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The evolution of asymmetric genitalia in spiders and insects

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ABSTRACT

Asymmetries are a pervading phenomenon in otherwise bilaterally symmetric organisms and recent studies have highlighted their potential impact on our understanding of fundamental evolutionary processes like the evolution of development and the selection for morphological novelties caused by behavioural changes. One character system that is particularly promising in this respect is animal genitalia because (1) asymmetries in genitalia have evolved many times convergently, and (2) the taxonomic literature provides a tremendous amount of comparative data on these organs. This review is an attempt to focus attention on this promising but neglected topic by summarizing what we know about insect genital asymmetries, and by contrasting this with the situation in spiders, a group in which genital asymmetries are rare.

In spiders, only four independent origins of genital asymmetry are known, two in Theridiidae (*Tidarren/Echinotheridion*, *Asygyna*) and two in Pholcidae (*Metagonia*, *Kaliana*). In insects, on the other hand, genital asymmetry is a widespread and common phenomenon. In some insect orders or superorders, genital asymmetry is in the groundplan (e.g. Dictyoptera, Embiidina, Phasmatodea), in others it has evolved multiple times convergently (e.g. Coleoptera, Diptera, Heteroptera, Lepidoptera). Surprisingly, the huge but widely scattered information has not been reviewed for over 70 years. We combine data from studies on taxonomy, mating behaviour, genital mechanics, and phylogeny, to explain why genital asymmetry is so common in insects but so rare in spiders.

We identify further fundamental differences between spider and insect genital asymmetries: (1) in most spiders, the direction of asymmetry is random, in most insects it is fixed; (2) in most spiders, asymmetry evolved first (or only) in the female while in insects genital asymmetry is overwhelmingly limited to the male. We thus propose that sexual selection has played a crucial role in the evolution of insect genital asymmetry, *via* a route that is accessible to insects but not to spiders. The centerpiece in this insect route to asymmetry is changes in mating position. Available evidence strongly suggests that the plesiomorphic neopteran mating position is a female-above position. Changes to male-dominated positions have occurred frequently, and some of the resulting positions require abdominal twisting, flexing, and asymmetric contact between male and female genitalia. Insects with their median unpaired sperm transfer organ may adopt a one-sided asymmetric position and still transfer the whole amount of sperm. Spiders with their paired sperm transfer organs can only mate in symmetrical or alternating two-sided positions without foregoing transfer of half of their sperm.

We propose several hypotheses regarding the evolution of genital asymmetry. One explains morphological asymmetry as a mechanical compensation for evolutionary and behavioural changes of mating position. The morphological asymmetry *per se* is not advantageous, but rather the newly adopted mating position is. The second hypothesis predicts a split of functions between right and left sides. In contrast to the previous hypothesis, morphological asymmetry *per se* is advantageous. A third hypothesis evokes internal space constraints that favour asymmetric placement and morphology of internal organs and may secondarily affect the genitalia. Further hypotheses appear supported by a few exceptional cases only.

Key words: asymmetry, genitalia, copulatory organs, mating position, Araneae, Insecta.

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I. INTRODUCTION

Bilateral symmetry is the default state in most higher animals, yet the breaking of symmetry is a pervading phenomenon that has attracted considerable attention (reviews in Ludwig, 1932; Neville, 1976; McManus, 2002; Levin, 2005). Widely known examples are fiddler crab claws, cricket stridulating wings, snail shells, flatfish, owl ears, mammalian hearts, and human brains. The multiple independent origins of morphological asymmetry, together with increasingly robust phylogenetic trees, permit generation of hypotheses about the evolution of asymmetry and even about modes of evolution (Palmer, 1996*a*, 2004, 2005). For example, transitions from random asymmetry (antisymmetry) to directional asymmetry have been used to argue for genetic assimilation (“phenotype precedes genotype”) (Palmer, 1996*a*, 2004).

Asymmetries are also widespread in arthropod genitalia, but in comparison to the above examples, genital asymmetries have largely been ignored. Arthropod genitalia often provide crucial taxonomic information, and primarily for this reason a huge literature exists containing countless scattered data on genital symmetry and asymmetry. However, the most recent serious review of available information dates from 1932, included in a general text on animal asymmetry (Ludwig, 1932). Since the book was written in German and has never been translated into English, its impact was limited. Before that, only Lamb (1922) and Richards (1927) reviewed part of the available evidence in the context of mating positions and sexual selection.

This review was initially born from an effort to understand genital asymmetry in spiders. In contrast to insects, spiders offer very few cases of asymmetry in general, and the first cases of genital asymmetry have been discovered only recently (Huber, 1997, 2004*a*, 2006; González-Sponga, 1998; Agnarsson, 2006). We reasoned that an explanation for the frequent evolution of insect genital asymmetries might throw some light on the rare evolution of spider asymmetries. We were surprised to find that such an explanation has never been proposed. Major contributions to the morphology and evolution of animal (or specifically insect) genitalia do not even mention asymmetry (Snodgrass, 1935, 1957; Matsuda, 1976; Eberhard, 1985).

The volume and language of Ludwig’s (1932) book may be an impediment, but we believe that the widely scattered distribution of the data in a group as immense as the insects is the most intimidating aspect in a review such as this. This is especially true for one of our aims: to simply document in which taxa genital asymmetry occurs. Our second aim was to trace the evolution of asymmetry. A few recent studies on certain fly, moth, true bug, and planthopper taxa have included genital asymmetry in matrices for cladistic analysis, but in most cases we had to map symmetry and asymmetry on available phylogenies. Missing data and unstable phylogenies often resulted in very preliminary conclusions. Our third aim was to test for a correlation between genital asymmetry and mating positions. This required reviewing still another segment of insect literature, but in this case we could largely build on the excellent review by Alexander (1964). The final important piece in the puzzle was genital mechanics. The details of genital movement and contact (especially ‘direct’ *versus* ‘inverse’ correlation, see below) relate genital morphology to mating positions.

Even though we have profited from the help of numerous specialists, we are uncomfortably aware of the incompleteness of our efforts. However, we anticipate that most of our conclusions rest on solid evidence and that the knowledge gaps we identify are real and will trigger new interest and research into a ubiquitous yet neglected phenomenon. In this sense, paraphrasing the last sentence in Eberhard’s (1985) seminal book on animal genitalia, this review is an attempt to bring genitalic asymmetry, long neglected by those evolutionary biologists outside of taxonomy, into the mainstream of evolutionary theory.

II. GENITALIA

In the last chapter of his book on animal genitalia, Eberhard (1985) remarked that his book had “the dubious distinction of questioning usefulness of its own title”. The problem results from the fact that genitalia are traditionally classified by their functional association with sperm transfer. However, some of the structures so classified may have additional or alternative functions like courtship or competitive insemination. This blurs the distinction between genitalia and certain ‘non-genital’ structures that also have specific functions during sperm transfer, like clasping or stimulating.

Despite these semantic problems, we will largely adhere to Eberhard’s (1985) operational definition of genitalia. In this sense, male genitalia are “structures that are inserted in the female or that hold her near her gonopore during sperm transfer”. This definition includes spermatophores, even if these are not always transferred directly by the male. Female genitalia are “those parts of the female reproductive tract that make direct contact with male genitalia or male products (sperm, spermatophores) during or immediately following copulation”. Excluded by these definitions are internal structures such as testes and ovaries, accessory glands, and usually also receptacles. Included are claspers and stimulatory structures close to the gonopore, excluded are structures with the same functions during copulation but located elsewhere (e.g. male sminthurid antennae, male boreid wings, male embiid mandibles, etc.). Even though the distinction may be somewhat fuzzy, it agrees very well with what taxonomists and morphologists do or do not classify as genitalia (or terminalia in insects). Major texts on animal genitalia use or imply similar or identical definitions (e.g. Snodgrass, 1936, 1957; Tuxen, 1970; Scudder, 1971).

A rather hotly debated topic regarding insect genitalia is homology and terminology (Snodgrass, 1936, 1957; Scudder, 1971). Many hundreds of terms are being used, and most insect orders have their own specific terminology (Tuxen, 1970). Terms like parameres may denote very different structures in different orders, and different terms often denote structures believed to be homologous. We will usually not enter this debate but simply adopt the terms used by taxonomists.

