

RAPID DIVERGENT EVOLUTION OF SEXUAL MORPHOLOGY: COMPARATIVE TESTS OF ANTAGONISTIC COEVOLUTION AND TRADITIONAL FEMALE CHOICE

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Abstract.—Male structures specialized to contact females during sexual interactions often diverge relatively rapidly over evolutionary time. Previous explanations for this pattern invoked sexual selection by female choice, but new ideas emphasize possible sexually antagonistic coevolution resulting from male-female conflict over control of fertilization. The two types of selection have often not been carefully distinguished. They do not theoretically exclude one another, but they have not necessarily had equally important roles in producing rapid evolutionary divergence. To date, most recent empirical studies of antagonistic coevolution have emphasized only a few taxa. This study uses the abundant but little-used data in the taxonomic literature on morphology to evaluate the roles of antagonistic coevolution and traditional female choice over a wide taxonomic spectrum (61 families of arthropods, mostly insects and spiders). Groups with species-specific male structures that contact females were checked for coevolution of species-specific female structures that are contacted by the male and that have mechanical properties that could potentially defend her against the male. Facultatively deployable, species-specific female defensive structures, a design that would seem likely to evolve frequently under the sexually antagonistic coevolution hypothesis, were completely absent (0% of 106 structures in 84 taxonomic groups). Although likely cases of sexually antagonistic coevolution exist, using conservative criteria, 79.2% of the 106 structures lacked even potentially defensive female coevolution. A common pattern (53.8% of 106) was a nearly complete absence of female change in areas contacted by species-specific male structures. Post-hoc arguments invoking possible coevolution of defensive female behavior instead of morphology, or of female sensitivities and responses to male sensory traps, could enable the sexually antagonistic coevolution hypothesis to explain these data. No case of such coevolution of female behavior or sensitivities has been demonstrated, and there are additional reasons to doubt that they are general explanations for the data presented here. Detailed studies of female resistance behavior could help illuminate several issues. The possibility of a greater role for antagonistic coevolution in reproductive physiology than in morphology and the possibility that female choice and sexually antagonistic coevolution have both been important in some lineages are discussed.

Key words.—Antagonistic coevolution, female choice, genitalia, male-female conflict, sexual selection.

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Analyses of evolutionary interactions in terms of conflicts between the reproductive interests of participating parties have a long and distinguished record of providing useful insights (e.g., Hamilton 1964a,b; Trivers 1972, 1974; Eberhard 1980, 1990; Haig 1993; Drummond 2001; Rice and Chippendale 2001). It is thus logical to attempt to analyze the reproductive interactions between male and female animals during sexual reproduction in terms of potential conflicts in their reproductive interests. But there is currently confusion regarding the importance and ubiquity of such conflict (Holland and Rice 1998; Chapman et al. 2003; Pizzari and Snook 2003; Cameron et al. 2003; Cordero and Eberhard 2003).

This paper attempts to evaluate support for sexually antagonistic coevolution due to male-female conflict by focusing on the sweeping evolutionary tendency for male morphological traits that are specialized to contact females during sexual interactions to diverge relatively rapidly and thus be species specific (West-Eberhard 1983; Eberhard 1985, 1996; Andersson 1994). Such traits are often more divergent in closely related species than are other nonsexual traits of the same organisms, and are thus often used in taxonomic studies to distinguish closely related species. The relatively rapid divergence of such traits has traditionally been thought to be due to sexual selection by female choice (Darwin 1871; West-Eberhard 1983; Eberhard 1985). Recently a hypothesis, which had been briefly explored earlier (Parker 1979) and which is based on possible conflicts of reproductive interests

between males and females (Rowe 1994; Alexander et al. 1997; Partridge and Hurst 1998; Holland and Rice 1998; Gavrillets 2000), has been widely discussed. It proposes that males and females often engage in evolutionary arms races or antagonistic coevolution for control of reproduction. The rapid divergence in male traits that affect copulation and fertilization of eggs is hypothesized to result from the coevolution of female traits that also affect these aspects of reproduction. Improvements in male abilities lead to more intense selection on females favoring increased female abilities to counteract his effects (“defensive” female traits), and thus results in improved female defenses; these improved defenses in turn lead to more intense selection on males to improve still more. The result is a continuing cyclical process (Holland and Rice 1998) or evolutionary chase (Alexander et al. 1997) of sexually antagonistic coevolution that produces rapid divergent evolution.

Part of the current confusion regarding relations between sexually antagonistic coevolution and traditional female choice stems from inconsistencies in use of the phrase “conflict of interest.” In the broad sense, the idea that the reproductive interests of males and females are not identical is obviously not new: every time a male attempts to mate with a female and is rejected, there is a conflict of reproductive interests (Eberhard and Cordero 2003; Pizzari and Snook 2003). The possible evolutionary importance to males of being able to overcome female resistance to mating has been recognized ever since evolutionary biologists became aware

of natural and sexual selection (Darwin 1859, 1871), and traditional models of female choice include this type of male-female conflict. What is novel, and potentially important in the new sexually antagonistic coevolution models (in their more narrow sense, which will be used below) concerns the benefits that the female may gain by sometimes rejecting males.

Traditional explanations of why females accede to some males and not others have invoked either direct benefits to the female (often in terms of greater numbers of offspring produced), or indirect gains (greater genetic quality of offspring produced) (Andersson 1994; Kokko et al. 2003). The new male-female conflict ideas suggest instead that females resist some males to avoid the male-imposed costs that females suffer from unwanted courtship and copulation, such as increased predation (e.g. Rowe 1994), reductions in oviposition (e.g. McLain and Pratt 1999), food intake (e.g., Sakaluk et al. 1995), fertility (Warner et al. 1995), offspring survival and survivorship (Chapman et al. 1995; Civetta and Clark 2000), infection by ectoparasites and disease organisms (Daly 1978), inferior offspring from genetically incompatible males (Zeh and Zeh 1996), damage to her own reproductive tract (Wing 1982; Crudgington and Siva Jothy 2000), or other male effects that reduce her reproductive success and are associated with loss of female control over fertilization (Alexander et al. 1997). Female avoidance of these costs thus produces sexual selection on males. Discussions of antagonistic coevolution have emphasized the payoff to a female of avoiding the types of male-inflicted damage that result in reduced numbers of offspring (Holland and Rice 1998; Rice 2000; Gavrillets et al. 2001; Chapman et al. 2003). In this view, the sexual selection on males that results from female rejections becomes a side effect of natural selection on females (Rowe 1994). A traditional view of female choice, on the other hand, would suppose that costs to the female of accepting a male, when they exist, are on average compensated by benefits to the female in terms of increased number or quality of her offspring.

In theory, both antagonistic coevolution and traditional female choice have the potential to produce rapid divergent evolution (Andersson 1994; Gavrillets 2000; Chapman et al. 2003; Kokko et al. 2003), and in fact antagonistic coevolution and traditional female choice are not strict alternatives (Cordero and Eberhard 2003, unpubl. ms., Kokko et al. 2003; Pizzari and Snook 2003). Both types of selection could theoretically affect the same male traits simultaneously, either reinforcing or counteracting each other. However, this does not mean that both have acted with equal frequency or intensity in evolution.

This empirical question of the relative historical importance of the two types of selection is as yet unresolved. The balance between the two types of selection is not easily predicted theoretically (Kokko et al. 2003), and it is likely to be influenced by complex factors (Cordero and Eberhard, unpubl. ms.). Here I examine this question empirically by comparing predictions of the two hypotheses with morphological data from a large number of groups of terrestrial arthropods, mainly insects and spiders. This study is largely complementary to recent reviews of sexually antagonistic coevolution (Chapman et al. 2003; Kokko et al. 2003; Pizzari

and Snook 2003; Cordero and Eberhard 2003), which concentrated on theory and evidence from direct experimental tests. It also complements two other empirical studies that were based on other predictions of sexually antagonistic coevolution and traditional female choice (Eberhard et al. 1998; Eberhard 2004a). It attempts to respond to the problems noted by Chapman et al. (2003) and Córdoba-Aguilar and Contreras-Garduño (2003), that functional interpretation of female traits has often been lacking in discussions of sexually antagonistic coevolution, and that data used to test the theory have come from very few taxa.

Coevolution of Defensive Female Morphological Traits with Species-Specific Male Morphological Traits

Alexander et al. (1997; p. 9) noted that a clue to detecting sexually antagonistic coevolution “. . . will often be evidence of forcing or manipulation by one sex, usually the male.” A corollary, on which much of this paper is focused, is that there will often be evidence of defense against such forcing or manipulation, usually by the female. For morphological traits, sexually antagonistic coevolution predicts arms races whose results should often resemble lock-and-key type evolution. In species with species-specific male traits, females should have species-specific defensive traits that are appropriately designed to counteract the species-specific aspects of male traits (and which will subsequently favor further modifications of the male). This prediction of species-specific defensive traits can be evaluated for female morphological structures, which are known to be contacted by species-specific structures of the male during sexual interactions. This has been done, for instance, by Arnqvist and Rowe (1995, 2002a) for *Gerris* water striders, and they claimed (with no supporting references) that “correlated evolution between the sexes in morphology. . . is a rule rather than an exception.” (2002a; p. 941) Alexander et al. (1997) note that in some groups the female structure that is contacted by the male may have some other important function, and may thus not be free to evolve to defend against the male. However, in such a cases, the antagonistic coevolution hypothesis would predict that males should lack species-specific differences (there would be no female differences to which they would need to adjust). The empirical focus of this study (see e.g., Appendix) is on groups in which male structures are species-specific in form, and on possible explanations for why rapid divergent evolution has occurred in these structures.

For a concrete example of these ideas, consider an evolutionary lineage in which males and females have been engaged in a coevolutionary race over the male's ability to grasp the female. The females should often have species-specific structures in the parts of their bodies that are contacted by the male that physically impede the grasping action of male organs. Because a female must also mate at least once, the most advantageous female defenses would seem to be those that can be deployed optionally, or be occasionally overcome by males. Possible examples of such facultative female defenses would be erectable spines, inflatable sacs, or mobile structures that can shield the female contact area from the male or reduce his mechanical support when he attempts to seize or couple with her. The crucial point is that females

should have species-specific traits whose properties are appropriate to defend the female against the species-specific aspects of male structures. These traits should not have selectively cooperative designs, such as grooves, slots, or pits into which the male can fit and that would thus facilitate rather than impede meshing, grasping, and holding by male structures.

