia. Recalculating the totals after omitting the 'no mention' genera, there was still no significant trend (Fig. 6). Male genitalia were species-specific in 79.5% of the 224 remaining genera with protected females, and in 84.3% of the remaining 102 genera with unprotected females ($\chi^2 = 1.07$, d.f. = 1, $P = 0.30$). Discarding genera in which genitalia were not mentioned was undoubtedly overly drastic, because consultation with expert taxonomists showed that some groups in which genitalia were not mentioned in taxonomic works do indeed lack species-specific differences (e.g. ichneumonid wasps, which had genera with both protected and unprotected females, I. Gauld, personal communication).

Another possible problem is that it is possible that the sample of genera may have been unconsciously biased against the new arms race hypothesis by more thorough searches for data on mating behaviour and genitalia in some taxa than others. The data on Diptera give one test of this suggestion, because I was both more rigid and more thorough and successful in tracking down every taxon that was mentioned in the literature on mating behaviour. The data from Diptera again give no sign of the predicted trend. Genitalia were species-specific in 82.3% of 79 genera with protected females, and 72.7% of 44 genera with unprotected females ($\chi^2 = 1.55$, d.f. = 1, $P = 0.21$). The corresponding numbers when those genera of Diptera with 'small' and 'very small' genitalic differences are reclassified as lacking differences are, respectively, 79.7% and 68.2% ($\chi^2 = 2.05$, d.f. = 1, $P = 0.15$). A further test for the effects of an unconscious bias is to adhere more strictly to the original list compiled from the behavioural literature, and to delete all species that were included either because I happened to have personal knowledge of their mating behaviour and from those groups (Enicocephalidae, Gryllidae, and Trichoptera) in which I decided to make a more thorough literature search (these genera are marked with '$' in Tables 2–4). The new totals show the same lack of the trend predicted by new arms race models: 73.5% of 196 genera with protected females have species-specific genitalia, compared with 70.4% of 98 genera with unprotected females (Fig. 6) ($\chi^2 = 0.31$, d.f. = 1, $P = 0.58$).

One further possible problem is related to phylogenetic inertia. Perhaps the sample was biased against the new arms race predictions by the inclusion of large numbers of related genera that happened to have particular combinations of traits (e.g. protected females and species-specific male genitalia) only because their common ancestors had these combinations. The lack of phylogenetic trees for most groups precludes making a formal test of this possible phylogenetic effect. Nevertheless, one can make a preliminary test of possible bias by collapsing data from related genera together, and repeating the analysis using families as the taxonomic units. This is an extremely conservative test, given the evolutionary lability of genitalic morphology and mating systems. The results again failed to conform to the predictions of the new arms race models. When spider and insect data were combined, and ditrysian moths were counted as a single family (they actually include closer to 100 families), there were 80 families with protected females and 66 with unprotected females. Of these, 26 had both protected and unprotected species (again indicating that mating systems are evolutionarily flexible). Of the remaining 54 families that had only protected females (marked with '*' in Tables 2, 3 and 5), in 7.4% the genitalia were not species-specific ('N', 'N?', and 'no mention' were counted as not species-specific); while of 40 families with only unprotected females (also marked with '*' in Tables 4 and 5), this number was 22.5%. This difference is weakly significant ($\chi^2 = 4.39$, d.f. = 1, $P = 0.037$), but the trend is again opposite

Table 5. Genera of araneoid spiders with and without giant females and dwarf males (from Hormiga *et al.*, 2000), and use of male genitalia to distinguish congeneric species. Letters in parentheses following genus names indicate separate evolutionary origins of male dwarfism and female gigantism according to Hormiga *et al.* (2000), except for *Allocyclosa* (see footnote 8). Families without genera with dwarf males are marked with '*'. 'med.'=medium

	Dwarf males or giant females?	Differences between congeneric species	Genitalia: Degree of complexity	References
Theridiidae				
Latrodectus[1] (A)	Yes	No/small	Med. simple	Levi (1967, 1983*a*)
Steatoda	No	Clear	Med.	Levi (1967), Knoflach (1996), Hann (1994)
Tidarren (B)	Yes	Clear[2]	Med. complex	Levi (1955), Knoflach & van Harten (2000)
Nesticidae				
Nesticus	No	Very clear	Complex	Kaston (1948), Hedin (1997), Huber (1993)
Linyphiidae				
Linyphia	No[3]	Clear	Complex	Kaston (1948)
Pimoa	No	Clear	Complex	Hormiga (1994)
Theridiosomatidae				
Theridiosoma	No	Very clear	Complex	Coddington (1986)
Tetragnathidae				
Azilia	No	Clear[4]	Med. simple	Levi (1980)
Dolichognatha	No	Clear[5]	Med. simple	Levi (1981)
Nephila (C)	Yes	Small[6]	Med. simple	Levi (1980), Schult & Sellenschlo (1983), Levi & Eickstedt (1989)
Other Tetragnathidae (e.g. *Tetragnatha*)	No	Med. clear	Simple	Levi (1981)
Araneidae				
Chorizopes	No	Clear[4]	Med. complex	Levi (1964)
Witica (D)	Yes	Clear	Med.	Levi (1986)
Mecynogea	No	Clear	Complex	Levi (1980, 1997)
Cyrtophora (E)	Yes	Clear	Med. complex	Levi (1997)
Neogea (E)	Yes	Clear	Med.	Levi (1983*b*)
Argiope (E)	Yes	Very clear	Complex	Levi (1983*b*)
Gea	No	Very clear	Complex	Levi (1983*b*)
Mastophora (F)	Yes	Small[7]	Med. simple	Gertsch (1955), Eberhard (1980), H. W. Levi (in prep.)
Hypognatha	No	Very clear[5]	Very complex	Levi (1996)
Xylethrus (G)	Yes	Clear	Med. complex	Levi (1996)
Chaetacis	No	Med. clear	Med.	Levi (1978, 1985)
Micrathena	No	Med. clear	Med.	Levi (1978, 1985)
Gasteracantha (H)	Yes	Clear	Med. simple	Levi (1996), Emerit (1973)
Isoxya	Yes	Clear	Simple	Emerit (1973)
Scoloderus	No	Clear[4]	Med. complex	Levi (1976)
Acanthepeira	No	Clear	Med. complex	Levi (1976)
Other Araneinae (e.g. *Araneus*)	No	Clear	Complex	Levi (1971, 1988, 1991, 1996), Harrod *et al.* (1990)
Zygiella	No	Very clear	Complex	Gertsch (1964), Levi (1974)
Metepeira	No	Med. clear	Med. complex	Levi (1977), Piel (2001)
Kaira (I)	Yes	Clear	Complex	Levi (1993)
Cyclosa	No	Clear	Med. complex	Levi (1999)
Allocyclosa (J)	Yes	Clear[8]	Med.	Levi (1999)