Important early papers on mating positions and genital mechanics in insects (Lamb, 1922; Richards, 1927) have introduced a complex terminology that we will adopt only in part. Instead of terms like ‘linear position’ or ‘male vertical position’ we use more intuitive terms like ‘end-to-end position’ or ‘male-above position’ (Fig. 1). We adopt the term ‘false male-above’ position, meaning that the male sits above the female but bends his abdomen sideways around her so that his genitalia contact the female from below. Instead of ‘pose’ and ‘position’ we use initial (coupling) and final (mating) position, without implying that specific functions like sperm transfer or stimulation are restricted

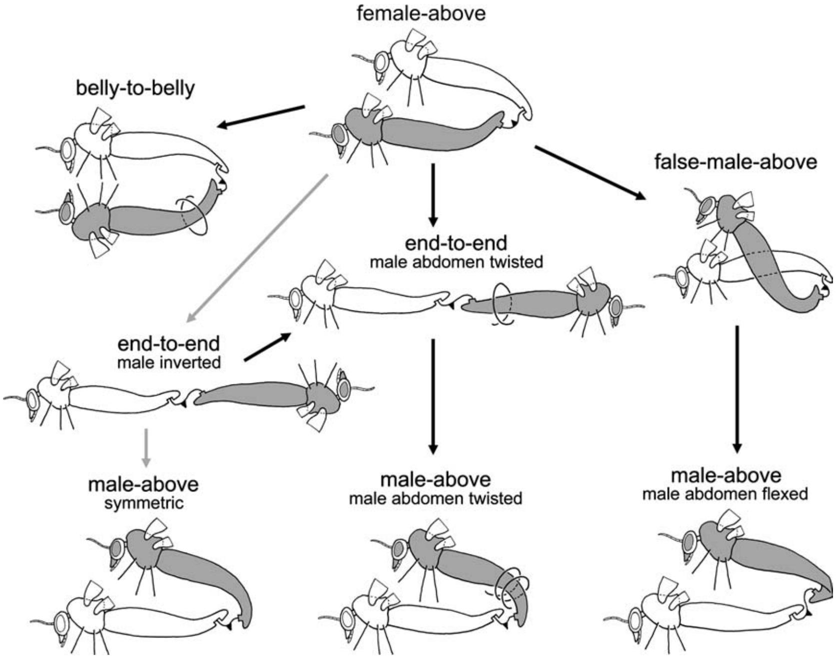

Fig. 1. Most common insect mating positions, schematic, with proposed evolutionary changes. Males are shown in grey. Grey arrows indicate the only possible way for the male to get on top of the female without involving asymmetry. All other deviations from the plesiomorphic female-above position result in asymmetry due to flexing or twisting of the male abdomen (or genitalia, not shown here). Note that the dorsal sides of the male genitalia (marked with small triangles) always contact the ventral sides of the females (inverse genital correlation). Modified from McAlpine (1981).

to any of these positions. We use twist and flexure as proposed by Lamb (1922): the former implies rotation along the longitudinal axis, the latter not. Male and female genitalia (and abdomens) may contact in two ways: morphological dorsal sides against each other ('direct correlation') or dorsal against ventral ('inverse correlation').

III. ASYMMETRY

Most authors have followed van Valen's (1962) distinction of three main categories of asymmetries. (1) Fluctuating asymmetry refers to the ubiquitous, usually small deviations from perfect symmetry due to the organism's inability to develop in precisely determined paths. (2) Antisymmetry refers to cases where both left- and right-sided individuals occur within a population, with no or few symmetrical individuals. (3) Directional asymmetry occurs when all individuals (except occasional freaks) in a population are either left- or right-sided. A more fundamental and important dichotomy was noted by Palmer (1996*b*) who distinguished between "well-behaved characters" (those that show fluctuating asymmetry) and "poorly behaved characters" (those that show adaptive, i.e. directional or bidirected asymmetry). Characters in the former category have an *a priori* ideal: perfect symmetry. Any departure from symmetry in this category is fluctuating and due to developmental noise. In characters of the second category, departures from symmetry are at some point affected by direct action of genes, although the direction of the asymmetry may not be heritable in species where direction is random (Palmer, 2005). In these cases, asymmetry is often conspicuous and not an accident but the organism's response to selection.

Recent decades have seen a flood of papers on fluctuating asymmetry, mainly due to its value as a tool for quantifying developmental stability (Palmer & Strobeck, 1986; Møller & Swaddle, 1997). In comparison, conspicuous asymmetries have received much less attention (see Palmer, 2005, and references therein, for exceptions). Arthropod genitalia offer a huge but almost completely unexplored source of information on the origin of conspicuous asymmetries, and it is only these asymmetries that are the focus of our review. The only conspicuous genital asymmetries we ignore are those resulting from gynandromorphism. Gynandrous individuals are a recurring phenomenon both in insects and in spiders (e.g. Meisenheimer, 1930), but their asymmetry is accidental and not adaptive.

A unified terminology for biological asymmetries was recently proposed by Palmer (2005). We largely follow this proposal but deviate in two minor respects. First, for reasons of simplicity and lack of data, we do not differentiate between (pure) antisymmetry (both forms explicitly equally frequent) and enantiomorphy (no statement about frequency). When we use antisymmetry we imply that both forms occur and that none of them represents just an occasional reversal. Second, we prefer to use the terms 'one-sided' and 'random-sided' (rather than 'handed' and 'random-handed') in combination with behaviour (mating position, direction of abdomen twisting). When an individual male can mate either on the left or right side of the female (or twist his abdomen in either direction), we call this a random-sided mating position (or twist). When the side/direction of twist is fixed, we call this a one-sided position/twist. When an individual male uses both positions in succession (as in many spiders and in a plokiophilid true bug), we call this an alternating two-sided position. Use of the alternative set of terms (handed, random-handed) would result in awkward combinations.

IV. SPIDERS

(1) Pholcidae

Genital asymmetry occurs in two of the currently 83 pholcid genera: *Metagonia* and *Kaliana*. The genus *Metagonia* has a wide distribution in the New World, with currently 81 described species ranging from Mexico to Argentina (Huber, 2000, http://www.uni-bonn.de/~bhuber1/genera/metagonia.htm). Females are externally symmetrical, but the internal genitalia of many species are asymmetric (Gertsch & Peck, 1992; Huber, 1997, 1998, 2000, 2004*a*; Huber, Rheims & Brescovit, 2005; Pérez González & Huber, 1999). In most species studied with regard to this detail, these are cases of antisymmetry (Huber, 1997, 2000). In only three species has the internal morphology been studied using serial sections, and these studies have shown that the asymmetric structures are ducts and receptacles located in the narrow space between the uterus externus and ventral body wall (Huber, 1997, 2004*a*). However, for all other species the only information comes from cleared preparations of the female genitalia, and the resulting drawings often do not allow a clear decision about asymmetry or about the nature of the structures involved (e.g. figures in Gertsch, 1977, 1986).

A single species of *Metagonia* (*M. mariguitarensis*) is known to have directionally asymmetric female internal genitalia (Huber, 2004*a*). This is also the only species (and the only spider) known to have asymmetric male genitalia. Male asymmetry in this case is also directional, and by far more conspicuous than female asymmetry (Huber, 2004*a*).

Based on outgroup comparison, female symmetry appears to be plesiomorphic in *Metagonia* (Huber, 2000), but a formal cladistic analysis of the problem has not been conducted. Molecular data support the inclusion of *M. mariguitarensis* in a species group characterized by antisymmetric females (Astrin *et al.*, 2006), suggesting that directional asymmetry evolved from antisymmetry. These data also indicate clearly that male asymmetry in *Metagonia* evolved after female asymmetry.

Mating behaviour has been studied in *M. rica* only, a species with antisymmetric female genitalia. The copulatory position was identical to those in all other pholcids studied: both partners hang upside down in the web, the male facing in the opposite direction to the female and symmetrically inserting both genitalia (palps) simultaneously. This is the plesiomorphic mating position in spiders (von Helversen, 1976). The facts that (1) male pholcids press their chelicerae against the female external genitalia during copulation (Huber & Eberhard, 1997; Huber, 2002), and (2) male chelicerae and female external genitalia of *M. mariguitarensis* are symmetric (Huber, 2004*a*), suggest that even in *M. mariguitarensis*, mating is probably symmetric.

The monotypic Venezuelan genus *Kaliana* was described based on the male only, but the morphology of the recently discovered female and molecular data strongly suggest that *Kaliana yuruani* is just an unusual representative of the species-rich South American genus *Mesabolivar* (Huber, 2006; Astrin *et al.*, 2006). All known representatives of *Mesabolivar* have symmetric male and female genitalia. The same is true of the *K. yuruani* male, but female genitalia are asymmetric (Huber, 2006). Surprisingly, the structures involved in this asymmetry are extremely similar in principle to those in *Metagonia* (see above). Just like in *Metagonia*, there is a system of ducts and folds between the uterus externus and ventral body wall. Only four female specimens were available for clearing or sectioning, and these were all same-sided. However, more specimens need to be studied to decide if this is a case of directional asymmetry or antisymmetry.

As in *M. mariguitarensis*, the symmetry of the male chelicerae and the female external genitalia of *K. yuruani* suggest a symmetric mating position, but mating has never been observed in this species nor in any species of *Mesabolivar*.