Female defenses against male morphological traits could also be behavioral or sensory rather than morphological (Eberhard and Pereira 1996; Alexander et al. 1997; Eberhard 2001a). Nevertheless, it seems reasonable to expect females to frequently coevolve defensive morphology that is adjusted to male morphological adaptations, given the great abundance of groups in which the morphology of males has diverged rapidly, and the need to explain the advantage of particular aspects of the male's morphology that are species-specific in form (simple female avoidance or generalized resistance is not enough; see the Discussion for a more complete examination of these points).

The prediction of traditional female choice regarding the female structures that are contacted by species-specific male structures is somewhat different. Females could choose males on the basis of how well male and female morphologies mesh, and in such cases female morphology would coevolve with male morphology (Eberhard 1985; Eberhard and Huber 1998). Expected female designs adjusted to males could include devices to fend off males (as with sexually antagonistic coevolution) if other female traits (e.g., behavioral avoidance of male contact) are not sufficient to avoid copulation. Females using mechanical criteria to select among males would also be expected to use selectively cooperative designs, such as grooves and pits that facilitate clasping by males that have designs, but not by others with other designs. Still another expectation, when females use stimulatory criteria to select among males, would be a frequent lack of female morphological coevolution with males. When female screening processes occur via stimulation received from the male structure, female choice criteria could involve more cryptic traits, such as the distribution of female sense organs, the number or types of synapses made by the sensory neurons that are stimulated by the male clasping structure, or connections deeper within in her nervous system.

METHODS

Morphological evidence has several advantages. First and foremost, pertinent morphological data are available for a huge range of species, due to extensive use of morphology in the massive taxonomic literature. Published accounts typically include descriptions of many closely related species. Extensive close taxonomic comparisons, which are crucial to test possible rapid divergent evolution, are quite rare for other types of traits.

Groups included in the Appendix had to meet two conditions: (1) the male structures that contact the female are species-specific in form; and (2) the mechanical mesh of the male structures with the female has been described. Species-specificity of male structures was determined by checking taxonomic studies to see whether these structures were used to distinguish congeneric species. Coevolution was judged

to have occurred in female structures that are contacted by the species-specific male structures when taxonomic papers on the group used these female structures to distinguish congeneric species. This criterion was conservative, because some rapid divergent evolution of female structures may not represent morphological adjustments to fit with the male (see e.g., Fig. 2).

I omitted cases in which male structures are inserted into soft female sacs or ducts that are membranous. This was an attempt to eliminate false negatives for female coevolution, which might involve more cryptic female characters, such as muscular valves or inflatable barriers that could impede penetration by the male but that might have been overlooked. I included some soft but more or less planar external female structures such as pleural and intersegmental abdominal membranes of flies that were likely to be unable to change in form sufficiently to exclude males. I also included (or would have included if they had occurred) soft sacs or membranes that could be inflated or extended to cover the female's genitalia or other contact zones.

A second advantage of morphology that was exploited is that the probable functions of many morphological structures can be deduced with fair certainty from their designs. This is especially true for structures that are more or less rigid, and whose positions and movements during sexual interactions are known. At the very least, it is usually possible to eliminate some possible functions on the basis of morphological design (Anderson 1997; Huber 1999; Arnqvist and Rowe 2002a). Female designs that I took to be potentially defensive included the following: erectable spines, inflatable sacs, or other structures in the area of the female contacted by the male that could hold the male structure away; mobile sacs or shields that could cover the area of the female that is contacted by the male and thus protect it from contact by the male; fixed spines, bristles, ridges, or bumps on the contact area of the female that would hold the male away; long, highly coiled ducts into which the male inserted a long structure; and hardened (sclerotized) or thickened membranous areas where sharp male genitalic structures might otherwise perforate the female. Some female defenses may be subsequently rendered ineffective by male evolutionary responses, with the result that the fit between male and female structures no longer gives the impression of conflict (Alexander et al. 1997). For instance, a female spine that originally evolved to fend off the male could later be grasped by the male to hold on to her. Nevertheless, the potentially defensive properties of the spine would still be evident, and all potentially defensive female structures were counted as defensive. This classification as defensive was conservative in that female structures with potentially defensive properties could also be used in traditional female choice to filter males to obtain superior sons.

The data in the Appendix were not collected systematically. Instead, they represent a gradual accumulation over many years (the first version was table 11.1 of Eberhard 1985). The techniques I used varied, and included systematic attempts to amass literature on lock-and-key ideas of genitalic evolution (especially in Diptera), my own morphological studies of particular groups, and accidental finds made while reading for other projects or conversing with colleagues. One

might object that this unstructured sampling may have been biased against groups showing patterns predicted by sexually antagonistic coevolution. However, I never consciously failed to follow up a lead because it appeared to fit particular predictions, and some of my own studies document possible antagonistic coevolution in the Appendix (e.g., *Macrodactylus* and *Phyllophaga* beetles).

The taxonomic units in the Appendix vary. The minimum unit that allowed assessment of species specificity in male structures, a prerequisite for inclusion in the Appendix, was a genus. In some cases multiple genera in larger taxonomic groups shared the same combination of male and female traits (e.g., the male abdominal appendages of many genera in several families of damselflies and dragonflies). These groups were collapsed into single entries in the Appendix, and were counted as single taxa when the data were analyzed. This means that the numbers of taxa given in the results are substantial underestimates of the numbers of genera involved. When multiple male and female structures were checked in the same taxon, they were counted separately unless noted otherwise.

RESULTS

Part A in the Appendix presents data on female genitalic designs in groups in which male genitalia are species specific; part B presents similar data on females in groups in which nongenitalic male contact structures are species specific. The data show two important trends. When each structure in the Appendix was counted separately, the number of cases in which female structures failed to coevolve with males was 15 (34.9%) of 43 structures in 34 taxonomic groups with species-specific male genitalia, and 42 (68.3%) of 63 groups in 53 taxa with species-specific male nongenitalic structures ("?" and "sometimes" were not included in this category). The total was 57 (53.8%) of 106 structures in 84 taxonomic groups. An example of a group with species-specific nongenitalic male structures that lacked female morphological coevolution is illustrated in Figure 1. A clear example in genitalia occurs in *Bombus* bumblebees: "... the stipes, volsella, and squama, that is the most complex [and interspecifically variable] part of the [male] genitalia, do not enter the abdomen of the female at all, but grip the sides of the sixth sternite . . . , a part of the female which is identical (or nearly) in all species." (Richards 1927, p. 262)

The second important trend was that in those groups in which females had species-specific structures in the area contacted by the male, the majority of the female designs were not potentially defensive. For genitalia, potentially defensive female genitalic structures were lacking in at least 16 (57.1%) of 28 structures in 23 taxonomic groups, and in nongenitalia the number was 11 (52.4%) of 21 structures in 19 groups (conservative criteria were used in both cases, so all "?" and "sometimes" were not included). The total was 27 (55.1%) of 49 structures in 39 taxonomic groups. Combining these data with the numbers of groups in which females did not coevolve with males (above), females clearly failed to show coevolved potentially defensive structures in 31 (72.1%) of 43 genitalic structures, and 53 (84.1%) of 63

nongenitalic structures, or a total of 84 (79.2%) of 106 structures in 84 taxonomic groups.

Instead of defensive designs, females in many groups in which females coevolved with males had grooves, pits, and indentations that would facilitate stronger rather than weaker meshes with males (for female genitalia, see Rentz [1972] and Nadig [1994] on orthopterans, Downes [1978] on flies, Grasshoff [1973], Huber [1994a, 1995a,b] and Knoflach and van Harten [2000] on spiders, Peretti [2002, 2003] on an amblypygid and scorpions; for nongenitalia, Freitag [1974] on tiger beetles, Corbet [1999] on odonates, Toro and de la Hoz [1976] on bees, Kraus [1984] and Huber [2003] on pholcid spiders, and Huber [1995a] on dictynid spiders). Female facilitation of this sort is selective rather than random. It favors only those males with appropriate processes that can fit into the grooves or pits (for especially strong correlation between male and female in a genus of spiders see Huber 2003), a design that results in selective cooperation and that is compatible with the female choice hypothesis.

Spiders are especially well documented with respect to female genitalia, because figures of the female's external genitalia (epigynum) are routinely included in taxonomic descriptions in most groups. The epigynum is a rigid, platelike structure surrounding the entrances to the paired, highly sclerotized insemination ducts, which lead internally to the sclerotized spermathecae. The epigynum often has complex grooves, furrows, and ridges, and the insemination ducts are often long and tortuously curved. Not a single example of the species-specific facultatively deployable defensive structures that were expected to frequently result from sexual antagonistic coevolution (erectable spines, moveable hoods, or other mobile external closing mechanisms that would facultatively impede entry into the duct) is described in any of the studies of copulation just cited, nor in the thousands of species included in general faunal works (Kaston 1948; Forster 1970; Forster and Wilton 1968, 1973; Dippenaar-Schoeman and Jocque 1997), and in other extensive recent taxonomic reviews (Griswold 1987, 1990, 1991, 1994, 1997; Platnick and Forster 1989; Jocque 1991; Levi 1991a,b, 1992, 1993, 1995a,b, 1996, 1997, 1999; Hormiga 1994, 2000; Platnick 2000, 2002; Piel 2001).