1. No data were presented on dimorphism *per se*, but '... the black widow spiders (Theridiidae, *Latrodectus*) probably represent an additional case of female gigantism ...' (Hormiga *et al.*, 2000, p. 442).
2. Conductor and embolus differ only slightly, but cymbium 'differs considerably'.
3. Males are subequal in size, and sometimes cohabit with females for extended periods during which they may reduce her prey capture (see Rovner, 1968).
4. Genitalia of only one species were drawn, but genitalic traits were mentioned in the text that distinguish species.
5. Male genitalia are especially diagnostic.
6. Contrary to new arms race predictions, the conductor, which in *N. plumipes* has the potentially conflictive function of a hold-fast device (Elgar *et al.*, 2000), is not particularly elaborate or species-specific in this genus (references in Table 5, plus Uhl & Vollrath, 1998). Nevertheless, indirect evidence regarding the mesh of male genitalia with those of the female suggests that the conductor may not be introduced into the female's insemination duct, where it can become lodged, in some other species (Schult & Sellenschlo, 1983), and in some species a different male sclerite, the embolus, sometimes breaks off within the female (Schult & Sellenschlo, 1983; Uhl & Vollrath, 1998). Further data on genitalic functions in this genus would be interesting.
7. 'The palpi of different species are surprisingly similar and the males present a challenge to determine' (H. W. Levi., in prep.).
8. *Allocyclosa* is a monospecific genus previously included in *Cyclosa*; its genitalia differ from those of other *Cyclosa* species (Levi, 1999).
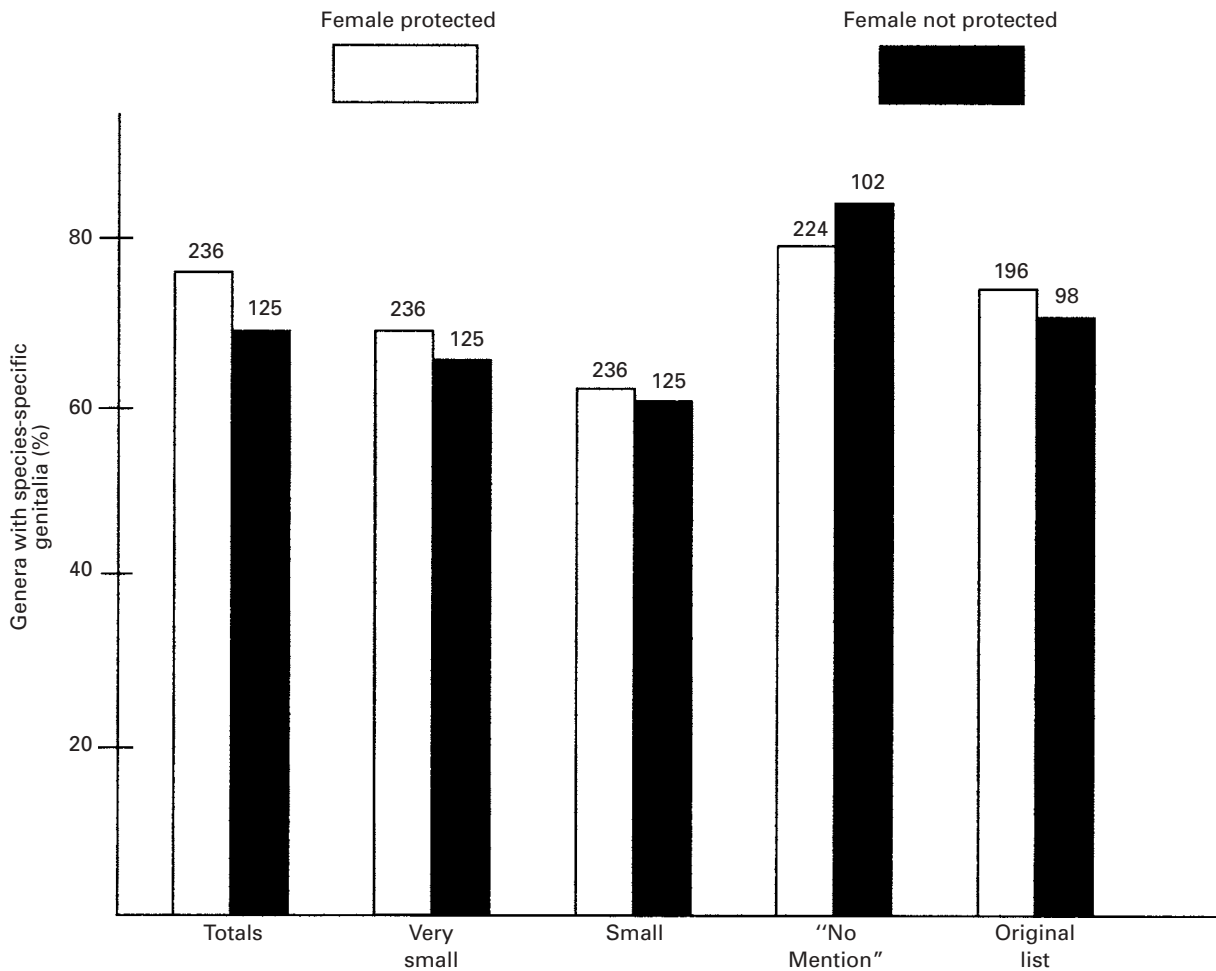
Fig. 6. Proportions of genera in which male genitalia are species-specific in groups with protected and unprotected females. 'Totals' – grand totals combining all genera of insects and spiders; 'Very small' – totals after reclassifying all groups with 'very small' interspecific differences in male genitalia as 'no difference'; 'Small' – totals after reclassifying all groups with either 'small' or 'very small' interspecific differences in male genitalia as 'no difference'; 'No mention' – totals after omitting all groups in which no mention was made of genitalia; 'Original list' – totals after omitting all groups that were added to original list of genera compiled from reviews of mating behaviour. In no case is the difference between groups with protected and unprotected females statistically significant.

to that predicted by the new arms race models. When these data were adjusted as discussed above to correct for possible biases, they still did not fit the new arms race predictions. When families with 'very small' differences were counted as no difference, the percentages for families in which females were and were not protected were, respectively, 20.4 % ($N=54$) and 27.5 % ($N=40$); and when both 'very small' and 'small' were counted as no difference, they were 24.1 % ($N=54$) and 35.0 % ($N=40$). When families with 'no mention' were omitted, the percentages of families without species-specific male genitalia were 5.7 % of 53 and 13.9 % of 36 groups which had, respectively, protected and unprotected females (none of these differences are statistically significant).

Data from ditrysian moths (the majority of species in Lepidoptera) were largely omitted from the preceding analyses because their uniform mating behaviour does not warrant genus-by-genus analyses. They represent a massive

trend in opposition to the new arms race predictions, and their inclusion in the numerical analyses just reported would push the numbers even more strongly away from the new arms race predictions. Females of this very large group (approximately 250 000 species) seem uniformly safe from unwanted male attentions, because male–female encounters seldom if ever occur unless females release long-distance attractant pheromones to attract males. The uniformity of female pheromone composition and their glandular origin throughout ditrysian moths '… is strongly suggestive of a monophyletic system that has undergone relatively little change during the evolutionary history of the over 100 moth families included in this group' (Phelan, 1997). Even in the few exceptions, in which males rather than females call pheromonally (Phelan, 1997), females appear to be protected from unwanted encounters with males. It is equally clear that, contrary to the new arms race predictions, male genitalia in the large majority of moths are highly elaborate

and species-specific in form, as shown in compendia reviewing thousands of species in the North American and Palaearctic fauna (Dominick *et al.*, 1971–1998; Amsel, Gregor & Reisser, 1965–2000; Forster & Wohlfahrt, 1952–1981; and Huemer, Karsholt & Lyneborg, 1996).