(2) Theridiidae

Genital asymmetry has been documented in three out of currently 86 theridiid genera: *Asygyna*, *Tidarren*, and *Echinotheridion*. In the recently described Malagasy genus *Asygyna*, females are antisymmetric, males are symmetric (Agnarsson, 2006). In contrast to *Metagonia* and *Kaliana*, female asymmetry includes both internal and external structures. Nothing is known about the reproductive biology of *Asygyna* species.

Males of the closely related genera *Tidarren* and *Echinotheridion* amputate one of their palps after the penultimate moult (Knoflach & van Harten, 2000*a*, 2001; Knoflach, 2002; Knoflach & Benjamin, 2003; Ramos, Irschick & Christenson, 2004). Left and right palps are amputated randomly, resulting in antisymmetry. In *Tidarren cuneolatum*, a given male inseminates only one female spermatheca, but it may inseminate either of the two paired and symmetrical spermathecae (Knoflach & van Harten, 2000*a*). This case differs from all others in this review in that asymmetry is not a direct result of genes on the development of the organ but a result of a unique male behaviour directed randomly towards one of two symmetric organs.

V. INSECTS

(1) Apterygote insects and Palaeoptera

Apterygote insects transfer sperm indirectly *via* spermatophores or sperm drops (reviews: Schaller, 1971; Proctor, 1998; see also Sturm & Machida, 2001). Spermatophores are usually deposited on the ground or on special silk threads. They are then picked up by the female, sometimes with active male participation and close physical contact between male and female, sometimes in dissociation. Both the organs involved and the spermatophores are symmetric (e.g. Birket-Smith, 1974; Betsch, 1980; Thys, 1989). We found no evidence for asymmetric female sperm(atophore) uptake positions. The only exception we are aware of occurs in *Petrobius* (Arachaeognatha), where the male deposits sperm directly on the female ovipositor, in an antisymmetric side-by-side position (Sturm, 1978). The "seemingly direct sperm transfer" in *Petrobius* resembles copulation in pterygote insects but it is considered derived among Archaeognatha and thus probably evolved independently (Sturm & Machida, 2001).

Either Ephemeroptera, or Odonata, or both taxa together (Palaeoptera) are the sister group of Neoptera (Hovmöller, Pape & Källersjö, 2002; Ogden & Whiting, 2003), and thus potentially informative regarding character polarity. However, both the genitalia and the mating position of extant Odonata are unique among insects and certainly apomorphic. Males transfer sperm from the gonopore at the ninth abdominal segment to a secondary copulatory organ on the second abdominal segment, and from here sperm is transferred to the female genitalia. The characteristic 'mating wheel' position results from the male clasping the female head or prothorax with his terminal appendices and from the female attaching her gonopore to the male copulatory organ (Quentin & Beier, 1968; Pfau, 1971). The structures involved in this process as well as the mating position are symmetric.

Exceptions to symmetry have recently been discovered in *Calopteryx haemorrhoidalis* damselflies, where the left curved process in the male distal genitalia was significantly longer than the right one, and the corresponding left female spermathecae were significantly more often emptied by males (Cordero Rivera *et al.*, 2004). Females of Italian *Calopteryx haemorrhoidalis* had symmetric numbers of sensillae on their vaginal plates, but other populations and other *Calopteryx* species were asymmetric in their number of sensillae (antisymmetric with a left-bias; Córdoba-Aguilar, 2003*a*, *b*). These asymmetries were interpreted as possible results of an intersexual arms race over the control of sperm transport within females (Córdoba-Aguilar, 2003*b*). Whether these are exceptional phenomena or not, and whether male or female asymmetry arose first remains to be established.

How the unique situation in Odonata evolved has long been the object of speculation (e.g. Fraser, 1939; Brinck, 1962). The giant 'protodonate' *Namurotypus* probably had no secondary genital apparatus but a paired penis, a pair of parameres and segmented gonopods (Bechly *et al.*, 2001). The gonopods appear asymmetric but this probably results from different views (outer and inner sides, respectively). There is no indication that Odonata ever had conspicuously asymmetric genitalia or mated in an asymmetric position. In fact, it is still controversial if ancient odonates copulated or had indirect sperm transfer (Bechly *et al.*, 2001 *versus* Whiting, 1996 – cited in Bechly *et al.*, 2001).

Ephemeroptera, on the other hand, resemble neopterous insects much more closely, both in the morphology of their genitalia, and in their mating position. Their penis is unusual in being paired, but it is probably homologous to the primary phallic lobes of Neoptera that usually develop into aedeagus and parameres (Snodgrass, 1957). We found no case of asymmetry, neither in the male nor the female genitalia.

Mating in Ephemeroptera usually occurs during flight but occasionally on the ground (Brinck, 1957; Takemon, 1990). The male approaches the female from below and grabs her wing bases with his long front legs and her abdomen with his clasping styli (without turning upside down!). The resulting position is a symmetric female-above position (Morgan, 1929; Snodgrass, 1936; Brinck, 1957; Despax, 1949; Illies, 1968; Takemon, 1990; Kluge, 2003).

(2) Lower Neoptera

(*a*) *Orthoptera*

Both male and female genitalia in Orthoptera are overwhelmingly symmetric (e.g. Snodgrass, 1937; Roberts, 1941; Randell, 1963, 1964; Chopard, 1965*b*; Dirsh, 1956, 1973; Eades, 2000; Kumashiro & Sakai, 2001). The only explicit mentions of asymmetry we found occur in the male genitalia of *Dambachia eritheles* (Gryllidae) (Nischk & Otte, 2000), and in the aedeagus of *Acanthacris* species (Mungai, 1987). The fact that only a single *D. eritheles* specimen is known suggests the possibility of a teratology. In *Acanthacris*, however, the aedeagus is consistently asymmetric, "usually gently twisted to right or left" (Mungai, 1987; the author does not specify if this is interspecific variation or antisymmetry). Another potential case of asymmetry occurs in *Proscopia scabra* (Proscopiidae), where the endophallus appears asymmetrically curved (figure E on plate 14 in Dirsh, 1956). In the genus *Pristoceuthophilus* (Rhaphidophoridae), a large basal penial spine is consistently bent to the left in one undescribed species, to the right in another one (T. J. Cohn, personal communication, April 2006). More cases may exist, but the available evidence strongly suggests that genital symmetry is the plesiomorphic condition in Orthoptera.

An interesting case of female antisymmetry has been reported for *Locusta migratoria*: the receptacular duct bends either to the right or left side (Mika, 1959). The functional significance of this duct during copulation is unknown, and the structure may not meet our definition of genitalia given above.

The surprising diversity of copulatory positions in Orthoptera (and related groups) has been suggested to be derived from a (symmetric) female-above position (Alexander, 1964; Alexander & Otte, 1967). This is the usual position of grylloids and some tettigonioids among Ensifera (e.g. Boldyrev, 1913*a*, *b*; Hohorst, 1937; Alexander & Otte, 1967; Sakai *et al.*, 1991). Some tettigonioids assume an end-to-end position with the male upside down, often holding on to the female ovipositor (Boldyrev, 1913*b*; Chopard, 1965*b*; Rentz, 1972). A comparable end-to-end position occurs also in a few grylloids and gryllacridoids, apparently due to copulation taking place in a burrow (Alexander & Otte, 1967). This positional change (whether evolutionary or during copulation) involves only a vertical rotation and results in no asymmetry.

In some gryllids (*Miogryllus*, *Anurogryllus*) the male turns out horizontally from under the female to adopt a final end-to-end position similar to cockroaches. This transitionally asymmetric position probably requires twisting of the phallic complex against the copulatory papilla (Alexander & Otte, 1967). Whether or not a male can turn out on either side seems not to have been documented.

In Caelifera, the male jumps on top of the female but lowers his abdomen on the side of the female to grasp her genitalia from ventrally using the hooks of the epiphallus and the cerci (Fedorov, 1927; Uvarov, 1966; Whitman & Loher, 1984). This position is two-sided in the sense that any side can be used by the male (Katiyar, 1952; Mika, 1959; Gregory, 1965; Whitman & Loher, 1984; F.M. Buzzetti & P. Fontana, personal communication, Sept. 2005). In *Locusta migratoria*, males that are unsuccessful on one side may immediately try the other side (Mika, 1959). The flexibility of the male abdomen ensures that his genitalia contact those of the female in an almost symmetric way (Fedorov, 1927; Blackith & Blackith, 1966). Derived positions occur when the male is very small relative to the female: in such cases, the male may sit beside the female or assume an upside-down, end-to-end position comparable to that in some grylloids and tettigonioids (Katiyar, 1952).