A possible limitation of these analyses is that no correction was made for possible phylogenetic inertia (Harvey and Pagel 1991). Such a correction here may well be inappropriate, because it can lead to errors when traits are rapidly evolving and nonconservative (Losos 1999). At least on the male side, the types of traits examined here are notorious for diverging rapidly. Nevertheless, two additional analyses were performed to explore the possible effects of phylogeny. In one, all cases in which data on multiple structures were presented for a given taxonomic group were collapsed, so the units were taxonomic groups rather than structures (genitalia and nongenitalia were combined in the three groups in which both types of data were available). The second involved analyzing the data at the level of families instead of lower taxonomic levels (families with both genitalic and nongenitalic structures were counted only once). These analyses gave very similar values to those given above. Female coevolution was absent in 57 (53.8%) of 106 structures (above), in 44 (52.4%) of 84 taxonomic groups, and in 30 (49.2%) of 61 families.

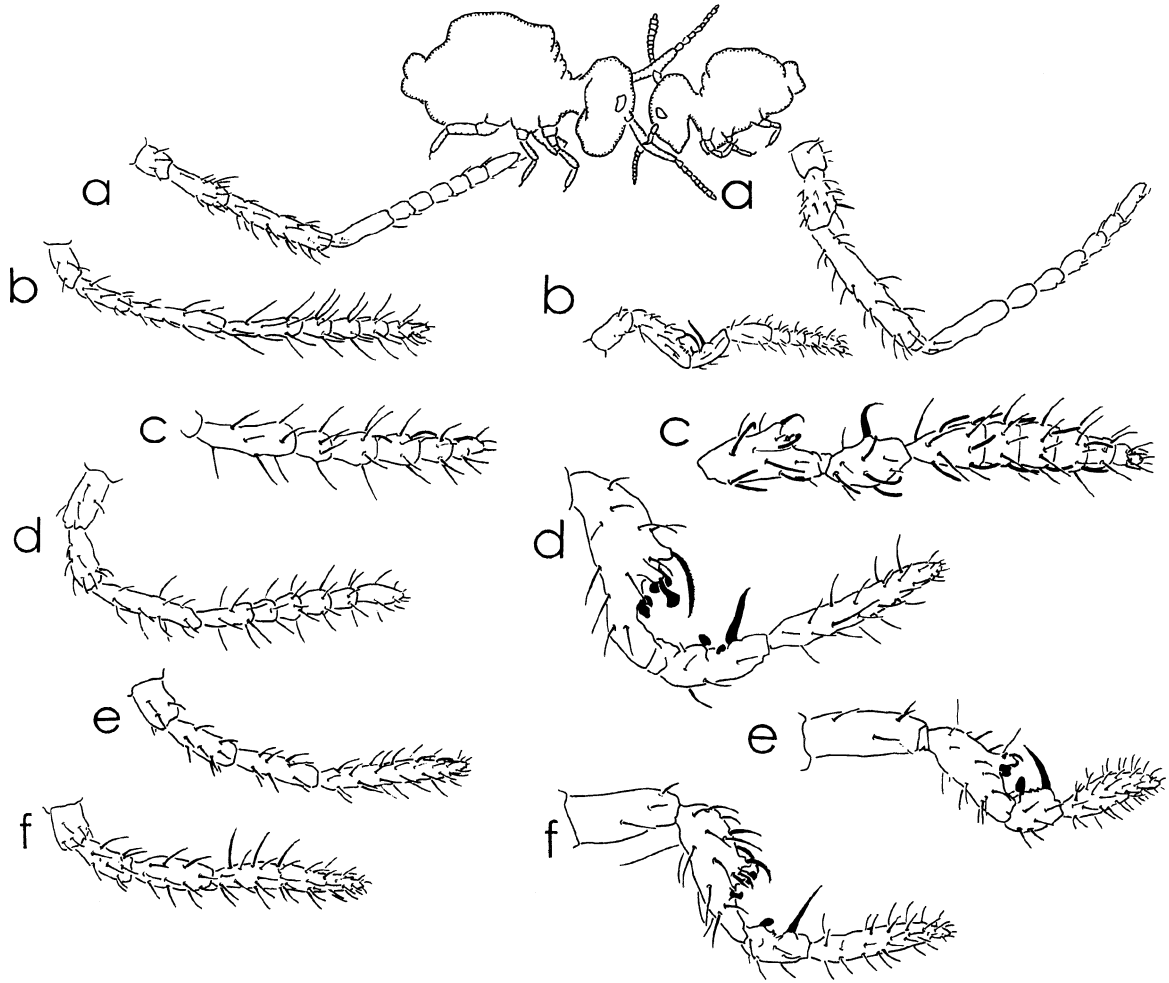


FIG. 1. One trend in the Appendix, lack of coevolutionary adjustments in females to species-specific differences in male structures, which contradicts sexually antagonistic coevolution, is illustrated in the antennae of symphypleone collembolans. The male uses the basal segments of his antenna to grasp the antenna of the female (upper drawing). In each pair of drawings below, the female antenna is on the left, and the male on the right. (a) *Bovicornia greensladei*; (b) *Yosiides himachal*; (c) *Smithuridia sphaeridioides*; (d) *Debouttevillea marina*; (e) *Denisiella* sp.; (f) *Jeannenotia stachi*. Upper drawing after Mayer (1957); lower drawings, to different scales, after Massoud and Betsch (1972).

Defensive female coevolution was lacking in 84 (79.2%) of 106 structures (above), 61 (72.6%) of 84 taxonomic groups, and 42 (68.9%) of 61 families (conservatively, all “?” and “both” were not included). The evolutionarily labile nature of the female structures (and thus the probable lack of importance of phylogenetic inertia) was evident from the fact that in seven (42.9%) of the 15 taxonomic groups with more than one structure (median = 2, range 2–5 structures/group), the different structures showed different patterns: female coevolution occurred in one structure and did not occur in the other.

There are complementary behavioral data on the male grasping structures of three groups in Appendix, part B, that give an additional reason to doubt the antagonistic coevolution argument that the species-specific aspects of the male’s clasping organs function to improve his ability to hold on to the female (on a damselfly, Loibl 1958; on a crustacean, Belk 1984; on a fly, Eberhard 2001b, 2002a). In all three groups, the species-specific portion of the male structure was exper-

imentally modified (removed in the fairy shrimp, trimmed in the damselfly, and covered with a lump of glue in the fly). In no case did this reduce the male’s ability to hold on to the female, even though in the fairy shrimp and the fly the females struggled more actively. Instead, in all three it reduced the likelihood that the female would copulate. The species-specific designs of these structures thus seem to function more to influence female choice than to simply hold on to her.

DISCUSSION

Female Morphology

Both genitalia and nongenitalia showed patterns that are opposite those predicted by the sexually antagonistic coevolution hypothesis. The type of female defensive design that would seem especially likely to evolve often under sexually antagonistic evolution—species-specific facultative morphological barriers that would allow the female to accept some

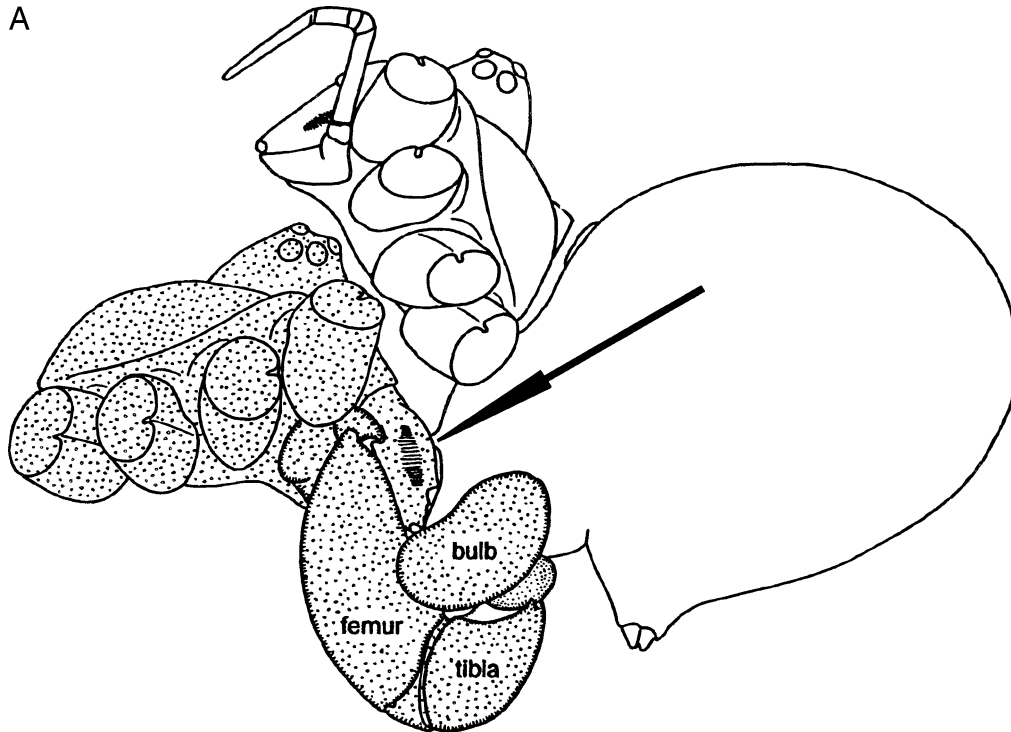


FIG. 2. The second trend in the Appendix that fails to conform to antagonistic coevolution predictions, species-specific female structures that contact species-specific male structures but that show no sign of defensive designs, is illustrated in some pholcid spiders. (A) During copulation the anterior surface of the chelicerae of the male (stippled) presses against a sclerotized area on the female's abdomen (the epigynum—arrow) while the male's genitalia (bulb) squeezes the epigynum against the basal segment of his chelicerae (left). The chelicerae thus form one side of a clamp that squeezes the female. (B) Each pair of male chelicerae (left) and female epigynum (right) is a different species in the genus *Trichocyclus* (drawings, to different scales, after Huber 2001). Species-specific male chelicerae combined with female epigyna that lack defensive designs are widespread in this family (e.g., Huber 1997a, 2000, 2001).

males and prevent others from engaging her—did not occur in a single species. Under the traditional female choice hypothesis, this lack may result from the effectiveness of female mechanisms to prevent males from coupling. A second unexpected result under sexually antagonistic coevolution was that in many of the groups in which female traits did coevolve with males, female designs were “selectively cooperative,” facilitating the male's purchase on the female, such as pits or grooves into which the male structures can fit. These patterns (especially the lack of facultative barriers) are especially well documented in spider genitalia, because of the huge sample of species in which female genitalia have been described (literally thousands of species). It is worth noting that my interpretation of the cooperative nature of female grooves and pits is supported by the reduction of one such presumably cooperative female structure in a group in which male-female conflict over copulation appears to occur. Females of many tettiioniids have pits or grooves near their external genitalia whose only known function is to receive a male clasping structure (the cercal tooth) that functions to grasp the female (Rentz 1972). These grooves are secondarily absent, and males have a robust cercal tooth in one katydid species (*Uromenus rugosicollis*) in which apparent male-female conflict over copulation has been documented (Nadig 1994; Vahed 1997; K. Vahed, pers. comm.).