(*b*) *Analyses at higher taxonomic levels*

Analyses at higher taxonomic levels allow inclusion of more details of behaviour and natural history, and thus offer tests that are in some respects stronger. One group in which lack of support for the new arms race predictions is particularly clear is the family of non-biting midges, Chironomidae. Natural history and behaviour data have been summarized by Thienemann (1954) and Oliver (1971) for this large family of >5000 species [there are more than 400 species in Britain (Pinder, 1978), and up to several hundred species in a single stream in Costa Rica – C. De La Rosa, personal communication]. Several aspects of the relatively uniform natural history of adult chironomids imply especially strong protection of females from male harassment. Males and females are relatively short-lived, and usually do not feed. Immature stages occur under water, and adults emerge at the water surface from aquatic pupae, and fly to terrestrial resting sites where egg development is completed. Males usually form swarms over markers such as light-colored stones, trees, haystacks, etc. at particular times of the day. Females oviposit on the surface of water away from swarm sites. The localized nature of swarms, the arbitrary sites of swarm markers with respect to female oviposition sites, and the special 'offering flights' of females ready to mate (Gibson, 1945; Syrjämäki, 1964, 1966; Downes, 1969) all indicate that females are relatively well protected, except in the few cases in which males search out emerging females (Table 4). Males in swarms are attracted only at close range to the flight sound of females. Copulation is initiated without apparent preliminaries only when the female enters the swarm, and generally lasts only a few seconds (Syrjämäki 1965, 1966; Hilsenhoff, 1966; Downes, 1969; Oliver, 1971; Paasivirta, 1972; Downe & Caspary, 1973; Neems, Lazarus & Mclachlan, 1992), or at most a few minutes (Gibson, 1945; Syrjämäki, 1966). The pair typically drops or flies away from the swarm (Edwards, 1929; Gibson, 1945; Syrjämäki, 1965, 1966, 1968; Hilsenhoff, 1966; Young, 1969; Neems *et al.*, 1992). So further male harassment is not possible. Male claspers (gonocoxa, gonostylus) clearly function in chironomids (as in other related nematocerans), to clasp the female externally. Due to the very brief copulations, conflict with respect to the possible male genitalic clasper function of retaining females for extended periods seems especially unlikely. Nevertheless, chironomids, with only a few exceptions (Lindeberg, 1963, 1967) are characterized by clear differences in genitalic claspers, even among closely related species (Table 2). These differences are so general, and so important in distinguishing species, that a guide to the chironomids of Britain (Pinder, 1978) basically consists of a compendium of beautiful figures of male genitalic claspers.

The biting midges (Ceratopogonidae) also generally mate in male swarms (Downes, 1955, 1969). Swarms are not usually associated with oviposition or feeding sites (although there are exceptions – see Glukhova & Dubrovskaya, 1974); copulation is not especially long (Downes, 1955; Linley & Adams, 1972); females are apparently free to escape after a single copulation (Downes, 1955; Linley & Adams, 1972); and in some species it is clear that females actively seek out swarm markers (Downes, 1955) rather than flying into them by chance. Nevertheless ceratopogonids have divergent, species-specific clasping male genitalia in many groups (Table 2). These midges offer an opportunity to test for the effects of morphological male–female conflict at a second taxonomic level. In contrast to chironomids, female ceratopogonids generally require a protein meal to mature their eggs. The six tribes in the subfamily Ceratopogodinae whose natural history is known have contrasting behaviour that leads to contrasting predictions by the new arms race models. In three relatively derived tribes (Heteromyiini, Sphaeromiini, Palpomyiini) (Downes, 1978) females regularly cannibalize the relatively small males during copulation, and in several genera the genitalia of a cannibalized male remain attached to the female, thus presumably preventing her from remating at least temporarily (the male's genitalia must eventually be dislodged for the female to oviposit). Females and males may be in conflict if females attempt to prey on males without copulating, or if they attempt to avoid being plugged by the male following copulation. The situation with respect to plugging may resemble the male-inflicted damage models of Johnstone and Keller (2000). In the other three, more basal tribes, females never (Culicoidini) or seldom (Ceratopogoniini, Stilobezzini) have their genitalia plugged by male genitalia (Downes, 1978). In some of these (Culicoidini) females remate (Linley & Adams, 1972). The probability of male–female conflict in the cannibalistic ceratopogonines thus seems higher; but they did not show a trend to have more diverse or complex genitalia than the others (Tables 2 and 4). In fact, the one ceratopogonid genus in which male genitalia are clearly not species-specific (*Probezzia*) is one in which both cannibalism and plugging regularly occur (Downes, 1978), contrary to the predictions of the new arms race models.

Still another indication of a lack of new arms races in biting midges comes from the morphological mesh between male and female genitalia. In most species, the male genitalic claspers (gonocoxae and gonostyli) grasp the female's eighth abdominal segment. In the tribes with genitalic plugs, the female's sternite, instead of having potential resistance structures, such as erectible spines that could make it more difficult for the male genitalia to hold on to the female, often has an indentation or invagination that seems designed to aid rather than impede males: the indentation 'in many species of these three tribes … probably serves to anchor the claspers' (Downes, 1978, p. 51). The relatively simple mechanical action of male clasper organs, and Downes' access to specimens killed while still coupled lend weight to his assessment of the lack of female resistance structures (for another apparently selectively cooperative female structure in a different group of flies, see footnote 3 of Table 1).

Females of firefly beetles (Lampyridae) are also generally extremely protected from male harassment, because males cannot find a female unless she produces flashes of light in

response to male flashes. Nevertheless, male genitalia are often species-specific in form (Table 3), and a close examination of an exceptional case shows a trend opposite to that predicted by the new arms race models. The genus *Photuris* is unusual among fireflies in that males can sometimes encounter females that have not given overt signs of willingness to mate. Female *Photuris* prey on males of other species by responding to their flashes, and male *Photuris* sometimes trick these 'femme fatale' females by emitting the flash patterns of the prey species (Lloyd, 1997). But instead of having unusually distinctive male genitalia compared with other lampyrids in which females are more protected, the male genitalia of *Photuris* are unusual in being especially uniform (McDermott & Buck, 1959; McDermott, 1964; Lloyd, 1997).

One group, bugs in the small family Eniocecephalidae, appears to conform to new arms race predictions. They are very unusual among Heteroptera in forming mating swarms (apparently a primitive trait for this family – Wygodzinsky & Schmidt, 1991; Štys, 1981, 1995), and also in having highly reduced and simple male genitalia with few or no species-specific traits (Wygodzinsky & Schmidt, 1991) (see Schuh & Slater, 1995 for other Heteroptera). It is not clear, however, whether variation within this family is in accord with new arms race predictions. Swarming may occur throughout the less derived subfamily Aenictopecheinae (only a few species have been observed), and the male genitalia in this group are relatively simple (Wygodzinski & Schmidt, 1991). In four genera of the more derived Eniocephalinae and Alienatinae, females are wingless, thus indicating that males are able to encounter females by other means (it is not known whether or not the wingless females attract males chemically from a distance). Male genitalia in these groups are even more reduced (phallus lost, parameres fused) and less distinct (Wygodzinsky & Schmidt, 1991). A crucial missing piece of evidence is whether females mate more than once. If they are monandrous, then both the male–female conflict and the traditional female choice hypotheses predict simple, only slowly evolving male genitalia (Eberhard, 1985*a*; Arnqvist, 1998).

IV. DISCUSSION

(1) Genitalic functions in Diptera

Clasping the female and interacting with her internal structures so as to promote intromission and insemination appear to predominate strongly over other functions of male genitalia in Diptera; their combined total was 85.7 % of the functions documented in Table 1. This impression is probably somewhat misleading, however. These two functions are particularly easy to deduce from observations of the positions of genitalic structures. Clasping on the outside of the female is especially easy to document, because it does not require dissections or sections of copulating pairs. In addition, researchers have probably been predisposed to look for these two functions compared with others. Functions such as stimulation of the female are much more difficult to deduce, especially when only dead animals are

observed (as in most studies to date), and when the structures are hidden from view (see Eberhard & Huber, 1998 for an especially clear example of this problem; indirect evidence strongly suggested some internal movements which could not be confirmed directly).