(*b*) *Phasmida*

The male genitalia in stick insects usually consist of an asymmetric phallic organ, a sclerotized ventral structure (the vomer), and a pair of cerci that may assist in copulation (Günther, 1970). Directional asymmetry appears to be present throughout the order (e.g. Walker, 1922; Günther, 1970), but strong asymmetry is rare and an apparent synapomorphy of Pseudophasmatini + Anisomorphini (O. Zompro, personal communication, March 2006). Asymmetry is also present in *Timema*, where it involves phallus, cerci, epiproct, paraproct, and the left genital process (a potential homologue of the vomer in other Phasmida) (Snodgrass, 1937; Vickery, 1993; Tilgner, Kiselyova & McHugh, 1999; Bradler, 1999). *Timema* has long been proposed as the putative sister taxon to all other Phasmida (review in Bradler, Whiting & Klug, 2003), and molecular data have supported this hypothesis (Whiting, Bradler & Maxwell, 2003; Terry & Whiting, 2005). According to Zompro (2004), however, *Timema* is not a phasmid but more closely related to Embiidina. Whatever the true position, it seems safe to assume that male directional asymmetry was present in the most recent common ancestor of Phasmida, and possibly even of 'Eukinolabia' (Phasmida + Embiidina; Terry & Whiting, 2005).

Female genital asymmetry does not seem to exist in Phasmida. Even in *Timema* with its conspicuous male asymmetries, female genitalia are symmetric (Vickery, 1993; Tilgner *et al.*, 1999).

Mating is apparently quite uniform across the order despite variation due to differences in the relative sizes of males and females across species (Carlberg, 1983). The male climbs onto the back of the female, passes his abdomen down and around one side of the female's abdomen to engage his genitalia with hers (Bedford, 1978; see also Gustafson, 1966; Bradler, 2001). Whether this position is one-sided or random-sided was not explicitly mentioned by any of these authors, but the available evidence suggests that males of most species bend down their abdomen on the right side of the female (Henry, 1937; Carlberg, 1983; Bradler, 2001; S. Bradler, personal communication on *Pseudosermyle phalangiphora*, April 2006). This is in agreement with the position in Embiidina (see below). However, photographs of mating *Diapheromera femorata* clearly show the male bending his abdomen around the left side of the female (C. Moxey, personal communication, April 2006).

(*c*) *Embiidina*

Male asymmetry in Embiidina usually involves not only the structures immediately adjacent to the ejaculatory duct but also the cerci and even the tergites and sternites of the abdominal tip (Fig. 2D; Krauss, 1911; Walker, 1922; Kaltenbach, 1968; Ross, 1970*a*, *b*, 1984, 2000*a*; Szumik, 1991, 1997, 1998, 2001, 2002). All male embiids are asymmetric, even though representatives of the genus *Clothoda* (Clothodidae) are often cited as being symmetric or "almost perfectly symmetrical" (Ross, 2000*a*). The asymmetry in *C. nobilis*, the supposedly "most plesiomorphic species of the order" (Ross, 2000*a*) is inconspicuous but clearly present (fig. 40A in Ross, 2000*a*). Interestingly, the family Clothodidae, and in particular the genus *Clothoda*, is traditionally considered primitive (Walker, 1922; Tillyard, 1926; Snodgrass, 1937; Szumik, 1996, 2004; Ross, 2000*a*), suggesting that the most recent common ancestor may have been symmetric (*cf.* fig. 120 in Davis, 1938). The available cladistic analyses of the order (Szumik, 1996, 2004) root the cladograms with *Clothoda* and thus unfortunately provide no test of the origin of asymmetry within the order. The proposed sister-group relationship of Embiidina + Phasmida ('Eukinolabia', Terry & Whiting, 2005) suggests that genital asymmetry arose before the split into these two orders.

Male asymmetry in Embiidina is directional (e.g. Walker, 1922; Snodgrass, 1937; Szumik, 1997, 1998, 2001, 2004). For example, it is always the left cercus that is modified to clasp the female, while the right cercus is not visibly different from a female cercus (Fig. 2D). Side-reversed specimens occur occasionally, as do secondarily symmetric specimens with one side duplicated on the other (Ross, 2000*a*), but whether such "anomalous" males mate or not is apparently unknown, as are the exact percentages.

Females have very simple genitalia that are barely used in taxonomic studies and that seem to be symmetric throughout. Even though females are consistently clasped on the right side (see below), there seems to be no corresponding female abdominal modification (Krauss, 1911; Ross, 1970*a*, *b*, 2000*a*).

A correlation between male asymmetry and mode of copulation has been assumed for a long time (e.g. Snodgrass, 1937). The male sits either on top or on the right side of the female and directs his terminalia beneath

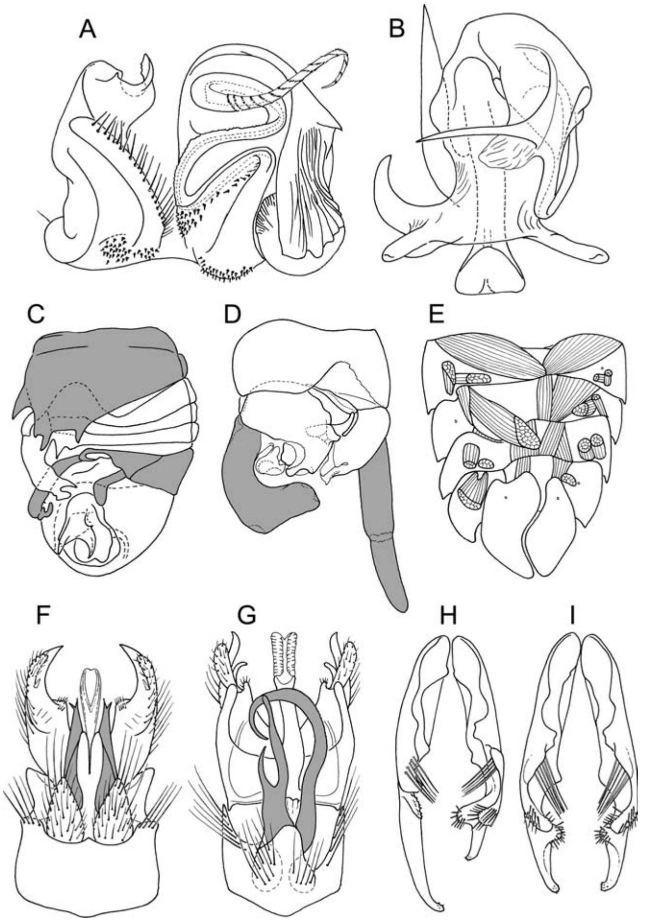

Fig. 2. Male insect genitalia and abdomens, showing some of the phenomena reviewed herein. (A) *Brachyptera braueri* (Plecoptera), strongly asymmetric paraprocts in ventro-posterior view (from Berthélemy, 1979). (B) *Hyalesthes productus* ('Homoptera'), strongly asymmetric aedeagus in dorsal view (from Hoch & Remane, 1985). (C) *Harpago medium* (Heteroptera), abdomen in dorsal view, showing that asymmetry extends to pregenital segments (abdominal tergites 3 and 8 in grey; from Plutot-Sigwalt & Péricart, 2003). (D) *Embonycha interrupta* (Embiidina), dorsal view of terminalia, showing that asymmetry extends to cerci (cerci in grey; from Ross, 2000*a*). (E) *Corixa dentipes* (Heteroptera), ventral and lateral abdominal muscles in dorsal view, showing that asymmetry extends to internal organization (from Larsén, 1938). (F, G) Dorsal views of genitalia of two closely related species, one symmetric (F: *Poecilopsyche pandu*, Trichoptera), the other asymmetric (G: *P. durdhyodhana*); projections of tenth segment in grey (from Schmid, 1968). (H, I) *Erynnis funeralis* (Lepidoptera), dorsal views of valvae of normal asymmetric specimen (H) and abnormal symmetric specimen (I) (from Burns, 1970).

the right side of the female, then upward and leftward (Friederichs, 1934; Stefani, 1953; Kaltenbach, 1968; Ross, 1970*a*, *b*, 2000*b*; Szumik, 2002). This is also the case in the slightly asymmetric *Antipaluria urichi* (Clothodidae) (Janice S. Edgerly-Rooks, personal communication, Sept. 2005), but mating behaviour in *Clothoda* seems to be unknown. The male cerci play a crucial role during copulation, clasping the female's abdomen (Stefani, 1953; Kaltenbach, 1968; Ross, 1970*a*, *b*).