More direct evidence regarding defensive female coevolution with species-specific male traits also showed a trend

opposite to that predicted by sexually antagonistic coevolution. Female morphology was often not species specific in groups in which the male morphology was species specific (53.8% of 106 structures in 84 taxonomic groups); and when female morphology did evolve rapidly, it tended not to show any sign of a potentially defensive design adjusted to male designs (55.1% of 49 structures in 39 taxonomic groups). Combining these data, potentially defensive female morphological coevolution was lacking in 79.2% of 106 structures in 84 groups.

Previous general surveys of insects have come to the same conclusion regarding the frequent lack of male-female coevolution documented here, both with respect to nongenital structures (Robson and Richards 1936; Eberhard 1985) and genitalia (Robson and Richards 1936; Eberhard 1985; Shapiro and Porter 1989; see also Peretti 2003 on scorpions, and Kraus 1966 on millipedes). The claim that correlated evolution between the sexes in the morphology of these types of structures is a rule rather than an exception (Arnqvist and Rowe 2002a) is, as far as I can determine, simply incorrect.

The frequency of apparent accord with sexually antagonistic coevolution expectations (20.8% of the structures) probably seriously overestimates how often such coevolution has occurred. In *Gerris* water striders there is a very strong case for sexually antagonistic coevolution (e.g., Arnqvist 1997; Arnqvist and Rowe 2002a, Rowe and Arnqvist 2002). But closer examination of several other cases in the Appendix

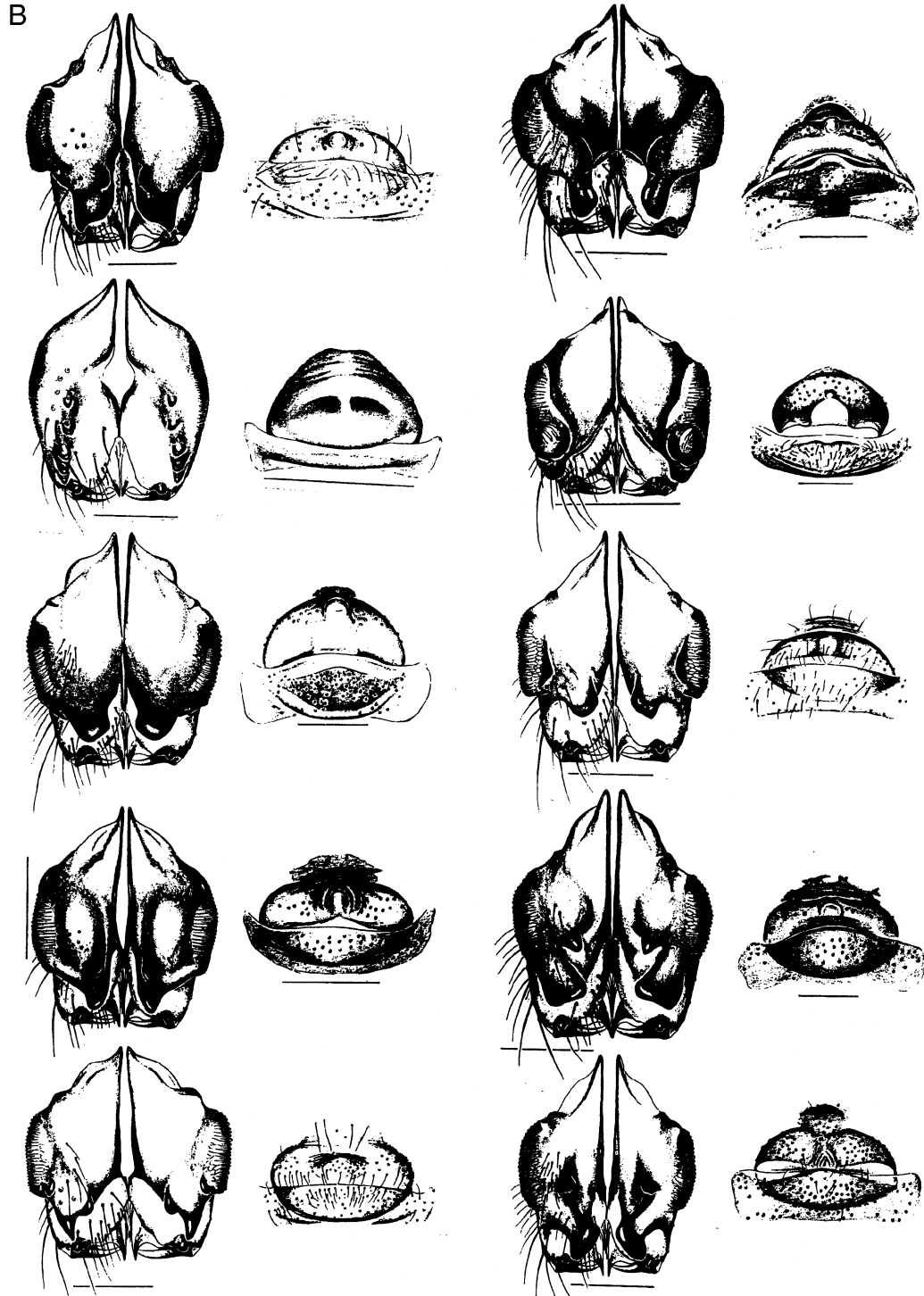


FIG. 2. Continued.

suggests they are unlikely examples of sexually antagonistic coevolution. In *Chelymorpha* beetles the “defensive” female structure is her long, highly sclerotized, and tightly coiled spermathecal duct. In *C. alternans*, however, there is no sign of the female struggling against coercive male behavior, as would be expected if males are inflicting damage on females. If a female is not receptive, she responds by lifting the tip

of her abdomen so that it is protected under her elytra, and the male discontinues his courtship (tapping her elytra gently with his antennae and mouthparts) and dismounts (Rodriguez 1995). The female’s long spermathecal duct is probably involved in producing a bias in paternity, favoring males with longer genitalic processes (Rodriguez et al. 2003); there is no indication that this genitalic process reduces the female’s

reproductive output. In the spider *Tetragnatha*, strong spurs on the large chelicerae of both males and females appear to facilitate the mutual cheliceral clasp that precedes copulation. Again the female's behavior shows signs of being cooperative rather than defensive. Clasping occurs after she turns toward the male, approaches him, and opens her chelicerae (Bristowe 1958; W. G. Eberhard, pers. obs.); clasping is not possible if the female does not face the male and open her chelicerae.

Other cases cited in the Appendix are also doubtful examples of sexually antagonistic coevolution. In females of some species of the pholcid spiders *Physocyclus* and "*Blechnroscelis*" there are fixed epigynal (genital) spines or apophyses that could keep the male away. But in *Physocyclus* the pair of spines is spaced so that the male can just fit between them, and during coupling there are no signs that females move so as to use them to reject males (A. Peretti, pers. comm.). Similarly, the epigynal apophyses of species ID 2 can also keep the male at a distance, but they are combined with an epigynal "hood" that facilitates mechanical coupling with those males whose cheliceral apophyses are long enough to reach the cavity formed by the hood (Huber 1999). Huber (1999, p. 137) concluded that this design "may reflect selective female cooperation (the female provides a hood for those males able to overcome her obstructive apophyses) rather than female resistance to coercive males. Revealingly the females of several putative close relatives have the cooperative structure (the hood). . . [and] their males' cheliceral apophyses are rather inconspicuous . . . but nevertheless species-specific in form." Although some female odonates have possibly defensive ridges in the area grasped by males, many have apparently cooperative structures such as furrows and indentations (Jurzitza 1974; Battin 1993; Corbet 1999). Still further cases in the Appendix, such as the thickened lining of the female reproductive tract or abdominal cuticle that may reduce male abrasion in *Lucilia* and *Glossina* flies (female species specificity is uncertain in the former), and the female projections that are hooked by male genitalia in *Hispona*, *Tetrix*, and *Clubiona* spiders, have alternative female choice interpretations (e.g., Cordero and Eberhard, unpubl. ms.) that have not been eliminated.

The frequency of lack of female coevolution was lower with genitalic than nongenitalic traits (34.9% vs. 66.7%; $\chi^2 = 10.3$, $df = 1$, $P < 0.005$). This may be the result of my inclusion of data on the genitalia of so many spiders. Spiders are atypical in that in that they lack nerves in their external genitalia, and this lack of innervation may have resulted in unusually frequent male-female morphological coevolution (Eberhard and Huber 1998). The data from nongenitalic structures (which speak more strongly against sexually antagonistic coevolution) may thus be more representative of general trends.

One limitation of the data in the Appendix is their taxonomic bias: they include only arthropods, and mostly only insects and spiders. I have not made a systematic survey of other taxa, but it is clear that the same lack of female morphological coevolution in groups with species-specific male morphology also occurs in at least some taxa. The bursa of nematodes, a flaplike extension of the male cuticle that assists in holding copulating pairs together (Hope 1974; Croll and Wright 1976) is often species specific in form, whereas the

area of the female's body that it contacts seems not to differ between species (Chitwood and Chitwood 1974). Antagonistic female coevolution of female genitalic morphology with that of male genitalia is not evident in primates, a group in which some taxa have elaborate, species-specific male genitalia: "I have been unable to identify a single case among the primates where the mechanical conflict of interest hypothesis might be applicable." (Dixson 1998, p. 247). Whether these cases are representative of other taxa remains to be determined.