Thus, little weight can be attached to the particular numerical values in Table 1. Nevertheless these data are important, because they demonstrate that clasping and penetration functions are common. These particular functions are among those over which male–female conflict should be reduced or absent in species in which females are protected from male harassment (see Section II). In addition, the evolution of male clasping structures in Diptera is typical of genitalia in general, in that the clasping structures show great diversity (Wood, 1991; Sinclair *et al.*, 1994; Cumming *et al.*, 1995). Even within the suborder Nematocera, design features show that clasping involves a variety of different structures in different groups: clasping by closing the gonostyli against each other, against extensions of the gonocoxae, against the epandrium, against the cerci, against the parameres, and even against other processes of the same gonostylus (Wood, 1991) (see Fig. 5). Structures that are apparently homologous with the clasping gonostylus and gonocoxa of lower Diptera also occur in related orders (Hymenoptera, Trichoptera, Lepidoptera, and Mecoptera: Wood, 1991), and genitalic structures that grasp the female also occur in more distantly related groups such as Ephemeroptera (e.g. Edmunds *et al.*, 1976) and Odonata (e.g. Corbet, 1999). It is thus clear that clasping is a common genitalic function in insects.

The general importance of the conclusion that these potentially 'non-conflictive' functions are common for the arguments herein is that it implies that the tests of the new arms race predictions in the second part of this study are realistic. Genitalic functions over which there might be male–female conflict in species with unprotected females, but not in species with protected females, are common in Diptera. By extension, unless this order is atypical, they are also common in other insects and spiders. Therefore it was reasonable to expect to be able to find differences in genitalic species-specificity between groups with protected and unprotected females, if the new arms race models are correct.

One additional point concerns the probability that some 'claspers' are used to stimulate the female rather than to restrain her. For instance, male genitalic surstyli of some sepsid flies clearly grasp the female tightly, and early observations of dead animals led to the conclusion that the surstyli function to hold the female to allow intromission (Eberhard & Pereira, 1996). More detailed observations of living animals, and of animals frozen at the moment just before intromission showed, however, that this conclusion was wrong: the male surstyli of some sepsids do not clasp the female until after intromission has occurred (Eberhard, 2002*a*); and once they clasp the female, they deliver complex, rhythmic patterns of squeezes that appear designed to stimulate her (Eberhard, 2001*b*). Rhythmic movements of male 'claspers' during copulation have also been seen in other insects (Squire, 1951 on tse-tse flies; Lorkovic, 1952 on a nymphalid butterfly; Alexander, 1959 on a carabid beetle; K. Brown, personal communication and Tyler *et al.*, 1994

on papilionid butterflies; Lachmann, 1996, 1997 on dung flies; Eberhard, 2001*a* on a sciarid fly). Thus some structures classified as claspers in Table 1 probably function as stimulators. But this alternative, stimulation function does not reduce contradictions with the new arms race models. The new arms race ideas would predict that claspers should not function to stimulate the female, but rather to restrain her mechanically (except in the seemingly unlikely case that genitalic stimulation coerced the female into acting against her own best reproductive interests and reducing the number of her offspring). Thus observations that genitalia are moved rhythmically as if to stimulate females also argue, at least in general, against new arms race interpretations.

(2) Comparisons of groups with protected and unprotected females

(*a*) *Genus-by-genus comparisons*

(*i*) *Totals*

Comparisons between genera with protected and unprotected females failed to show the trend predicted by the new arms race models toward increased species-specificity in those genera in which females are susceptible to unwanted sexual advances by males. The predicted trend failed to emerge when the data were re-analysed in several ways to compensate for possible biases. It is not clear whether any one of these analyses is superior to the others; but none revealed the predicted trend, despite large sample sizes. The massive set of data from ditrysian moths, which was not included in these analyses, would have made the totals even less in accord with the new arms race predictions. Hundreds of genera in this group have both protected females and elaborate, species-specific male genitalia. The general conclusion is that in genera in which females are probably completely or nearly completely safe from unwanted sexual attentions of males during their normal non-sexual activities, males do not have less diverse or species-specific male genitalia as predicted.

The spider data also constitute strong evidence against male–female conflict ideas, because male courtship behaviour in araneoids is usually luring rather than coercive (Robinson & Robinson, 1982; Huber, 1998); in addition, females probably often lure males with pheromones (Tietjen & Rovner, 1982; Pollard, Macnab & Jackson, 1987; Papke, Riechert & Schulz, 2001). This means that, if anything, the data in Table 5 underestimate evidence against the new arms race hypotheses. Many groups should probably be reclassified as having protected females, but male genitalia are nevertheless clearly species-specific in most genera. Spider males in other families also tend to perform luring rather than coercive courtship behaviour, and male genitalia are nevertheless usually especially useful species characters in these groups also (Huber, 1998).

It is possible to save a weakened version of the new arms race ideas from at least some of these contradicting data. As noted in Section I, groups with protected females are expected to have reduced levels of male–female conflict in some but not all aspects of genitalic function during copulation. There are possible male genitalic functions that might still be in conflict with female interests in species with protected females: damage to the female reproductive tract that makes remating less likely or less effective, or facilitates entry of manipulative male seminal products into her body cavity (Wing, 1982; Eberhard, 1993*a*; Crudgington & Siva-Jothy, 2000; Johnstone & Keller, 2000; Blanckenhorn *et al.*, 2002); removal of sperm from previous males (Waage, 1979; Birkhead & Møller, 1998; but see discussion in Section II); and holding the female in copula for longer than is desirable from the female's point of view or to deposit plugs in her genitalia (e.g. to protect her against copulations by other males). If one limits the new arms race ideas, and argues that only these particular genitalic functions have been important in genitalic evolution, then the genitalic differences in groups with protected females do not contradict the theory. This modification of the new arms race ideas represents a substantial weakening of its predictive value, however, and also runs afoul of data from species with species-specific genitalic structures which have other functions (e.g. Tyler *et al.*, 1994; Eberhard, 2001*a*, *b*; Danielsson & Askenmo, 1999; Arnqvist & Danielsson, 1999), and species in which these functions are unlikely (e.g. Chironomidae – see Section III).

Once again, it should be kept in mind that inclusion in the 'protected female' category does *not* necessarily imply a lack of male–female conflict over mating. Rather, it implies that if and when such conflict occurs, it is likely to be due to female resistance whose function is to select among males, rather than to avoid male-imposed costs of copulation to the female's reproductive output, as postulated in new arms race models. It is also important to keep in mind that both new arms race models and traditional sexual selection models predict that other aspects of mating behaviour not considered here can be expected to affect relative rates of genitalic divergence. If females are strictly monogamous, for example, both types of selection will be absent (Eberhard, 1985*a*; Arnqvist, 1998). Sexual selection by female choice also predicts that in some species the behaviour rather than the morphology of male genitalia may diverge rapidly (Eberhard, 1985*a*, 1998*b*).

(*ii*) *Possible limitations of the analyses*

There are several reasons to question whether the data and analyses tested the predictions of the new arms race models appropriately.

(*A*) *Data on genitalia* The taxonomic literature has several potential biases that could result in underestimates of genitalic diversity. As noted above, lack of use of male genitalia by taxonomists to discriminate species in some groups is probably not the result of lack of genitalic differences, but rather to lack of study. Nevertheless, this was probably not a serious problem for the analyses of this study. The conclusions would be affected only if there were a bias toward underestimating rapid genitalic evolution more often in groups with unprotected rather than protected females; I know of no reason to expect such a bias. In addition, an attempt to correct for this problem by omitting all genera for which the data were equivocal ('no mention') did not

change the lack of support for new arms race predictions (Fig. 6).