(*d*) *Grylloblattodea*

All male Grylloblattodea have strongly asymmetric genitalia (Walker, 1922; Gurney, 1953, 1961; Scudder, 1970; Namkung, 1982). Asymmetry is evident early in ontogeny (Walker, 1922; Nagashima, 1991), involves both the penis, the coxites, the ninth sternum and the tenth tergite, and is directional: the left phallomere is elongate, curled, and sac-like, the right one is short and blunt, sclerotized, and probably functions as a clasper (Scudder, 1970; Nagashima, 1991). Female genitalia, by contrast, are symmetric (Scudder, 1970).

Copulation has been studied both in the American *Grylloblatta campodeiformis* (Vissher *et al.*, 1982) and in the Japanese *Galloisiana nipponensis* (Nagashima, Ando & Fukushima, 1982). Both species assume a false male-above position, with the male prosoma on top of the female, but his abdomen bent around the female abdomen to reach her genitalia from below. For *Ga. nipponensis* it is explicitly noted that males consistently lower their abdomen along the right female side, resulting in a one-sided position (see also figs 3C, D in Nagashima *et al.*, 1982). The same side is used by the *Gr. campodeiformis* males shown in figures 1-6 in Vissher *et al.* (1982), but it is not stated how many pairs these figures represent and if all 14 copulations observed showed the same pattern.

(*e*) *Mantophasmatodea*

All extant species of this recently described order are subsaharan, with one species known from Tanzania (*Tanzaniophasma subsolana*) and eleven further species from Namibia and South Africa (Klass *et al.*, 2003*b*). This geographic dichotomy is potentially relevant in the present context, because *T. subsolana* is the only species with almost symmetric male genitalia (Klass, Damgaard & Picker, 2003*a*). All other species are strongly directionally asymmetric, with male genitalia consisting of highly complicated left parts and smaller right parts. In some species, even the cerci are slightly asymmetric.

The male genitalia of *T. subsolana* differ from those of other species by being almost symmetric and by being simpler due to the absence of certain structures (Klass *et al.*, 2003*b*). Asymmetry concerns the vomeroid (fig. 2C in Klass *et al.*, 2002), the cerci (figs 2A, B in Klass *et al.*, 2002), and a pair of membranous lobes at the gonopore (K.-D. Klass, personal communication, Sept. 2005). Unfortunately, the cladistic analysis of Mantophasmatodea presented by Klass *et al.* (2003*b*) does not include *Tanzaniophasma* (for lack of specimens available for sequencing), leaving open the question about plesiomorphic or derived condition of symmetry and simplicity within the order.

Females are symmetric throughout (Klass *et al.*, 2003*b*). The only mention of female asymmetry (Zompro, Adis & Weitschat, 2002: cerci in *T. subsolana*) rests on a printer's error (the male signs were replaced by female signs; Klass *et al.*, 2003*b*, p. 52).

The copulatory position is a false male-above position in all species where mating has been observed (figs 1K, M in

Klass *et al.*, 2003*b*; figure in Adis *et al.*, 2002; M. Picker, personal communication, Sept. 2005). The asymmetry appears to be one-sided, with males passing down their abdomen along the right side of the female. The photographs in Klass *et al.* (2003*b*) show the opposite, but this is due to a reversal of the original slides (M. Picker, personal communication, Sept. 2005).

(*f*) *Plecoptera*

Most stoneflies have symmetric genitalia, even though in males the various parts may be asymmetrically folded at rest (Brinck & Froehlich, 1960). Exceptions to structural symmetry occur in Nemouroidea. In males of Brachypterainae, a subfamily of Taeniopterygidae, the paraprocts and epiprocts are directionally asymmetric: the left inner paraproct usually forms a guide, the right some sort of flagellum (Fig. 2A; Illies, 1966; fig. 51 in Brinck, 1970; Berthélemy, 1979; Zwick, 2000; Krno, 2004). Asymmetry does not occur in Taeniopteryginae, the sister group of Brachypterainae. The origin of asymmetry in Brachypterainae was also supported by the cladistic analysis of Nelson (1984, character 92). In certain Nemouridae, male epiprocts are asymmetric (*Soyedina*, *Mesonemoura*, certain *Indonemoura*; P. Zwick, personal communication, March 2006). Male genitalia are also asymmetric in *Capnia glabra* and *C. scobina* (Capniidae) (Nelson & Baumann, 1989), and cladistic analysis suggests that asymmetry evolved independently in the two species (C.R. Nelson, personal communication, April 2006). Thus, present evidence suggests at least four independent origins of asymmetry in Plecoptera (*cf.* cladogram in Zwick, 2000). We found no clear case of female genital asymmetry in Plecoptera (certain asymmetries that appear in figures but are not mentioned in the text are probably artificial, e.g. figs 19-22 in Berthélemy, 1979).

During mating, the male usually takes an oblique position dorsally on the female, lowers his abdomen to one side of the female, and curves his abdomen to achieve genital contact (see figures in Wu, 1923; Stewart, Atmar & Solon, 1969; Moreira, 1998). The resulting position is the false male-above position, but small and brachypterous males may sit beside rather than above the female (Brinck, 1956; Moreira, 1998). The mating position in all symmetric taxa studied is random-sided. This is documented by Brinck (1956) and Stewart & Stark (1977) for various representatives of Perlodidae, Chloroperlidae, Taeniopterygidae (*Taeniopteryx*), Leuctridae, and Nemouridae, and by Stewart *et al.* (1969) and Moreira (1998) for representatives of Perlidae. In 24 observed copulations of *Perlesta placida*, left- and right-side copulations were made in an equal ratio (Stewart *et al.*, 1969). Mating position in asymmetric Brachypterainae was said to be random-sided by Berthélemy (1979). This contradicts one of the major trends we document in this paper and we therefore suggest that this detail needs confirmation.

(*g*) *Dermaptera*

The male external genitalia of Dermaptera comprise a basal penis (phallobase) with one or two penis lobes, and a pair of parameres (Hincks & Popham, 1970). The plesiomorphic condition was assumed to be symmetric by these and earlier authors. In 'higher' Dermaptera, however, the penis lobe on one side tends to be flexed, reduced, or even absent, implying an origin of asymmetry within Dermaptera (Hincks & Popham, 1970; Kamimura, 2004, 2006).

These assumptions are partly supported by recent phylogenetic studies (Haas, 1995; Haas & Kukalova-Peck, 2001; Kamimura, 2004; Jarvis, Haas & Whiting, 2005). In Jarvis *et al.*'s (2005) study, Pygidicranidae is sister taxon to all other Dermaptera, and in this taxon both penis lobes are equally developed, both pointing forwards and directed backwards during mating (Hincks & Popham, 1970). The cladogram in Jarvis *et al.* (2005) further suggests that the next evolutionary step was an asymmetric position of the otherwise symmetric penis lobes: in Apachyidae, Labiduridae, and Anisolabididae, one penis lobe is flexed forwards and not used. Previously it was suggested that in these taxa the left penis lobe is non-functional. However, studies on two *Anisolabis* species and *Euborellia plebeja* (Anisolabididae) have shown that right- and left-'handed' males occur with equal frequencies (Giles, 1961*a*; Kamimura & Matsuo, 2001). Moreover, in *Euborellia plebeja* (Anisolabididae), both penis lobes are functional, one serving as a 'spare' organ in case of damage (Kamimura & Matsuo, 2001). In *Labidura riparia* (Labiduridae), structural symmetry is still preserved, but males predominantly use the right penis lobe for insemination (Kamimura, 2006).

The next evolutionary step apparently was a complete reduction of the left penis lobe, found in Eudermaptera (Forficulidae, Chelisochidae, Spongiphoridae) and convergently in the archaic Karschiellidae. This sequence of evolution was also suggested by Haas & Kukalova-Peck (2001). A single penis lobe also occurs in all species of *Hemimerus* (Hemimerina) but in this case, the single penis lobe is interpreted to be formed by the fusion of both mesomeres (Hincks & Popham, 1970). Thus, reduction to a single penis lobe clearly occurred more than once. Furthermore, in Karschiellidae the morphology is so unique that an independent origin has been assumed here too (Haas, 1995). Several independent origins of male genital asymmetry were also proposed in studies that did not include a formal phylogenetic analysis (e.g. Popham, 1965; Matsuda, 1976). Due to the lack of available specimens, Karschiellidae were not included in some recent studies (Haas, 1995; Colgan, Cassis & Beacham, 2003; Jarvis *et al.*, 2005), but in fact they might be the sister taxon of all other extant Dermaptera (Haas & Kukalova-Peck, 2001; Haas & Klass, 2003), possibly shedding a different light on the origin of asymmetry in Dermaptera.