A second limitation is the omission of soft membranous female structures contacted by species-specific male structures. I see no reason why such difficult-to-read female structures should be more prone to having defensive traits, but further research will be needed to test this possibility.

Species-Specific Female Defensive Behavior?

I noted above that the antagonistic coevolution hypothesis could be rescued from the contradictions with morphological data if male morphological arms-race traits have generally been counteracted not by female morphology, but rather by female behavior (see also Eberhard and Pereira 1996; Arnqvist and Rowe 2002a,b). Perhaps rapid divergence in the male structures in the Appendix has been driven by rapid divergence in female resistance behavior, and the species-specific differences in male morphology are the means by which males overcome the different behavioral defenses of females of different species. Note that female resistance per se (e.g. Arnqvist and Rowe 2002b) is not enough to fulfill the antagonistic coevolution prediction. It is necessary to show that (1) there are species differences in female behavior, and (2) that these differences are particularly effective (can be considered adaptations) against species-specific traits of the males. To my knowledge, no single case of species-specific female resistance has ever been documented. However, Detailed studies of female resistance are rare, so perhaps this is not a strong criticism. Careful study of female resistance behavior could illuminate these issues.

There are several reasons, however, to doubt that antagonistic coevolution of female behavior is a general explanation for the species-specific male traits of the species in the Appendix. In some groups it is very difficult to imagine any type of forceful female resistance that could possibly select for the ornate species-specific male structures. Take, for example the pholcid spiders in Figure 2B. What female behavior could select for two large flattened cheliceral knobs in one species (upper right corner), rounded knobs in another (second from top at right), double knobs in another (bottom right), and a series of bumps in still another (second from top at left)? In fact, the epigynum of a copulating female pholcid is clamped tightly between the male's chelicerae and his powerful pedipalps, and observations of copulation in numerous genera have never revealed any potentially defensive movements of the epigynum (*Anopsicus*, *Holocnemus*, *Metagonia*, *Spermophora*, *Pholcus*, *Physocyclus*, *Psilochorus*, and *Modisimus*; Huber 1994b, 1995c, 1996, 1997a, 1998a, 2001, 2002; Uhl et al. 1995; Huber and Eberhard 1997; B. Huber pers. comm., A. Peretti pers. comm.). In several other groups in the Appendix that I have observed directly, I saw

no female behavior that could select for the species-specific male designs (in most of them such behavior seems physically impossible, because of mechanical constraints on the female: the mobile thumb of the surstylus of *Microsepsis* flies that presses and twists a female abdominal sternite; the sternal brushes in *Themira*, *Palaeosepsis*, and *Pseudopalaeosepsis* flies that tap the dorsal surface of the female's abdomen; the sternal forks in *Ptilosphen*, *Taenioptera*, and *Micropeza* flies that hold or rub the tip of the female's abdomen; the ventral spines in *Macroductylus* beetles that rub the female's elytra; the setose front legs in *Phyllophaga* beetles that rub the female's pronotum; the superior genitalic claspers in *Glossina* flies that rhythmically squeeze the ventral abdominal membrane of the female; the gonostylus spines in *Hybosciara* flies that rhythmically squeeze female intersegmental membranes; and the surstyli in *Ceratitis* flies that clamp the rigid tip of the female's ovipositor).

Indeed, an argument based on female resistance behavior is not even feasible in several groups in the Appendix, because it is the female that seizes the male rather than vice versa: *Schizomus* schizomids, *Argyrodes* spiders, several genera of erigonine spiders, *Modisimus* spiders, *Leucauge* spiders, *Collops* beetles, *Meleoma* lacewings, and *Julius* and *Chordeuma* millipedes. In still other groups, a female resistance behavior argument seems unreasonable because the male structure is designed to deliver stimuli but not to overcome physical female resistance behavior: the semitransparent platelike male fore tibiae are held against the female's eyes in *Crabro* wasps and apparently provide species-specific visual stimuli; and the genitalic setae of the male apparently provide tactile stimulation of the female's abdomen during copulation in *Aelurus* wasps. Still another set of data that are difficult to reconcile with supposedly species-specific female defensive behavior are the selectively cooperative species-specific female modifications such as pits and grooves that facilitate rather than impede the mechanical mesh of the male with the female.

One further reason to doubt that species-specific female resistance behavior is a general explanation for the lack of female coevolution is that it does not explain why females should so often fail to use potential morphological counter adaptations, and rely instead on behavior. Simple spines, for instance, like those of gerrid females (Arnqvist 1997) would seem to offer a relatively cheap, simple, and effective female defenses.

Female Defensive Sensibilities: Antagonistic Seduction and Sensory Traps

What about the possibility that female defensive counter-adaptations to male morphology are not morphological and not behavioral, but sensory? Perhaps species-specific male morphology stimulates the female in ways that elicit female responses that, because of preexisting female sensitivity and responses that evolved in other contexts, are advantageous to the male but are disadvantageous to the female in the sexual context. Perhaps males are using sensory traps (Ryan 1990; Christy 1995), and female antagonistic coevolution occurs in her sensory system or in the properties of her central nervous system rather than in her morphology.

An example of how this might work is found in a damselfly, in which males stimulate receptors in the female reproductive tract that originally evolved to sense the presence of an egg on its way down the oviduct during oviposition (Córdoba-Aguilar 1999, 2002). Stimulation of these sensilla induces movement or transport of sperm from the female storage organs to the oviduct. The male can thus induce movement of the sperm of previous males to a site where he can then remove it. Females have apparently responded by reducing the number of sensilla. This is not a certain example of antagonistic coevolution, because (1) no disadvantage to the female from having fewer sensilla (e.g., greater numbers of unfertilized eggs) has been demonstrated, and (2) possible benefits to females with fewer sensilla from sons that are better stimulators (due to a stronger bias in paternity in favor of more stimulating males) have not been evaluated. A number of the male structures in the Appendix are moved rhythmically or have other traits that suggest that they function to stimulate the female (see asterisks in the Appendix). But male stimulation does not necessarily imply that the female's response to the stimulus reduces her reproduction. Sensory traps per se are not necessarily damaging to a female's direct reproductive output, and female responsiveness could enable her to obtain sons that are superior stimulators.

I see no way to make direct tests of the possibly antagonistic coevolution of female sensibilities with the data at hand. However, several of the indirect arguments just made with respect to behavior also argue against sensory traps. Antagonistic female sensitivity seems unable to explain cases in which females voluntarily expose themselves to the supposedly damaging stimuli from the male, such as schizomids, *Collops* beetles, *Meleoma* lacewings, *Julius* and *Chordeuma* millipedes, *Argyrodes*, *Modisimus*, *Leucauge*, and erigonine spiders (unless one invents still other antagonistic, irresistible male stimuli that induce this female behavior). Nor does it easily explain the cooperative pits and grooves in females of many taxa. Also unanswered is the question of why female morphological defensive evolution should be so frequently superseded by defensive sensory evolution, when morphological defenses seem simple and effective defenses against antagonistic male seduction.

A more theoretical problem is that an argument that sensory traps result in seriously damaging antagonistic manipulations of the female requires that females be very simple automatons. If females are suffering from being trapped in this way, any female ability to perceive the male's presence, to distinguish between the two types of stimuli, or to sense differences in contexts in which she receives the two types of stimuli, would give her an opportunity to evolve to respond to the male only when it is advantageous for her to do so. Such female limitations often seem unlikely. For instance, it seems very unlikely that a female odonate is unable to perceive any difference between mating and normal oviposition and is thus unable to adaptively modulate her responses to stimuli received from sensilla in her oviduct during mating. In other words, the fact that a male uses a sensory trap in courtship or mating is not evidence that he can coerce a female into acting against her own best interests. Sensory traps are likely to have played important roles in initiating female responses to male stimuli (the "nudge" of Kokko et

al. 2003), especially to male stimulation during copulation (Eberhard 1996). But their continued influence through maladaptive female responses, once sexual selection begins to result in rapid diversification of the male stimuli, is less certain. A related point was made by Thornhill and Alcock (1983): there is a crucial difference between a female perceiving a male signal, and a female responding positively to it. Of course, even if females evolve to reduce the effectiveness of male traps, even a small payoff from a sensory trap that only raises the male's chances of fertilizations slightly can nevertheless be advantageous to the male. Selection is likely to act on males to maintain and improve traps as long as females give even partial responses. The upshot is that sensory traps may often be incompletely effective.

In sum, the possibility that antagonistic stimulation with species-specific male structures that is counteracted by changes in female sense organs and CNS properties cannot be ruled out in many cases. Nevertheless, there are reasons to doubt that it has occurred in several groups, and that it is a general explanation for the trends in the data in the Appendix.

General Implications of the Morphological Data

Selection resulting from female choice does not exclude sexually antagonistic selection, nor vice versa. Both can theoretically act on the same structures at the same time, either reinforcing or counteracting each other (Kokko et al. 2003; Cordero and Eberhard 2003, unpubl. ms.). They could also act sequentially, with for instance sexually antagonistic selection giving an original nudge that then triggers a bout of Fisherian female choice. Deducing the detailed history of the types of selection that have acted on a given trait from its present morphological design does not seem possible.

What, then, can be deduced from the trends in the Appendix? I have argued that many of the data there fail to fit easily with predictions from the sexually antagonistic coevolution hypothesis. Such failures represent evidence against the possibility that sexually antagonistic coevolution is the sole explanation for the rapid divergent evolution of these male genitalic and nongenitalic traits. This does not, however, constitute evidence that sexually antagonistic selection never acted on these male (and female) traits. The hypothesis tested in the Appendix is relatively simple and extreme. Failure to confirm this version does not rule out other more complex and perhaps more realistic versions.