A second, related limitation is that different parts of the male genitalia often show different degrees of interspecific differences. The taxonomy of tephritid flies illustrates both this and the previous problem (Fig. 7). One might expect that taxonomists would generally use the most distinctive characters available to distinguish species, but this is not always the case. Some studies of tephritids ignore the male genitalia, and use only the complex markings on wings and body to separate species (Foote, 1960; Drew & Hancock, 1995). Some authors explicitly state that possibly useful genitalic characters have been ignored for practical reasons (Foote & Blanc, 1963). Other studies use the more difficult to observe male epandrium, which generally shows only minor differences between species (Fig. 7) (Steyskal, 1977; Condon & Norrbom, 1994; Norrbom, 1997). Still others include the small tip of the aedeagus (the glans), which must be observed with a compound microscope. The glans is moderately to extremely complex, and at least in some groups it is much more divergent than the epandrium (McAlpine & Schneider, 1978; Stoltzfus, 1988; Han & Wang, 1997) (Fig. 7). In some groups in which genitalia are not included in current taxonomic works, such as *Ceratitis* (DeMeyer, 2000), the glans nevertheless shows clear interspecific differences (W. Eberhard, unpublished observatons of *C. capitata*, *rosa*, and *catiorii*). Otherwise cryptic subdivisions in the genus *Blepharoneura* that were revealed by study of the glans were confirmed by molecular analyses (Condon & Steck, 1997). The upshot is that some taxonomic studies of tephritids give underestimates of genitalic divergence.

Another related possible problem involves the likelihood that aspects of genitalic structure that are used by taxonomists to discriminate species are not always the same as those that are important to the females of the species involved. As noted earlier, this same criticism can also be applied to attempts to quantify morphological differences (Arnqvist & Thornhill, 1998; Arnqvist, 1998). For instance, different patterns of movements of morphologically similar genitalia, or the inflation of membranous structures that are difficult to observe in preserved specimens (Flowers, 1999) might be important. The result of this possible bias would probably be data that underestimate the frequency of relatively rapid genitalic divergence. Again there is no reason to suppose that this problem is consistently associated with protected or unprotected females. It is worth noting that previous studies which used techniques similar to those used here to test predictions concerning genitalic evolution succeeded in finding trends (Eberhard, 1985 a; Dixson, 1987; Roig-Alsina, 1993).

A potentially more serious problem is that genitalia are probably included in some species descriptions even when they have not diverged especially rapidly (Hedin, 1997; Hausmann, 1999; Huber, in press). In contrast to the preceding problems, this bias could result in overestimates of rapid genitalic divergence. When I attempted to correct for this possibility by reclassifying all groups in which I judged interspecific differences to be very small, however, there was no change in the general pattern of failure to conform to new arms race predictions. The criterion for

'very small' was, of course arbitrary, but repeating the analysis with the more inclusive 'small' criterion still failed to reveal even a weak trend in the predicted direction. As mentioned above, these corrections were probably overly severe in at least some groups. In some genera with very small genitalic differences between species, taxonomists nevertheless emphasized that they had to rely heavily on genitalia to distinguish species (McDermott, 1964; Galley, 1999) (Fig. 1). I do not wish to make any claims regarding the general importance of my 'small' and 'very small' criteria: it is important to keep in mind that the core data of this study are based on judgements of the highly trained eyes of professional taxonomists.

A related problem is that over-reliance on genitalia in some taxonomic studies could lead to failures to distinguish species in which their genitalia have not diverged especially rapidly. These groups could have cryptic species with identical genitalia. The result would be that genitalia may have evolved less rapidly and may be less distinct between closely related species than the taxonomic literature on these groups would suggest (Eberhard, 1985 a; Huber, in press). An example of this problem is the black widow spider genus *Latrodectus*, where the usual practice in spider taxonomy of emphasizing male and female genitalic traits led to an underestimate of species numbers, and an overestimate of the rapidity of divergence in male genitalia (Levi, 1983 a). It is not feasible to test for this possible bias by simply reclassifying data as above. Nevertheless there are reasons to expect that this problem is probably not especially serious for the tests performed here. In the first place, underestimates of species numbers would only affect the comparative analyses presented above if this kind of mistake was more common in genera with protected females. I see no *a priori* reason to expect such an association. In addition, cryptic species with identical male genitalia should be less common in groups in which taxonomists also routinely use the traits of immature stages to distinguish species. Three such groups which are well represented in this study are chironomid midges, mosquitoes, and mayflies (e.g. Goetghebuer & Lenz, 1936; Carpenter & LaCasse, 1955; Edmunds *et al.*, 1976; Berner & Pescador, 1988). These groups clearly show widespread species-specific male genitalia in genera with protected females (Table 2), contrary to predictions by the new arms race models.

Another possible problem concerns differences among taxonomists in the degree of difference they use for recognizing species. Taxonomists who are lumpers at the species level would presumably tend to recognize species in which the differences among the genitalia were accentuated; lumping at the genus level would have the same effect. Splitters would have opposite effects. I see no way to correct for this problem, but also see no reason to expect that lumpers would tend to work more on genera with protected females. Both this and the preceding problem seem more likely to introduce noise into the analyses, rather than produce consistent biases against the trends predicted by new arms race hypotheses.

(*B*) *Data on mating behaviour* The mating behaviour data also have possible weaknesses. The categorical classification
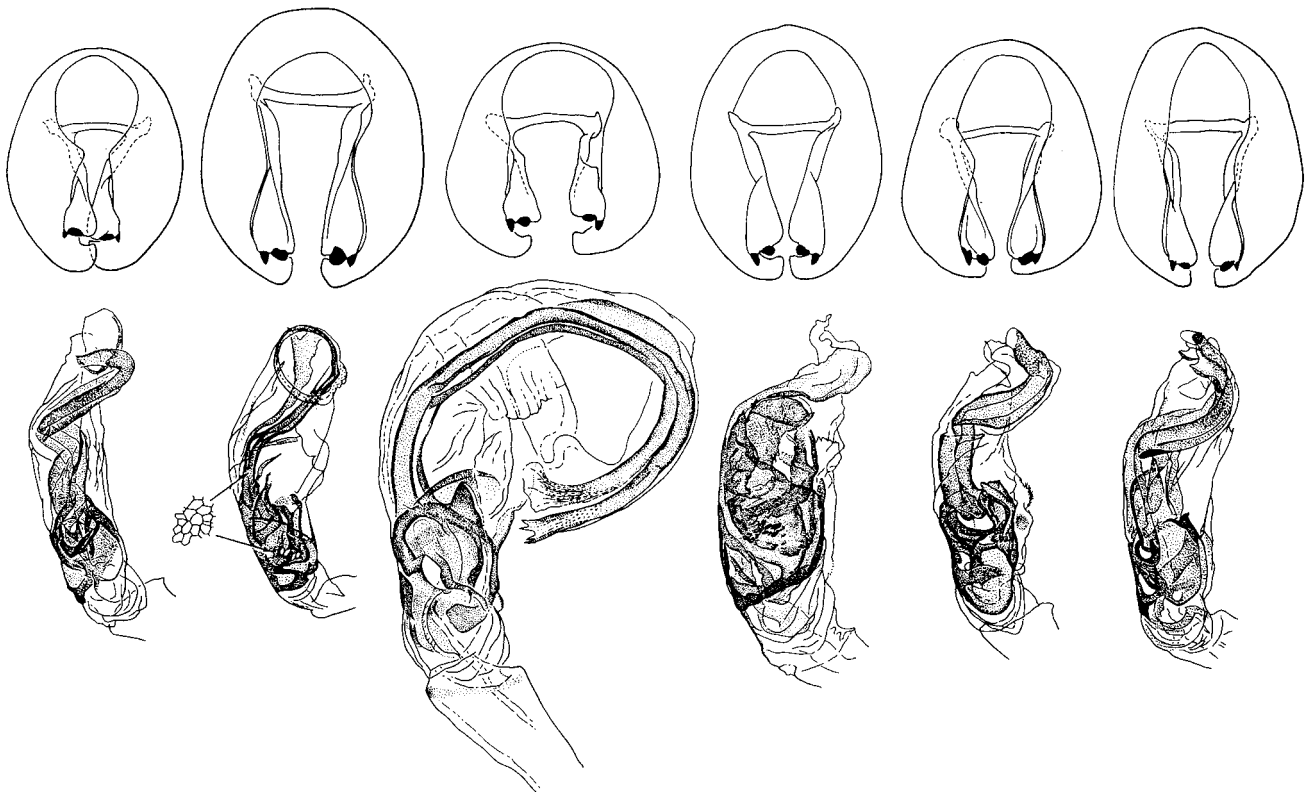
Fig. 7. Different portions of the male genitalia show different degrees of complexity and species-specificity in the six species of the fruit fly genus *Neaspilota* (from Freidberg & Mathis, 1986). For each species the epandrium (upper row) is above the aedeagus tip (lower row). Although aedeagus structure is generally more complex and differs more dramatically, aedeagus structure is not included in many taxonomic studies of tephritids. Thus the lack of use of genitalic structures is not conclusive evidence that they do not differ among congeneric species (drawn to different scales).