In addition to the penis lobes, the cerci of males (but rarely of females) may be asymmetric. Dermapteran cerci or forceps are used both in male intrasexual competition and in courtship (Moore & Wilson, 1993; Briceño & Eberhard, 1995), but also in prey capture, wing unfolding, and defence. At least in some taxa they do not play a role during copulation and might therefore not fit the definition of genitalia used herein. In most species, the cerci are symmetric, but asymmetry occurs, usually in the form of directional asymmetry (Tomkins & Simmons, 1995, 1996; White, Borror & Peterson, 1998, p. 99). For example, in some species of *Euborellia, Carcinophora* and *Anisolabis* (all: Anisolabididae), the right cercus is more strongly curved that the left one (Hoffmann, 1987; Briceño & Eberhard, 1995).

Female genitalia in Dermaptera are less well studied (Klass, 2003*b*) since they are not used in species or higher taxon identification. No female genital characters are included in the morphological matrices published (Haas, 1995; Haas & Kukalova-Peck, 2001; Jarvis *et al*., 2005). Female genital asymmetry is apparently rare and seems to have evolved after male asymmetry. *Anisolabis* species, for example, as well as *Labidura riparia* (Labiduridae), have symmetric female but asymmetric male genitalia (Walker, 1922; Giles, 1961*b*; Bhatnagar, 1964; Hincks & Popham, 1970). In *Forficula auricularia* (Forficulidae), both male and female genitalia are asymmetric (fig. 7 in Popham, 1965; fig. 84 in Hincks & Popham, 1970). The last loop of the spermatheca is directed towards the left side of the body (Hincks & Popham, 1970), indicating directional asymmetry.

Most earwig males appear to approach the female in an end-to-end-position, and copulation takes place in a fairly straight position (Herter, 1965; Popham, 1965; Briceño & Eberhard, 1995; Briceño, 1997). The male of *Prolabia arachidis* starts copulation alongside the female and then turns to the end-to-end position (Herter, 1965). Males rotate their abdomens along the longitudinal axis before genital coupling, often by up to 180° (Fulton, 1924; Kuhl, 1928; Herter, 1963, 1965; Popham, 1965; Briceño & Eberhard, 1995; Walker & Fell, 2001), resulting in inverse correlation of the genitalia. In some species, the male cerci end up at the side of the female abdomen (Briceño & Eberhard, 1995), indicating a substantial degree of asymmetry in the relative positions of male and female genitalia. In *Pseudomarava prominens* (Spongiphoridae), the male initially holds the female with his mouthparts, then bends his abdomen towards her to start copulation (Briceño & Eberhard, 1995). Thus, an end-to-end position throughout copulation seems to be the plesiomorphic condition in Dermaptera, but positional asymmetries occur in various taxa, and the copulation behaviour of archaic earwig taxa remains virtually unstudied.

Information on one crucial aspect is largely missing: whether behavioural (rotation of abdomen) and positional asymmetries are one-sided or random-sided. The only explicit statements we found are by Walker & Fell (2001) on *Forficula auricularia*, where rotation is anticlockwise, and on *Labidura riparia* by Kamimura (2006), where rotation is either clockwise or anti-clockwise.

(*h*) *Zoraptera*

Zoraptera comprise about 40 known species of small, cryptic, mostly tropical insects. As a result, their genitalia are rather poorly known, and taxonomic drawings are the almost exclusive source of information. In at least some species, male genitalia are directionally asymmetric. For example, the penis of *Zorotypus hubbardi* consists of a slender left 'titillator' and a large right lobe bearing a hook (Walker, 1922). Both processes might actually be ontogenetically derived from the left side, meaning that the corresponding right side structures are reduced (Walker, 1922). Taxonomic drawings show asymmetries in various further species (e.g. figs 6, 11, 28 in New, 1978; fig. 4 in Choe, 1989; fig. 10 in Rafael & Engel, 2006). In some species, like *Z. snyderi*, no asymmetry has been described/illustrated (e.g. fig. 45 in Delamare Debouteville, 1970; see also Gurney, 1938), but even *Z. snyderi* has slightly asymmetric male genitalia (M. Engel, personal communication, April 2006). Unfortunately, most papers do not mention asymmetry in the text, and it often remains unclear to which degree asymmetries in drawings result from artefacts during preparation of the tiny genitalia. In a rare mentioning of symmetry, the 'phallosome' in *Z. weidneri* is said to consist of "two distinct symmetrical parts" (New, 1978), but figures 11 and 13 in New (1978) clearly show asymmetries. More research is necessary to evaluate Engel's (2004) generalization that Zoraptera have asymmetric male genitalia.

Female genitalia in this order are difficult to study, being lightly sclerotized and "virtually undetectable following maceration" (New, 1978). Most taxonomic drawings show symmetric structures, and some asymmetries may be artefacts like in males (e.g. fig. 15 in New, 1978). However, the notion that female genitalia in Zoraptera are symmetric (Delamare Debouteville, 1970) may be an unjustified generalization. In *Z. gurneyi*, the entrance to the spermathecal duct appears shifted to one side (fig. 5 in Choe, 1989) (it is not evident from the drawing to which side).

This poor knowledge of zorapteran genitalia, combined with a very rudimentary resolution of relationships within the order (Engel, 2003), allows no meaningful conclusion regarding the origin(s) of asymmetry in this taxon.

Mating has been studied in some detail in only two species: *Z. barberi* and *Z. gurneyi* (Choe, 1994, 1995, 1997). In *Z. barberi*, the male first faces the female, presenting his cephalic secretion, then curles and rotates his abdomen towards the female. In this side-by-side position the genitalia are coupled. Unfortunately, it is not clear from the published accounts if males consistently approach females from the right side (as illustrated in Choe, 1995, 1997), or if either side can be used. As soon as coupling is accomplished, the male slides into the final end-to-end and upside-down position that is maintained for the rest of copulation (Choe, 1995). By contrast, *Z. gurneyi* lacks male cephalic secretions, and copulation is initiated in the end-to-end position. Soon after genital coupling, the male slides into an upside-down position (Choe, 1994), suggesting that abdominal twisting occurs before genital coupling. The rudimentary description of mating in *Z. hubbardi* by Gurney (1938) suggests that the pair started copulation in a female-above position.

(*i*) *Dictyoptera*

The three dictyopteran orders (Blattaria: cockroaches, Mantodea: mantids, Isoptera: termites) are here treated under one heading because male genital asymmetry probably evolved before a split into the orders Blattaria and Mantodea (Grandcolas, 1996; Klass, 1997; *contra* Mizukubo & Hirashima, 1987), and because the monophyly of the group is well supported (Terry & Whiting, 2005 and references therein). Male genital asymmetry in Mantodea and Blattaria is usually directional, with genitalia being composed of a 'right phallomere' and a 'left complex' (Grandcolas, 1996; Klass, 1997). The 'left complex' includes the left phallomere, an elongated structure with a hooked apex. In the families Blaberidae and Pseudophyllodromiidae (= Plectopterinae) the asymmetry is reversed, but substantial similarity strongly argues against an independent origin of asymmetry (Bohn, 1987; Grandcolas, 1996; Klass, 1997; *contra* Mizukubo & Hirashima, 1987). Moreover, reversals may occur even within a genus, as for example in *Ectobius* (Brown, 1975; Bohn, 1987). Such reversals affect only the posterior end of the abdomen while other asymmetries (wing crossing, gut curvature, mandibles) are unaffected. Similar cases of reversals have been reported for mantids (Balderson, 1978). The only case of antisymmetric male genitalia in Dictyoptera known to us occurs in a *Ciulfina* species (Mantodea; Balderson, 1978).

Male genitalia in Isoptera are not only symmetric but also simpler than those of Blattaria and Mantodea, both with regard to the external morphology and the muscles (Klass, 2000; Klass, Thorne & Lenz, 2000). Since most recent analyses place Isoptera within a paraphyletic Blattaria (Eggleton, 2001; Deitz, Nalepa & Klass, 2003; Klass, 2003*a*; Terry & Whiting, 2005 and references therein) the obvious conclusion must be that isopteran symmetry and simplicity are secondary rather than primitive. This view has been expressed long ago, for example by Walker (1922) who considered asymmetric genitalia "doubtless present in the forebears of the Isoptera" and simplificity of genitalia in the order "without doubt a secondary condition". *Mastotermes* and *Stolotermes* have comparatively complex genitalia (Roonwal, 1970; Klass *et al.*, 2000) and *Mastotermes* is considered "the most basal termite group" (Eggleton, 2001). Simplicity has been explained as a consequence of strict monogamy and the resulting decrease of sexual selection (Eberhard, 1985). We will argue that the re-establishment of symmetry may also be related to the same factors.