Take, for example, the sepsid flies, a group in which the failure to confirm sexually antagonistic coevolution predictions is relatively clear for the species-specific wing clamping structures on the male front leg (Fig. 3), and in which additional experimental evidence favors female choice. Female coevolution has generally been absent in response to male femoral wing clamps of sepsid flies (Eberhard 2001b, unpubl. ms.; on *Sepsis cynipsea*). No major differences in female shaking (resistance) behavior that could explain the species-specific aspects of male clamping structures are known (Eberhard, unpubl. ms.), and female sensilla near the area grasped by the male also do not show defensive modifications (Eberhard 2001b, unpubl. ms.). In one species, experimental modifications of the male clamping structure and of the female

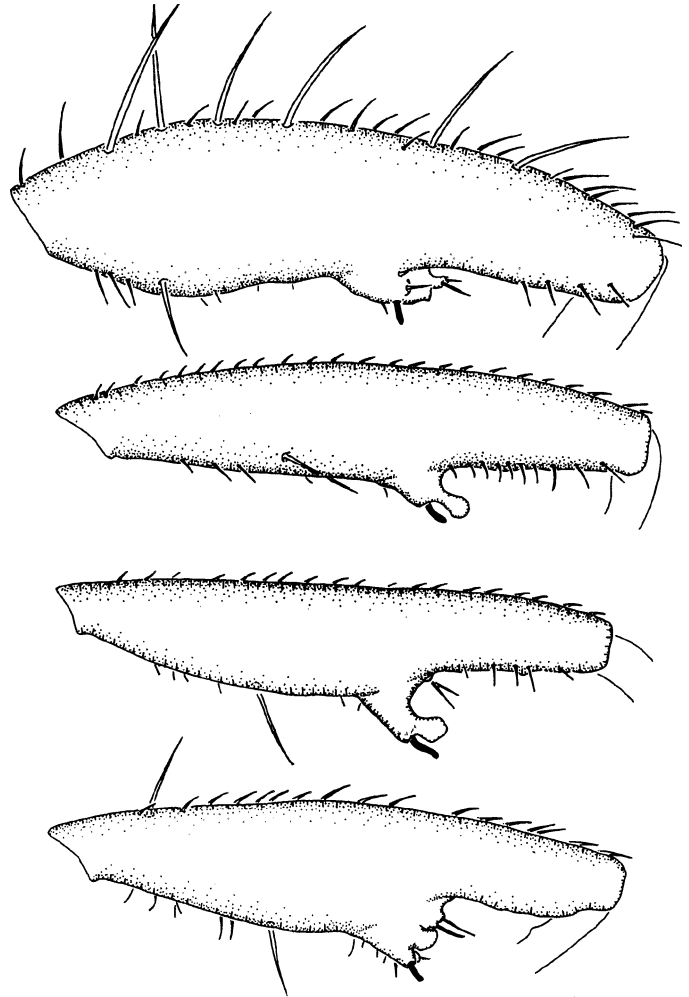


FIG. 3. Lateral views of the male front femur in four species of *Archisepsis* flies, showing the species-specific modified ventral surface that clamps the wing of the female.

structure that it clamps did not reduce the male's ability to hold on to the female, but both strongly reduced her tendency to copulate (Eberhard 2002b), suggesting a female choice function for the male clamp. As in most insects, males cannot physically force intromission (Eberhard 2002a). Nevertheless, a possible role for sexually antagonistic selection at particular stages in the evolution of these male structures cannot be ruled out. For instance, energetic female shaking behavior to dislodge males may have arisen when males first started to mount females, because male riding behavior reduced the female's ability to avoid predators. Early modifications of male femur structure, by coupling the male more tightly to the female's wing, may have represented an antagonistic coevolutionary male response to this female behavior. Later modifications of the male to produce the present diversity may have then evolved due to sexual selection imposed by female choice that favored particular male designs because of their stimulatory rather than their mechanical properties. In addition, the females of one species have evolved a potentially defensive structure on the wing (Eberhard 2001b), so perhaps sexually antagonistic coevolution

also occasionally occurred later in certain lineages. In sum, female choice was probably largely responsible for the details of the designs in the present array of species-specific designs of male front legs in sepsids; but sexually antagonistic coevolution could possibly have occurred at particular times, and have played key roles at certain steps in the process.

Generalization from Morphology to Physiology?

Is it reasonable to generalize from these conclusions and those from other wide-ranging taxonomic surveys that are also based on morphology (Eberhard et al. 1998; Eberhard 2004a) and that also failed to support sexually antagonistic coevolution predictions? Can one predict that rapid divergent evolution of other behavioral and physiological traits involved in male-female interactions have also been only weakly influenced by sexually antagonistic coevolution? The most conservative supposition might be that other types of traits will follow the same pattern documented for morphology. However, there are at least two reasons that sexually antagonistic coevolution might be more likely in physiological traits than in morphology. First, male seminal products may be particularly powerful weapons. In many insects and ticks, male seminal products have strong effects on female reproductive physiology, and indeed the male sometimes uses the same signaling molecules that are used by the female in her own body (summaries in Chen 1984; Eberhard 1996; Wolfner 1997). It may be difficult for a female to exclude such powerfully manipulative products during sperm transfer, and to fail to respond to them once they have entered her body. In a sense, male use of the female's own reproductive hormones is the ultimate sensory trap. Second, male weapons such as seminal products may not be expected to be uniform and simple, because the effectiveness of the male function is not determined by the relatively invariant laws of mechanics, as in morphology, but rather by the perhaps more flexible and variable aspects of female physiology, such as the numbers and properties of membrane receptor molecules.

On the other hand, the female may have many potential ways in which she can control the entry and fate of male products in her body, and thus avoid male-imposed reproductive damage (Eberhard 1996; Pizzari and Snook 2003). Female defenses against chemical weapons could be as simple and cheap as sequestering or degrading seminal products, elevating her response thresholds, reducing the size of her genital cavity where male products are deposited, or decreasing the permeability of her reproductive tract to seminal products. The sex peptide of *Drosophila melanogaster* offers an illuminating example of multiple documented female effects of this sort. Prior to the arrival of the sex peptide at its target in her CNS, the female can potentially modulate its effects by cleaving (or not cleaving) the peptide from the sperm (which carry it from the male to the female); by pumping (or not pumping) it across the cells of her reproductive tract (which have receptor molecules) and into her hemolymph; by degrading (or not degrading) it in her hemolymph; by sequestering (or not sequestering) it in cells associated with her heart before it reaches her CNS; and by binding (or not binding) it with receptor molecules in her CNS (Kubli 1996, 2003, pers. comm.; Ding et al. 2003; Liu and Kubli 2003).

It is probable that there are often multiple possible defensive female mechanisms of this sort (due to the fact that the critical events occur within the female's own body). This implies that at any given moment in evolution females may usually be able to counteract male products and avoid suffering reproductive damage from them. The experimental demonstration of male potential to damage females physiologically (e.g., Rice 1996) is not equivalent to showing that males actually damage females under natural (or even under laboratory) conditions. Further data are needed to test these ideas.

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APPENDIX

Frequency of coevolution of female structures that mesh with species-specific male structures. Male structures are species-specific in all groups; characteristics of the female structures that they contact (species-specific modifications, possible defensive designs) are given. Species specificity was counted when congeneric species differed. The “likely functions” given for nongenital male structures do not include possible stimulation of the female. Asterisks indicate groups in which movements of the male, or the design of male structure (e.g. glands associated with structure that is seized by the female with her mouth), strongly suggest male structures used to stimulate females.

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
A. Male genitalia (primary or secondary) and spermatophores							
Orthoptera							
Tettigoniidae							
<i>Anonconotus cerci</i>		lateral memb. abd.	no		no ^a	Vahed 2002	Carron et al. 2002
<i>Uromenus cerci</i>		copulatory groove	yes		no ^b	Rentz 1972	Nadig 1994
Hemiptera							
Gerridae							
<i>Gerris</i>	length clasper	spines, ventral	yes		yes	Rowe 1994; Arnqvist 1997	Arnqvist and Rowe 2002a; Arnqvist 1989
<i>Aquarius</i>	phallus	genital segs.	no		no	Fairbairn et al. 2003	Fairbairn et al. 2003
Homoptera							
Cicadellidae							
<i>Euscelis</i>	penis	reprod. tract	no ^b		? ^d	Müller 1957	Müller 1957
Diptera							
Sepsidae							
<i>Archisepsis*</i> , <i>Themira</i> , <i>Microsepsis*</i> , <i>Sepsis*</i> , <i>Sepsidomorpha</i> , <i>Pseudopalaeosepsis</i>	surstyli	abd. sternite VI and the surrounding membranes	no		no	Eberhard and Pereira 1996; Eberhard 2001a, 2003, unpubl. ms.	Pont 1979; Steyskal 1987; Eberhard and Pereira 1996; Eberhard 2001a, 2002a, unpubl. ms.
<i>Archisepsis</i>	aedeagus	dorsal proj. bursa	no		no	Eberhard and Huber 1998	Eberhard and Huber 1998
Sciaridae							
<i>Hybosciara gigantea*</i>	gonostylus	abd. memb.	no		no	Eberhard 2002d	Eberhard 2002d
Ceratopogonidae							
Several tribes	gonostylus	abd. sternite	?yes		no ^b	Downes 1978	Downes 1978
Drosophilidae							
<i>Drosophila</i> (4 spp.)*	genital arch	abd. tergite	no ^e		no ^e	Robertson 1988; Eberhard and Ramirez, in press	Robertson 1988; Eberhard and Ramirez, in press
	surstyli	oviscape valves	no ^f		no	Eberhard and Ramirez, in press	Eberhard and Ramirez, in press
Tephritidae							
<i>Ceratitis</i>	surstyli	aculeus	yes		no ^g	Eberhard and Pereira 1994	DeMeyer 2000