of mating behaviour used in Tables 2–4 undoubtedly over-simplifies the behaviour of some groups in which males have alternative mating tactics. In some species of swarming mosquito, for instance, some copulations occur away from swarms (Roth, 1948; Nielsen & Greve, 1950; Nielsen & Nielsen, 1958). It is very probable that alternative male be-havioural tactics have been missed in some species (Evans & O'Neill, 1985). The importance of the problem of alterna-tive male tactics depends on the degree of difference in the coerciveness between primary and alternative mating tactics, and the fraction of male–female interactions involv-ing alternative rather than primary male mating tactics. In some species, alternative male tactics would not change the classification of the species. In the scarabeid *Podischnus agenor*, both major (fighting) and minor (non-fighting) males attract females to feeding burrows (Eberhard, 1977a, 1982). Some other alternative male tactics would involve changes in the categories to which species are assigned, however. For in-stance, males of the medfly *Ceratitis capitata* lure females to mate at leks in the morning, but accost them at oviposition sites in the afternoon (apparently much less often – Eberhard, 2000c). In the sciarid fly *Hybosciara gigantea*, males probably generally mate with females at swarms, but they may also sometimes attempt to mate with them at feeding sites (Eberhard & Flores, 2002). It seems likely that most of the observations on which the classifications were based,

including those species with alternative male tactics, rep-resent the reproductively most important male tactic.

A related problem is that entire genera were typified as having a particular type of mating behaviour, usually on the basis of studies of only one or a few species. An indication of the possible extent of the lack of knowledge is the fact that several genera in which the mating behaviour of especially large numbers of species have been studied had both pro-tected and unprotected females. The expected effects of both typological thinking and of possible ignorance on the analyses performed above will be serious only if there is a systematic bias against the associations predicted by the new arms race hypotheses. I see no *a priori* reason to expect such a bias.

A probably more important bias is that my classification of mating behaviour almost certainly overestimates the likelihood that males can physically coerce females to copulate. Although there are exceptions, probably most male insects and spiders have genitalia whose design pre-cludes their use to forcefully achieve intromission. In most insects, the female must instead spread or open abdominal structures that otherwise cover her external genital opening before intromission can occur (Snodgrass, 1935; Eberhard, 2002a); and in many spiders the female must assume a special acceptance posture or otherwise actively cooperate if mating is to occur (Huber, 1998; also Watson, 1993). The

most probable effect of this bias is to make the tests of new arms race models performed here overly conservative. The females of some of the species which are classified as 'female unprotected' are probably in fact not at risk from unwanted copulations, because the male is unable to force his way into her body. This underestimate of the degree to which females are protected would increase even further the failure of the new arms race predictions in species with protected females (see below).

One could use arguments developed in chase away selection models (Holland & Rice, 1998) to suggest that females of some genera were misclassified as 'protected', when they in fact are at risk of being coercively seduced. For example, 'luring' male courtships may be thought to manipulate females against their best interests if they involve use of effective sensory traps (West-Eberhard, 1984; Ryan, 1990; Christy, 1995). Because of selection in other contexts, the female may respond to stimuli from a male that mimic stimuli that signal, for instance, food or helpless offspring. This idea of antagonistic seduction is unappealing, however, for several reasons. In the first place, it requires that females be very simple automatons. Any variability in female responsiveness, or any female ability to distinguish male signals from the stimuli to which she evolved to respond (triggered by perception of the male's presence, or his failure to mimic the model stimuli perfectly) before she is close enough for the male to be able to seize and mount her would provide the opportunity for selection on females to avoid males when it is advantageous for them to do so. Living animals seldom if ever give such consistent responses. Stated in other words, the fact that males may often use 'sensory traps' in their courtships is not evidence that males can coerce females into acting against their own best interests. Attracting a female's attention with a stimulus like the odour of a flower which she sometimes visits, or a visual cue she uses to find shelter when attacked by a predator, is a far cry from actually obliging her to copulate.

In any case, antagonistic seduction arguments will not work in the many swarming and lekking species in Table 2, in which males are highly localized and their attractant signals (if any) are effective at best over only a short range. Males that await females on hilltops, or swarm over light-coloured stones or tree tops at particular times of day, could not 'trap' a female until she approached closely. Nor can antagonistic seduction explain the many groups in which the female releases a long-distance attractant pheromone herself without ever being exposed to male signals (Table 4). There is just no sensory trap with which a male could seduce such females.

Finally, it is possible that the sample of study groups, which was determined in large part by the availability of evidence on mating behaviour, was not truly random with respect to genitalic evolution. Perhaps I unconsciously favoured inclusion of groups which did not fit the new arms race predictions. However, exclusion of groups which were added to the original list because I happened to be familiar with their mating, or followed up leads to investigate further did not reveal a trend in the direction predicted by new arms race models. Another attempt to control for this possibility (by being more strict regarding inclusion of Diptera in the

study, and then analysing Diptera separately) also failed to reveal the predicted trend.

One could still argue that this control is inadequate, because Diptera is not typical of all insects. Flies are, after all, especially prone to mate in swarms (which are rare in most other groups), and they also generally have species-specific male genitalia. Or perhaps it was incorrect to suppose that the fact that genitalic functions that are potentially non-conflictive in species with protected females in Diptera can be extended to other groups, so that the conclusion that these genitalic functions are also common other groups was incorrect. Failure of the new arms race models, even in a single large group such as Diptera, however, seriously undermines any claim for generality.

(C) *The analyses* The general decision not to correct for phylogenetic relations among different groups could also be criticized. I argued that it was justified because genitalic form often evolves very rapidly and mating behaviour has also changed rapidly in some groups. Phylogenetic corrections are not appropriate for such rapidly evolving traits (Losos, 1999). In any case, additional analyses at the level of families, thus reducing possible unjustified inflation of sample sizes with closely related genera, showed the same clear lack of support for the new arms race predictions.