Female genitalia in Dictyoptera are symmetric or at most slightly asymmetric (e.g. Crampton, 1925; Marks & Lawson, 1962; McKittrick, 1964; Chopard, 1965*a*; Beier, 1974; Grandcolas, 1996; Klass, 1998). Asymmetries commonly occur in some Blattaria, but these are usually rather subtle and inconspicuous (e.g. McKittrick & Mackerras, 1965; Bohn, 1987; Grandcolas, 1993, 1996, 1997*a*, *b*). In *Blattella germanica*, the genital sclerites of the 8th venter presumably hold the asymmetric spermatophore (Khalifa, 1950*a*), and they are quite asymmetric (directionally). Other, quite conspicuous asymmetries fall outside our definition of genitalia (above) or are unlikely to have any function in copulation: females of most or all Blattaria and Mantodea have highly asymmetric colleterial glands whose secretions combine to produce a hardened oothecal wall (Beier, 1974); in *Gromphadorhina*, the brood pouch is located over the left oviduct (Beier, 1974).

Copulatory positions vary among the three dictyopteran orders. In Blattaria, the male usually makes an effort to get the female to climb onto his back, both facing the same direction. Secretions from male tergal glands are used for this purpose. Once the female is in position, genital contact is accomplished and the male turns out from under the female to assume the final end-to-end position (review: Roth, 1970). Alternative mating positions (male-above and end-to-end) are probably derived (e.g. Sreng, 1993 on Bleberidae: Oxyhaloinae). A male-above position has also been reported for *Pycnoscelus* (Blaberidae: Pycnoscelinae; Roth & Willis, 1958; Roth & Barth, 1967), while certain *Gromphadorhina* and *Panchlora* species have been observed to start copulation in the end-to-end position (Roth & Willis, 1958; Barth, 1968). It is revealing that the hooks that in other taxa seize the female genitalia in the initial female-above position (see below) are missing in panchlorine genitalia (Roth, 1971).

The details of genital contact in cockroaches are comparatively well known. In *Periplaneta americana*, the hook on the left phallomere initially seizes the female (on which side is apparently unknown), while the right phallomere is used to hold the female once the end-to-end position is adopted (Gupta, 1947 - cited in Scudder, 1971). Similar results were obtained by Roth & Willis (1952) on *Blatta orientalis* and by Khalifa (1950*a*) on *B. germanica*. In the latter species, the hook on the left phallomere initially seizes the (fairly symmetric) female 'transverse sclerite', and only after assuming the final position, paired male sclerites and a sclerite of the right phallomere grasp the (symmetric) female ovipositor. In Khalifa's drawings (1950*a*, figs 5a-c) the left phallomere is hooked to the female sclerite both in the initial and the final positions. Since the ventral views of the final position (figs 5b, c in Khalifa, 1950*a*) show contralateral coupling (left male side to right female side) without crossover, this would require either crossover in the initial position (which unfortunately is shown in lateral view only) or change of contact site after change of mating positions. However, Roth & Willis (1952, p. 110) stated that abdominal twisting (180°) occurs during the change of positions, suggesting ipsilateral coupling of the internal structures that are twisted in the final position while the abdomen rotates back to an untwisted condition.

In Mantodea the male jumps on top of the female, lowers his abdomen on the right side of the female to couple the genitalia in a false male-above position (Beier, 1968; Maxwell, 1998; Ehrmann, 2002). This position is maintained throughout copulation. In Isoptera, the pair seals the nuptial chamber before copulation and the details of copulation seem to be poorly known. According to Becker (1952, and references therein) copulation is initiated in an end-to-end position; there is no change in position.

(3) Paraneoptera

(*a*) *Thysanoptera*

Genital asymmetry does not seem to be known in Thysanoptera. The initial mating position is a false male-above position where the male mounts the female but curls the posterior tip of his abdomen sideways and under the female (Pesson, 1951; Priesner, 1968; Terry & Dyreson, 1996). After coupling, the pair may assume a side-by-side position with a varying angle (~30° to >90°) between male and female (Terry & Dyreson, 1996). Whether the position is one-sided or random-sided has not been observed to our knowledge.

(*b*) *'Homoptera'*

Male genital asymmetries are rare or absent in some major homopteran taxa, but widespread in others. We found no cases of asymmetry in Sternorrhyncha (Psylloidea, Aleurodoidea, Aphidoidea, Coccoidea), the sister group of Euhemiptera (Bourgoin & Campbell, 2002). Within Cicadomorpha, genital asymmetry seems to be unknown (perhaps only unstudied) in Cicadoidea, Cercopoidea and Membracidae, but common in Cicadellidae. Within this family, aedeagus asymmetry is common, and in certain taxa additional structures are asymmetric like the paraphyses, the pygofer, and the styles (Young, 1977; Nielson, 1977, 1979, 1982; Ossiannilsson, 1983). The scattered occurrence of these asymmetries among genera suggests several convergent origins. In planthoppers (Fulgoromorpha), some taxa again seem to lack asymmetric representatives (e.g. Fulgoridae, Lophopidae). Asymmetric genitalia occur in Achilidae, Derbidae, and Tropiduchidae, and are nearly all-pervasive in Cixiidae and Delphacidae. In Achilidae, Cixiidae, Delphacidae, and Derbidae, the aedeagus and/or anal segment may be asymmetric (Fig. 2B; Fennah, 1969; Ossiannilsson, 1978; van Stalle & Synave, 1984; Asche, 1985; Hoch & Remane, 1985; J.-T. Yang & C.-T. Yang, 1986; Yang & Chang, 2000; Emeljanov, 2005). The distribution of asymmetric species among genera again suggests multiple convergent origins. For example, both symmetric and asymmetric species occur in the delphacid genera *Kelisia* and *Delphax* (Ossiannilsson, 1978), and the pygopher may be either symmetric or asymmetric in the *Hyalesthes productus* species group (Hoch & Remane, 1985). In Tropiduchidae, the genera *Trypetimorpha* and *Haliartus* are characterized by an unpaired lateral process of the periandrium that also affects the aedeagus (Bourgoin & Huang, 1990, 1991). An apparent case of reversal to symmetry has been documented in Hawaiian *Iolana* planthopper species (Hoch, 2006). In Coleorrhyncha, the sister taxon of Heteroptera, asymmetries do not seem to exist (e.g. Myers & China, 1929; China, 1962).

Whether male asymmetry is directed or bidirected is rarely mentioned, but whenever it is mentioned (usually indirectly), it is mostly directed (Fennah, 1969 and Yang & Chang, 2000 on Cixiidae and Delphacidae; Nielson, 1979 on Cicadellidae; van Stalle & Synave, 1984 and Hoch & Remane, 1985 on Cixiidae; Bourgoin & Huang, 1990 on Tropiduchidae; Emeljanov, 2005 on Achilidae). The only exception we are aware of occurs in a Dutch population of *Stiroma affinis* (Delphacidae) (Jong, 1986). However, the samples in some of the studies cited above are very small. We found no case of female genital asymmetry.

Mating positions vary widely among homopterans, but the details of how the abdomen tips of male and female contact during copulation seem to suggest that most or all positions are derived from a female-above position. Psyllidae and Aleurodidae mate or start mating in a side-by-side position, but the tip of the male abdomen is brought under the tip of the female abdomen and the male genitalia are inserted from below (Weber, 1930, 1931; Cook, 1963; White, 1970; Yang, Yang & Chao, 1986). After coupling, Psyllidae may change to an end-to-end position (White, 1970; Yang *et al.*, 1986). Aphididae and Coccidae mate in a male-above position (Weber, 1930, 1935; Manichote & Middlekauff, 1967; Hafez & Salama, 1969), but in *Protortonia primitiva* (Coccidae), the male bends his abdomen around to the ventral side of female, rather suggesting a false male-above position (Schrader, 1930).

Cicadomorpha mate in the side-by-side position, but again, the tips of male and female abdomens are actually in a female-above position (Weber, 1930, 1931; Hunt, 1993). The position (angle) may vary even during copulation (Weber, 1930, 1931), and in *Euscelis 'plebejus'* (= *incisus*) (Cicadellidae) the male starts in the side-by-side position and then quickly turns into an end-to-end position (Kunze, 1959). Most Fulgoromorpha mate in a side-by-side position, though with varying angles between male and female (Claridge & Vrijer, 1994). Males move their abdomens sideways under the female abdomen, again resulting in a female-above position of the genitalia (Delphacidae: Asche, 1985, p. 158; Heady & Wilson, 1990; Lophopidae: Soulier-Perkins & Bourgoin, 1998). The fulgorid *Hysteropterum grilloides* mates in an end-to-end position with the male lying on his back (Weber, 1930, 1931). Within Cixiidae, mating positions may vary within families, and include end-to-end positions with the male upside down (e.g. Hoch & Remane, 1985 on *Hyalesthes*) and side-by-side positions with both partners facing in opposite directions, inducing considerable twisting of the male genitalia (Sforza & Bourgoin, 1998; R. Sforza, personal communication, Jan. 2006).