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
Psychodidae <i>Phlebotomus aedeagus</i>	spermathecal duct		yes		yes (length)	Ilango and Lane 2000	Ilango and Lane 2000
Calliphoridae <i>Lucilia</i>	phallosome	bursa copulatrix	? ^h		yes (thickness)	Lewis and Pollock 1975; Merritt 1989	Lewis and Pollock 1975
Glossinidae <i>Glossina tabaniformis</i>	harpes	signum (ant. end uterus)	yes		yes (pre-vent abrasion)	Jordan 1963	Jordan 1963
<i>G. spp.*</i>	superior clasps	vent. surf. abd.	no		no ⁱ	Vanderplank 1948; Squire 1951; Pollock 1974; pers. obs;	Potts 1970; W. G. Eberhard, pers. obs.
	9th tergo-sternum	abd. tergite 9 (medio-dors. plate)	yes ^j		no ^j	W. G. Eberhard, pers. obs.	Patton 1936; Potts 1970; pers. obs.
Coleoptera Carabidae <i>Carabus insulicola</i>	cop. piece	vaginal apophysis	yes		? ^k	Takami 2003	Ishikawa 1991 in Takami 2003
Chrysomelidae <i>Chelymorpha alternans</i>	flagellum	spermathecal duct	yes		yes ^l	Rodriguez 1994; Rodriguez et al. 2003	Rodriguez et al. 2003
Melolonthidae <i>Macrodactylus</i>	paramere	hemisternite	yes		no (weak fit with male)	Eberhard 1993a, unpubl. ms	Carrillo and Gibson 1960; Eberhard 1993a, in prep.; Arce-Perez and Morón 2000
	internal sac	vagina	no ^m		no ^m	Eberhard 1993a, unpubl. ms	
Scarabeidae <i>Onthophagus</i>	internal sac	vagina/entrance spermathecal duct	yes		? ^c	Zunino 1988	Zunino 1971; Piera and Zunino 1983, 1984
Hymenoptera Apidae <i>Bombus</i>	stipes, volsella, squama	sternite	no ⁿ		?no ^a	Richards 1927	Richards 1927
Tiphiidae <i>Elaphroptera</i> _o	sternite VIII	tergite VI	yes ^p		no ^q	Toro and Carvajal 1989; Toro and Elortegui 1994	Toro and Carvajal 1989; Toro and Elortegui 1994

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
	paramere	tergite VI	yes ^p		no ^q		
	gonocoxite	sternite VI	yes ^p		no? ^r		
	penis valve	bar betw. rami	yes		? ^c		
	auricular process	ventral plate	yes		no ^b		
<i>Aeleurus</i>	paramere	gaster	no		no	Eberhard 2004b	Eberhard 2004b
Lepidoptera							
Satyridae							
<i>Maniola jurtina</i>	clasper	ovipositor	no		no ^p	Goulson 1993	Goulson 1993
Noctuidae							
<i>Apamea</i>	vesica	bursa, bursal duct	yes		no ^s	Mikkola 1992	Mikkola 1992
Papilionidae							
Several genera	claspers, harpes	abdomen	yes		? ^d	Jordan 1896; Tyler et al. 1994	Jordan 1896; Tyler et al. 1994
Araneae							
Nesticidae							
<i>Nesticus</i>	palpal bulb	epigynum	yes		? ^t	Huber 1993	Huber 1993
Agelenidae							
<i>Hispona, Tetrax</i>	palpal bulb, process	epigynum	yes		yes ^u	Huber 1994a	Huber 1994a
Dictynidae							
<i>Dictyna</i>	palp bulb, tib. apophysis	epigynum, abd.	yes		no ^b	Huber 1995a	Kaston 1948; Huber 1995a
Thomisidae							
<i>Misumenops, Philodromus</i>	palp bulb, tib. apophysis	epigynum	yes		no ^b	Huber 1995a	Kaston 1948; Huber 1995a
Salticidae							
<i>Euophrys</i>	palp bulb, tib. apophysis	epigynum	yes		no ^b	Huber 1995a	Kaston 1948; Huber 1995a
Anyphaenidae							
<i>Anyphaena</i>	palp bulb, tib. apophysis	epigynum	yes		no ^b	Huber 1995b	Kaston 1948; Huber 1995b
Clubionidae							
<i>Clubiona</i>	palp bulb, tib. apophysis	epigynum	yes		yes? ^u	Huber 1995b	Kaston 1948; Huber 1995b
Theridiidae							
<i>Tidarren</i>	palpal bulb	epigynum	yes		no ^b	Knoflach and van Harten 2000	Knoflach and van Harten 2000
Scorpiones							
Bothriuridae (many)	spermatophore	genital operculum, space betw. coxae	sometimes		no	Peretti 2003	Peretti 2003, pers. comm.

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
Diplopoda							
Spirostreptomorph							
Several	gonopod	vulva	no ^v		?no ^a	Kraus 1968	Kraus 1968
Chordeumidae							
<i>Taiyutyla</i>	gonopod	genitalia	no ⁿ		?no ^a	Shear 1976	Shear 1976
B. Nongenitalic male structures							
Odonata							
Several families	abd. appendages	head/thorax	often	grasp	yes/no ^w	Corbet 1962, 1999; Jurzitza 1974, 1975; Robertson and Patterson 1982	Kormandy 1959; Paulson 1974; Jurzitza 1975
Ephemeroptera							
Several genera	leg I	prothx, mesothx	no ⁿ	grasp	?no ^a	Spieth 1940; Edmunds et al. 1976	Edmunds et al. 1976
Plecoptera							
Several genera	abd.segs.	abdomen	no ⁿ	press	?no ^a	Brinck 1956a,b	Brinck 1956a,b
Zoraptera							
Zorotypidae							
<i>Zorotypus</i> *	tergal setae	sternites	no	tap	no	Choe 1995	Choe 1989
Dermaptera							
Labiidae							
<i>Labia</i>	forceps	forceps	no	grasp	no	Briceño and Eberhard 1995	Brindle 1976
Hemiptera							
Gerridae							
<i>Gerris</i>	abd. segs.	tip abd.	yes	grasp	yes	Arnqvist and Rowe 2002a	Arnqvist and Rowe 2002a
<i>Rheumatobates</i>	antenna	antenna	no ⁿ	grasp	no ^a	Silvey 1931	Hungerford 1954, pers. obs.
	leg III	body	no	grasp	no ^x	Silvey 1931	Hungerford 1954, pers. obs.
Diptera							
Sepsidae							
<i>Palaeosepsis</i>	front legs	base wing	no (n = 5)	grasp	no (n = 5)	Eberhard 2001b, unpubl. ms.	Port 1979; Steyskal 1987; Ozerov 1993
<i>Archisepsis</i>			yes (n = 1)		yes (n = 1)		
<i>Microsepsis</i>							
<i>Themira</i> *	sternal lobe	dorsum abd.	no	rub	no	Eberhard 2001c, 2002c, 2003	Ozerov 1998; Eberhard unpubl. ms.

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
<i>Palaeosepsis</i> *							
<i>Pseudopalaeosepsis</i> *							
Micropezidae							
Several genera	sternum 6	tip abd.	no	rub	no ^y	Ortiz 2002, pers. obs. ^y	Merritt and Peterson 1976; Paes de Albuquerque 1980; Steyskal 1987, pers. obs. ^y
Coleoptera							
Carabidae							
<i>Pasimachus</i>	mandibles	jct. pro-meso. thorax	no ^z	grasp	no	Alexander 1959	Bänninger 1950; Alexander et al. 1997
Meloidae							
<i>Meloe</i>	antenna	antenna	no ^z	grasp ^{aa}	no	Pinto and Selander 1970	Pinto and Selander 1970
<i>Pyrota</i>	antenna	antenna	no ^z	grasp	no	Selander 1964	Denier 1934
<i>Epicauta</i> (some)*	maxillary palp leg I	elytra leg III	no ^z	tap	no	Selander and Mathieu 1969	Selander and Mathieu 1969
	antenna	antenna	no ^{n,z}	wrap around	no? ^a		
Melyridae	maxillary palp	elytra, pygidium	no ^z	tap	no ^p	Pinto 1980	Pinto 1980
	<i>Collops</i>	antenna	mandibles	no ⁿ	seized by female	? ^d	P. Smith, pers. comm.
Melolonthidae							
<i>Macroductylus</i>	front leg	pronotum	no (n = 4) yes (n = 1)	grasp	no	Eberhard 1993a, unpubl. ms.	Carrillo and Gibson 1960; Eberhard, unpubl. ms.
<i>Phyllophaga</i> *	antenna	eye	yes	cover eye	yes	Eberhard, unpubl. ms.	Eberhard, unpubl. ms.
	abd. sternite	abd. tergite	yes/no	press	yes/no	Eberhard 1993b	Morón 1986; Eberhard 1993b
	front leg	pronotum	no	rub	no	Eberhard 1993b	Morón 1986; Eberhard 1993b
Neuroptera							
Chrysopidae							
<i>Meleoma</i> *	antenna frontal horns and cavity	head mouthparts	no ^{n,h} no ^h	grasp female feeds at it	?no ^a ?no ^a	Tauber 1969 Toschi 1965; Tauber 1969	Tauber 1969 Tauber 1969
Hymenoptera							
Apidae							
<i>Anthidium</i>	tergum gas- ter ^{bb}	sternum VI gaster	yes	press	no? ^{cc}	Batra 1978; Toro and Rodriguez 1997	Toro and Rodriguez 1997
	sternum gaster	tergum VI gaster	yes	press ^{dd}	no	Toro and Rodriguez 1997	Toro and Rodriguez 1997