There does appear to be at least one taxonomic pattern in the data: species-specific genitalia are especially uncommon in parasitoid Hymenoptera (perhaps due to the greater frequency of female monandry in this group, associated with selection on females to maximize the time spent hunting for hosts – see Eberhard, 1985a). These include groups with both protected and unprotected females, and there is no *a priori* reason to expect that this problem would be biased so as to obscure differences between groups with protected and unprotected females.

(D) *Summary of limitations* The data presented here are probably biased and imprecise in several ways. Many of the same problems also occurred, although generally unacknowledged, in previous comparative tests of hypotheses regarding genitalic evolution (Eberhard, 1985a; Dixson, 1987; Roig-Alsina, 1993; Arnqvist, 1998). Some biases are likely to result in underestimates rather than overestimates of the lack of support for the new arms race predictions. Other imprecisions could bias the data in other ways, but there is no reason to suppose that they would be biased so as to obscure the relationships predicted by the new arms race hypotheses. Nevertheless, the 'noise' that these biases produce could have obscured the predicted relations in this study. On the other hand, the lack of discernable trends, despite the very large sample of taxa examined here, means that if the trends do exist, they must be very weak indeed.

(b) *Large taxa with uniformly protected females*

A second way to analyse the data on genitalia takes advantage of the sweeping coverage of the taxonomic literature. Genus-by-genus comparisons such as those in Tables 2–5 are inevitably limited by the restricted number of genera in which mating behaviour has been observed. An alternative is to check genitalic evolution in especially large groups in which female protection is apparently uniform.

There are two very large groups in this study in which there are sufficient data to argue that most females are protected from male harassment – chironomid midges, and ditrysian moths. As noted in Section III 2 *a*, females of most species of Chironomidae are probably especially protected from unwanted male attentions and unlikely to be in conflict with males with which they mate, but male genitalia nevertheless clearly differentiate closely related species throughout the family (Pinder, 1978). Possible problems due to over-reliance on genitalia to distinguish species also seem relatively unlikely in this family, because independent traits in immature forms have also been used in taxonomic studies and thus serve as controls (Goetghebuer & Lenz, 1936; Lindeberg, 1967).

In addition, there are literally thousands of species of moths in which females initiate sexual interactions by attracting males with pheromones, and in which males nevertheless have both elaborate and species-specific genitalia. Long-distance female attractant pheromones are also clearly widespread in other groups of insects (the review 30 years ago by Jacobson, 1972 mentioned species in 35 different families belonging to nine orders in addition to Lepidoptera). Although there are exceptions (e.g. many Braconidae – Shaw, 1995), female attraction of males with pheromones is often combined with extremely ornate, distinctive male genitalia, as, for instance, in the large beetle genus *Phyllophaga* (more than 250 species known from Mexico alone) (Morón, 1986; Woodruff & Beck, 1989; Eberhard, 1993 *b*; Zhang *et al.*, 1997). Mating in caddisflies is poorly known, and female attractant pheromones have only recently been discovered, but they are now known to occur in three of the four infraorders (Solem & Petersson, 1987; Bjostad, Jewett & Brigham, 1996). Male swarming also occurs in many species in this order (Downes, 1969; Sivinski & Petersson, 1997), and mating pairs escape from possible harassment by leaving the swarm (Davis, 1934; Balduf, 1939; Petersson, 1989), so the females of many Trichoptera are probably protected. Nevertheless, male genitalia are extremely elaborate, and are species-specific throughout this order (Mosely, 1939; Malicky, 1983; Neboiss, 1986) (Fig. 4). Female attractant pheromones also occur in cockroaches (Bell *et al.*, 1977; Bell, 1982; Wendelken & Barth, 1987), which again have very complex and species-specific male genitalia (Walker, 1922; Hebard, 1943; Princis, 1951; McKittrick, 1964; Beier, 1970; Klass, 1997) (Fig. 4).

(*c*) *Other hypotheses and data*

Some other, independent data from genitalia also fail to fit new arms race predictions. The allometric slope of male genitalia seems to be relatively low rather than relatively high, when compared with the slopes of other non-genitalic traits that are not directly involved in sexual interactions (Eberhard *et al.*, 1998; Eberhard, Huber & Rodriguez, 1999). In addition, the expected female defensive genitalic structures are generally absent, and instead female structures often include forms such as grooves and pits that seem more likely to selectively aid males (e.g. Eberhard, 1997, 1998 *a*; footnote 3 in Table 1).

By a process of elimination, the evidence against the new arms race hypotheses strengthens alternative hypotheses to explain the rapid divergent evolution of male genitalia. The strongest of these involves classic sexual selection (Eberhard, 1985 *a*, 1997). The data presented here do not, however, provide guidance in distinguishing between different types of sexual selection, and in particular between the sexual selection by female choice hypothesis (Eberhard, 1985 *a*) and the more recent hypothesis involving sexual selection by male–male battles (Simmons, 2001). The male–male battle model proposes that male genitalia diverge under selection to function as hold-fast devices that defend against takeovers by other males after copulation has begun. A separate study would be needed to test thoroughly the male–male battle idea, which predicts a lack of genitalic divergence and diversity in groups in which other males do not attacking copulating pairs. A preliminary evaluation, based on genera with which I happen to have direct field experience, and in which I can thus evaluate the likelihood of such attacks, suggests that the prediction does not work. Several groups have species-specific male genitalia despite complete lack of forceful male–male battles during copulation: the beetles *Phyllophaga* (Melolonthidae) and *Macrohaltica* (Chrysomelidae); the flies *Ochthera* (Ephydridae), *Chymomyza* (Drosophilidae), *Microsepsis*, *Themira*, *Palaeosepsis*, and *Archisepsis* (except one species) (Sepsidae), and *Ceratitis* (Tephritidae) and the wasps *Auplopus* (Pompilidae) and *Trigonopsis* (Sphecidae) (for references on genitalic evolution in these groups, see Tables 2–4). In two nereid flies, *Glyphidops* and *Nerius*, males do attack copulating pairs; but, again in contradiction to the male–male battle predictions, the male genitalia are not elaborate and species-specific. In addition, in many genera of swarming flies and some swarming caddisflies with clear species-specific male genitalia (Table 2), copulating pairs immediately drop out of the swarm and are not pursued by other males (see footnote 3 in Table 2), so it appears that their generally species-specific male genitalia could not function in male–male battles. Observations of direct male–male struggles during copulation also appear to be very rare in spiders (e.g. no struggles of this sort were recorded in the very extensive observations of Robinson & Robinson, 1982). In most spiders the male repeatedly couples and uncouples his genitalia during copulation (Huber, 1998), and in at least some species, the male uncouples if another male approaches and turns toward the intruder (Rovner, 1968 on *Linyphia triangularis*; W. G. Eberhard unpublished observations of *Physocyclus globosus* and *Leucauge mariana*). Thus a hold-fast function to defend against other males is unlikely. Yet in general male genitalia are species-specific throughout spiders. The species-specific forms of genitalic structures in Diptera which function not to clasp the female, but rather to push open or past female structures (Table 1) also argue against the Simmons (2001) male–male battle hypothesis.

(3) **Non-genitalic traits**

The focus of this review is on male genitalia, but some of the data can also be used to examine, in at least a preliminary way, the likelihood that other morphological traits, that are involved in pre-copulatory courtship displays of males, have

diverged rapidly due to male–female conflict. The new arms race models predict that in groups with protected females, species-specific courtship traits of the male that are brought into play after the male and female have encountered each other, and that do not involve physical restraint of the female, should be absent. Traditional sexual selection by female choice, by contrast, predicts no such association, because female choice criteria are not necessarily limited to a single stage of sexual interactions, or to a single male trait, and multiple criteria can operate in a single species. The contrast between these predictions is clearer than in genitalia, because the mechanical functions of the non-genitalic structures are more limited and obvious, and because many male traits are not capable of producing post-insemination manipulations of the female that could result in male–female conflict. Only if one makes a seemingly improbable assumption, that male structures brought into play before but not during copulation are able to coerce females into particular responses during or following copulation, could many of these male traits be presumed to result in male–female conflict in species with protected females.

The prediction of the new arms race models that such non-genitalic structures should not occur in groups with protected females does not hold in several groups in Tables 2 and 3. For instance, male hind tarsi of the swarming platypezid flies *Calotarsa* are probably visual display devices, and are elaborately adorned with species-specific forms (Kessel, 1963). An alternative explanation, that these male structures function as species-isolating mechanisms, is also improbable due to the species' disjunct distributions (Sivinski & Petersson, 1997) (although present distributions are not necessarily the same as those when the species evolved). Male *Neoxabea* crickets sing to attract females, but they have moderately complex, species-specific metanotal structures (where the female is probably stimulated as she feeds on male products prior to and during copulation) (Walker, 1967). Males of several species of *Phyllophaga* beetles have species-specific modifications of the abdominal sterna or the front legs that contact or rub against the female during sexual interactions (Morón, 1986; Woodruff & Beck, 1989; Eberhard, 1993*b*), despite the fact that sexual encounters only occur after females have lured males with long distance attractant pheromones (Eberhard, 1993*b*; Zhang *et al.*, 1997). Similarly, in eight genera of the groups with species-specific non-genitalic male contact courtship structures listed in Table 11.1 of Eberhard (1985*a*), either the way in which the male structure functions (e.g. offer substances for the female to ingest) or other data suggesting that females are protected from male harassment (*Apis* and *Araneus*) indicate that the female could easily protect herself from the male's stimuli (e.g. not ingest the substance).

Again the most extensive data come from ditrysian moths, both because of the huge numbers of species involved, and because of the clear impossibility of male coercion with the traits used in pre-copulatory displays in most groups. Male moths have repeatedly evolved odours and odour-dispersing structures, sounds, and tactile and perhaps visual signals that are brought into play after the female has lured the male into her vicinity with a long-distance attractant pheromone (Birch, Poppy & Baker, 1990; Phelan, 1997). Scent organs

for such short-distance communication have evolved on virtually all parts of the male body, including his wings, thorax, abdomen, genitalia, legs, head, and antennae (Birch *et al.*, 1990). Male-specific sounds and sound-producing organs in moths are also varied and widespread. Female discrimination among males on the basis of these signals has been documented in several groups (Phelan, 1997). Less complete data on caddisflies also suggest a similar pattern. Diverse male courtship structures, such as the elaborate and species-specific scent-dispersing structures occur on the heads of male *Hydroptila* (Mosely, 1919, 1923; Eltringham, 1919), despite the fact that mating is characterized by protected females (male swarming or long-distance attractant pheromones produced by the female). In summary, males in several groups in which females are protected from male harassment possess a variety of non-genitalic traits that are apparently used to induce copulation and fertilization, contrary to the new arms race predictions.

(4) Can one generalize from genitalia?

As noted in Section I, much of the data cited in recent discussions of new arms race models involve possible male manipulations of female physiology. The data on such interactions are limited to very few well-studied groups, in particular *Drosophila melanogaster*, and thus fall short of documenting general trends. It is quite possible that some effects of male seminal products on females are peculiar to *Drosophila* and their relatives. Indeed, studies of some other groups have demonstrated that the negative effect of copulation on female longevity seen in *D. melanogaster* does not occur, and that the female may benefit rather than suffer from mating (Arnqvist & Nilsson, 2000; Wagner *et al.*, 2001). In addition, the *D. melanogaster* data do not provide completely convincing tests of new arms race interpretations, because possible pay-offs to females from more attractive sons were not taken into account, and evaluations of costs and benefits, measured in fruit fly culture bottles, are also not necessarily appropriate to understand the conditions under which these flies evolved (Cordero & Eberhard, 2003).

Is it reasonable to expect that the evolutionary forces which have shaped the morphology of genitalia are the same or similar to those which have shaped other traits involved in sexual interactions, such as the physiological effects of male seminal products on female reproductive physiology? The most conservative supposition is that other types of traits will follow the same pattern as morphology. There is at least one reason, however, to suppose that new arms races are more likely to occur in physiological effects than in morphology. This is because male seminal products may be particularly powerful weapons compared with, for example, sensory traps (Section IV 2*a* ii). In many insects and ticks, male seminal products have powerful effects on female reproductive physiology, and indeed sometimes involve the same signaling molecules that are used by females in their own bodies (summaries in Chen, 1984; Eberhard, 1996; Wolfner, 1997). It may be difficult for a female to exclude such powerfully manipulative products during sperm transfer. On the other hand, female defences against such effects could be simple (sequestration or degradation of seminal

products, elevated response thresholds, smaller genital cavities where male ejaculate is deposited, decreased permeability of the walls of the reproductive tract to seminal products). Demonstration that under artificial conditions in which male seminal products can evolve but female responses to them cannot, that the male products can evolve to have damaging effects on females (Rice, 1996) is not logically equivalent to showing that females under conditions which allow them to evolve suffer damage from males. More work will be necessary to sort this out.

V. CONCLUSIONS

(1) A survey of publications on 43 species in 22 families of Diptera showed that the most common function adduced for genitalic structures is achieving deeper penetration and transferring sperm; it accounts for approximately half of all attributed functions. Clasping the female accounts for about another third of the attributed functions.

(2) New arms race models, which propose that conflict of interests between males and females over control of reproduction results in the widespread tendency for male genitalia to evolve especially rapidly and divergently, were contrasted with traditional explanations based on sexual selection by female choice. The two types of models give different predictions: new arms race ideas predict that in species in which the probability of male–female conflict is reduced or lacking because unreceptive females are protected from harassment by males, male genitalic structures with certain functions (particularly penetration and sperm transfer) should tend to be less often species-specific in form; traditional sexual selection does not predict such an association.

(3) Because genitalic functions, such as penetration and sperm transfer, that are not expected to result in male–female conflict in species with protected females appear to be common (point 1), it is reasonable to expect a difference between genitalic evolution in groups with protected *versus* unprotected females if male–female conflict has been an important selective force causing rapid divergent evolution of male genitalia.

(4) A search for this predicted difference was conducted using the taxonomic literature on a sample of 361 genera of insects and spiders. There was no sign of the predicted trend: the differences found were generally not significant; when there were significant differences, they were in the opposite direction.

(5) Several limitations and weaknesses of the data and the analyses were discussed. Attempts to correct for some of these problems by re-analysing the data also failed to reveal the trend predicted by the new arms race models (Fig. 6).

(6) Inclusion of ditrysian moths, a very large group in which the predicted trend also does not occur, would have made the lack of confirmation even more dramatic.

(7) The implication of points 1–6 is that the new arms race models of male–female conflict over control of reproduction have not played an important role in producing the rapid divergent genitalic evolution that is widespread in insects and spiders.

(8) Other, non-genitalic courtship structures, such as stridulation devices and species-specific scent-dispersing structures that are employed prior to copulation, frequently show species-specific morphologies in species with protected females. They thus also appear to fail to fit the predictions of the new arms race models.

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