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
<i>Callonychium</i> <i>Xylocopa</i>	sternites gaster middle tarsi	tergites gaster eye	yes no	press ^{dd} cover eye	yes/no ^{ee} ?no ^a	Toro 1985 Anzelberger 1977	Toro 1985 Hurd and Moure 1963
<i>Leioproctus</i>	mandibles	tergite, gaster	yes	grasp	no ^b	Toro and de la Hoz 1976	Toro and de la Hoz 1976
Sphecidae <i>Crabro</i> *	front tibia	eye	no ^z	cover eye	no ^{ff}	Low and Wcislo 1992; Mat- thews et al. 1979	Bohart 1976, pers. obs.
Eulophidae <i>Mellitobia</i>	antenna	antenna	no ⁿ	manip.	?no ^a	Evans and Matthews 1976	Evans and Matthews 1976; R. Matthews, pers. comm.
Vespidae <i>Zethus</i> *, <i>Polistes</i> *	antenna	antenna	no ^z	stroke	no	Evans and Eberhard 1970	Bohart and Stange 1965; van der Vecht 1971, pers. obs.
<i>Belanogaster</i> *	antenna	antenna	no ^z	stroke	no	Piccioli and Pardi 1970	Richards 1982
Mecoptera Several groups	notal organ	body	usually no	grasp	no	Thornhill 1980;	G. Byers, pers. comm.;
<i>Boreus</i>	wings	antennae, rostrum	no ⁿ	grasp	? ^d	Cooper 1974	Cooper 1972
Collembola Symphyla (some)	antenna	antenna	no ^p	grasp	no	Mayer 1957	Massoud and Betsch 1972
Onychophora Peripatopsidae Several genera	head organ	vagina	no	insert sptop.	no ^{gg}	Tait and Briscoe 1990; Tait and Nor- man 2001; Reid 2000	Reid et al. 1995; Tait and Nor- man 2001; Reid 2000
Araneae Antrodiaetidae <i>Atypus</i>	chelicerae	chelicerae	no ^z	grasp	no	Coyle 1968; Coyle and Icenogle 1994	Coyle 1968
Araneidae <i>Araneus</i>	tibia of leg II	femur I, II	no	grasp	no	Grasshoff 1964	Grasshoff 1964
Dipluridae <i>Euagrus</i>	leg II	leg II	no ⁿ	grasp	no	Coyle 1986	Coyle 1986, 1988
Several ischno- thelines	leg II	pedipalp	no ^z	grasp	no	Coyle and O'Shields 1990	Coyle 1995

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
Linyphiidae Several erigonines*	cephalothorax	mouthparts ^{hh}	no ^z	seized by female	no? ^a	Bristowe 1958; Meijer 1977	Milledge 1980, 1981a,b; Hormiga 2000
Pholcidae							
<i>Anopsicus</i>	chelicerae	sternum/pedicel ⁱⁱ	no	lift	no	Huber 1998b	Huber 1998b
“ <i>Blechnoscelis</i> ”	chelicerae	epig. plate	yes	press	yes	Huber 1999	Huber 1999
<i>Holocnemus</i>	chelicerae	epig. plate	yes	press	no ^b	Huber 1995c	Huber 1995c
<i>Metagonia</i>	chelicerae	epig. plate	yes	press	no	Huber 1996	Huber 1996
	clypeal apophysis	epig. plate	no	press	no	Huber 1996	Huber 1996
<i>Modisimus</i> *	clypeal lobe ^{ij}	mpts.	no ^z	female feeds at it	?no ^a	Huber 1997c	Huber 1997a
	chelicera	epig. plate	yes/no	press	no ^b	Huber 1998a,b	Huber 1998b, 1999
<i>Pholcus</i>	chelicerae	epig. plate	yes	press	no? ^u	Huber 1995c; Uhl et al. 1995	Huber 1995c, 2001; Uhl et al. 1995
<i>Physocylus</i>	chelicerae	epig. plate	yes	press	no/yes ^{kk}	Huber and Eberhard 1997	Huber 1997a, 2000
<i>Psilochorus</i>	chelicerae	epig. plate	no	press	no	Huber 1994a	Huber 1997b
<i>Spermophora</i>	palp apophysis	abdominal pocket	?	brace genitalia	no ^b	Huber 2001	Huber 2001
Tetragnathidae							
<i>Leucauge</i>	ant.surf. chelicerae	chelicera	no	press ^{ll}	no	Eberhard and Huber 1998; Preston-Mafham and Cahill 2000	Chrysanthus 1963, pers. obs.
<i>Tetragnatha</i>	chelicerae	chelicerae	yes	grasp	?yes ^{mm}	Kaston 1948	Kaston 1948; Chickering 1959
Theridiidae							
<i>Argyrodes</i> *	cephalothorax	mouthparts ^{hh}	no ^z	seized by female	no ^a	Lopez and Emerit 1979	Exline and Levi 1962
Amblypyga							
Phryniidae							
<i>Phrynus gervaisii</i>	spermatophore	genital operculum	yes	press	no ⁿⁿ	Weygoldt 1998, 1999; Peretti 2002	Weygoldt 1998, 1999; Peretti 2002
Schizomida							
Schizomidae							
<i>Schizomus</i> *	telson	chelicerae	no ^z	seized by female	? ^d	Schaller 1971	Rowland and Reddell 1979
Scorpiones							
Buthidae (several)	pedipalp	pedipalp	no	grasp	no	Peretti 2001	Peretti 2001, pers. comm.

APPENDIX. (Continued)

Taxon	Species-specific male contact structure	Female structure contacted by the male structure	Female structure that meshes with male structure is species-specific?	Probable function	Female structure has a possibly defensive design?	References	
						Function	Female structures
Acari							
<i>Glycyphagus</i> (mite)	tibiae I,II	setae	yes (some)	grasp ^{oo}	yes	B. O'Connor, pers. comm.	B. O'Connor, pers. comm.
two gen. parasitids	leg II	leg IV	no ^z	grasp	? ^d	Hartenstein 1962	Hartenstein 1962
Crustacea							
Anostraca							
eubranchipods	2nd antenna	dorsum	no ⁿ	grasp	?no ^a	Pennak 1978; Belk 1984	Pennak 1978; D. Belk, pers. comm.

^a Deduced from lack of modification in the area of the female that is contacted by the male.

^b Grooves and pits in female probably serve to anchor the structures of the male.

^c Deduced from fact that males of different forms with different penis morphology bred readily with females of different forms.

^d Insufficient detail of fit to judge.

^e Conclusions to the contrary by Robertson (1988) are probably incorrect—see Eberhard and Ramirez, in press.

^f Small differences between species do not correspond to differences between male surstyli.

^g Modifications of female ovipositor tip (aculeus) probably associated with oviposition substrate; male surstylus does not grasp the portion of aculeus that is most often modified.

^h No mention of possible differences between females.

ⁱ Female sternite and intersegmental membrane simple and featureless, not mentioned in lists of characters used to separate species. In *G. palpalis* females have a soft "mating cushion" (Squire 1951) which may reduce damage inflicted by the male's superior claspers, but whose mechanical properties do not impede clasping by the superior claspers.

^j My observations are of species in the *morsitans* group, whereas comparative morphological data are of the *fusca* (Patton 1936) and *palpalis* (Potts 1970) species groups; the assumption is that the male's ninth tergo-sternum has similar functions in these groups. The female tergite 9 is very simple in form, and varies interspecifically in relatively subtle details; it differs less intraspecifically in *G. morsitans* than some male genitalic traits (Vanderplank 1949).

^k No defensive structures were noted in the long soft sac of the female, but proper fit may be necessary to align male genitalia to transfer sperm successfully.

^l The female duct is extremely long.

^m Soft, large cavity without apparent valve.

ⁿ Specific statement to this effect was made by author (Richards 1927).

^o Male carries phoretic female with genitalic coupling; female thus presumably gains from tight genitalic fit.

^p Deduced from drawing.

^q Species-specific traits of female tergite have no obvious relation to those of male sternite VIII or parameres. The parameres are not designed to exercise force on the female. Judging by their rigid pilosity, and the apparent stimulatory use in another thynnine (Eberhard 2004b), they may serve to stimulate the female.

^r Attributed function of male-female mesh is to aid the male penis to encounter the entrance of the female spermathecal duct.

^s Female modification involves expansions and different angles between more or less sclerotized ducts and outpouchings into which male spines and inflatable membranous sacs fit; no valves or blocking sclerites or spines are described.

^t Too complex to judge; no moveable female structure or valve that could facultatively block the male.

^u Male hooks female projection that might have previously fended off males; no moveable female structure or valve that could facultatively block the male.

^v Female described only as "saclike," in contrast to great complexity of male.

^w Some females have pits or grooves (not defensive), and others ridges (lamina) (possibly defensive). In some coenagrionid species, females have apparent sense organs in the region contacted by the male. In one damselfly, stimulation of this area of the female by the male abdominal appendages serves to elicit copulation by the female (Loibl 1958; Kreiger and Kreiger-Loibl 1958).

^x Relatively smooth surface and no defensive prominences.

^y Four genera observed.

^z Lack of species specificity deduced from lack of mention among characters used to distinguish species.

^{aa} Female can free her antennae with apparent ease, so physical restraint is apparently not the function.

^{bb} Could, on the basis of its design, also be used in male-male aggression; no direct observations available.

^{cc} Both grooves and notches (possibly cooperative) and projections (possibly defensive) exist in female, and mesh with complementary male contours; no sign of facultative female resistance designs.

^{dd} By pressing tightly against the female, the male may hold onto her more tightly or insert his genitalia more deeply.

^{ee} Two portions of female contacted by the male modifications project into male pockets (one is grasped there by the male) as if to fend off male; one other male structure (sternite III) presses the soft and unmodified distal margin of female tergite V.

^{ff} Semitransparent tibial plate has complex, species-specific color patterns, and thus probably provides an important visual stimulus rather than a tactile stimulus to the female.

^{gg} Vaginal insemination with head structure confirmed directly only for *Florelliceps* and *Planipapillus*; lack of female modification, deduced from lack of mention in species descriptions of this area of the female, is tentative because internal portion of the vagina, where male head structure is presumably inserted, was not described (however, see Reid 2000).

^{hh} Glandular tissue associated with male structures suggests chemical courtship of the female.

ⁱⁱ Long process present in some but not all species in the genus.

^{jj} Only one species in large genus with this lobe (which has an associated gland, suggesting chemical courtship).

^{kk} Pair of small spikes in *P. dugesii* could impede male mesh when he is misaligned, but not when he is aligned (A. Peretti, pers. comm.).

^{ll} Female grasps male rather than vice versa.

^{mmm} Both male and female must open chelicerae for grasp to occur, so grasp is not entirely coercive.

ⁿⁿ Female must open gonopore to allow spermatophore to enter.

^{oo} Leg with notch that apparently functions as a clamp; the species-specific male comb appears designed to contact (stimulate?) the female rather than forming a part of the clamp.