We have barely been able to find the crucial information about one-sided *versus* random-sided mating positions. The only two cases refer to taxa with symmetric genitalia: *Euscelis 'plebejus'* males start mating either on the right or left side of the female (Kunze, 1959), and *Trialeurodes vaporariorum* males were observed to try copulation on both sides of the female (Weber, 1930). Also, the details of genital mechanics have been studied in a few taxa only. Interestingly, both inverse and direct genital correlations exist within homopterans. Inverse correlation has been reported for certain Aleurodidae (Weber, 1930), Lophopidae (Soulier-Perkins & Bourgoin, 1998), and Cixiidae (Sforza & Bourgoin, 1998). Direct correlation has been documented for *Euscelis* and two *'Typhlocyba'* species (now *Ribautiana ulmi* and *Edwardsiana hippocastani*) (Cicadellidae, Kunze, 1959; see also Singh-Pruthi, 1925; Hamilton, 1983, fig. 392), and may also occur in Membracidae (Marcus, 1950). In *Euscelis*, the positional change from a side-to-side to an end-to-end position does not seem to involve any kind of twisting of the abdomen or genitalia (Kunze, 1959).

(*c*) *Heteroptera*

Asymmetry in male Heteroptera may occur in a variety of structures, including the phallus, the parameres and even pregenital segments (Fig. 2C; Schuh & Slater, 1995; Hernández & Stonedahl, 1999). Mapping symmetric and asymmetric male genitalia on a cladogram of Heteroptera suggests multiple convergent transformations within the order. Using as a basis the data in Schuh & Slater (1995) (both the data on asymmetry and the cladograms), asymmetry has evolved at least eight times convergently: in Dipsocoromorpha, Hebridae, some Veliidae, Nepomorpha without Nepoidea, some Reduviidae, Miroidea, Naboidea + Cimicoidea, and some Lygaeidae. This most parsimonious optimisation seems to imply several convergent reversals to secondary symmetry, for example within Nepomorpha. However, in the cladistic analysis of Nepomorpha by Hebsgaard, Andersen & Damgaard (2004) four independent origins of asymmetry just within this taxon was the most parsimonious optimisation. Similarly, the distribution of symmetric and asymmetric taxa in Reduviidae suggests that asymmetry has arisen multiple times convergently within this family (Wygodzinsky, 1966; Willemse, 1985). Asymmetry in some taxa is limited to inconspicuous and hidden structures, as for example the slight twist of the abdominal tip in *Nabis* (Ekblom, 1926) or the distal end of the phallus in Lygaeidae (Ashlock, 1957). A comprehensive analysis including such cases may bring the number of independent origins of asymmetry in true bugs to well over a dozen.

Male genital asymmetry in Heteroptera is overwhelmingly directional. For example, male asymmetry in Dipsocoridae is sinistral, in other Dipsocoromorpha it is dextral (Schuh & Slater, 1995); in Ochteroidea, the left paramere is reduced or absent; in *Nabis*, the genital segments are slightly twisted either clockwise (viewed from posterior) (*N. flavomarginatus*) or counter-clockwise (*N. limbatus*) (Ekblom, 1926); in Helotrephidae, the genital capsule is twisted 90° to the left (Schuh & Slater, 1995); in Miridae, one paramere (usually the left) is more strongly developed than the other one or may be provided with a hook (Kullenberg, 1947; Kelton, 1959; Schmitz, 1968; Cassis & Moulds, 2002; Chérot, Ribes & Gorczyca, 2006); in certain *Corixa* species, the right paramere is modified to guide the phallus during intromission, in other *Corixa* species and in certain Miridae the same function is performed by the left paramere (Keilbach, 1935; Larsén, 1938; Kullenberg, 1947); in Cimicidae and relatives, the left paramere is modified in the context of traumatic insemination (Carayon, 1977); in *Microvelia ayacuchana* the male genitalia extend toward the left side (Spangler & Froeschner, 1987); in *Naucoris cimicoides*, certain abdominal muscles are only or more strongly developed on the right side (Larsén, 1938); in Lygaeidae, the expanding phallus always rotates in the same direction (Ludwig, 1926; Bonhag & Wick, 1953). A notable exception to this dominance of directional asymmetry occurs in Thaumastocoridae. Their grossly asymmetric genitalia are usually either dextral or sinistral (i.e. directionally asymmetric), but in *Xylastodoris luteolus* the direction is variable within the species (i.e. antisymmetric; Cassis, Schuh & Brailovski, 1999). Similar cases have been reported in Corixinae, but here the antisymmetry is clearly biased (references in Larsén, 1938, pp. 263-264).

Female genitalia are mostly symmetric. This is rarely stated explicitly (e.g. by Larsén, 1938, p. 226; Kullenberg, 1944 for Miridae; Willemse, 1985 for the reduviid genus *Sirthenea*; Cassis *et al.*, 1999 for Thaumastocoridae), but inferred from figures and missing statements to the contrary (e.g. Slater, 1950; Davis, 1955; Scudder, 1959; Wygodzinsky, 1966; Jordan, 1972; Schuh & Slater, 1995). Importantly, female asymmetry seems to be restricted to taxa with male asymmetry (Larsén, 1938). Examples (other than those cited by Larsén, 1938, p. 226) are *Lygaeus equestris* (and relatives) and *Aphelocheirus aestivalis*, where the openings of the ducts of the seminal receptacles are slightly shifted to the right (Ludwig, 1926; Larsén, 1938). In *Lygaeus*, the duct is a left-hand spiral which is probably related to the spirally wound male phallus (see below). In *Nabis*, a pair of flaps covering the female genitalia may be either left over right (*N. flavomarginatus*) or right over left (*N. limbatus*), which is probably correlated with the twisted male abdomen mentioned above (Ekblom, 1926). In most Dipsocoromorpha, the seminal capsule is situated on the left side, and in two *Harpago* (Dipsocoridae) species the asymmetry even involves external structures (Plutot-Sigwalt & Péricart, 2003). In certain Helotrephidae the female 7th sternum is directionally asymmetric (Zettel, 1999), and the species-specific shape of this structure suggests that it meets our definition of genitalia. Directional female asymmetry also occurs in Cimicoidea, where traumatic insemination often occurs *via* a specific secondary copulatory organ (spermalege, copulatory tube) which in most cases is on the right side of the female abdomen (Carayon, 1977). Females of *Cardiastethus limbatellus* (Anthocoridae) have paired copulatory tubes and are considered secondarily symmetric (Carayon, 1977). The same is apparently the case in Plokiophilidae, where females are symmetric and males are symmetric or at most weakly asymmetric (Carayon, 1977; Schuh & Slater, 1995). Traumatic insemination and directionally asymmetric (always right-sided) female 'paragenitalia' have independently evolved in *Coridromius* (Miridae; Tatarnic, Cassis & Hochuli, 2006).

The most common position at genital coupling in true bugs is a male-above position, but the male usually stands obliquely on the female (e.g. Wefelscheid, 1912; Hase, 1918; Ekblom, 1926, 1928; Larsén, 1938; Rawat, 1939; Kullenberg, 1944, 1947; Wygodzinsky, 1966; Davis & Usinger, 1970; Jordan, 1972; Stork, 1981; Cassis *et al.*, 1999; Wheeler, 2001) or even beside her as in Leptopodomorpha (Cobben, 1957; Schuh & Polhemus, 1980) and some Miridae (Kullenberg, 1944). After genital coupling, the male may remain in the initial position [e.g. Saldidae, Nabidae, Gerromorpha: Ekblom, 1926; Nepomorpha: Ekblom, 1928; Larsén, 1938; Rawat, 1939; *Triatoma* and *Rhodnius* (Reduviidae): Hase, 1932] or he may turn to a V-shaped side-by-side or to an end-to-end position [e.g. Lygaeidae: Ludwig, 1926; Bonhag & Wick, 1953; Rodriguez & Eberhard, 1994; *Myrmus*: Ekblom, 1928; *Helopeltis*: Devasahayam, 1988; *Phymata* (Reduviidae): Balduf, 1941; *Elasmucha*: Jordan, 1958; many Miridae: Kullenberg, 1944, 1947; Wheeler, 2001]. The stinkbug *Euschistus conspersus* male omits the initial mounting phase and couples in an end-to-end position (Alcock, 1971).

The asymmetry of the coupling position can be either one-sided (Miridae: Kullenberg, 1944, 1947; Stork, 1981; Cimicoidea: Hase, 1918; Carayon, 1972, 1977; *Nabis*: Ekblom, 1926; *Aphelocheirus, Naucoris, Corixa, Notonecta*: Hagemann, 1910; Lehmann, 1922; Ekblom, 1928; Larsén, 1938; Rawat, 1939) or random-sided (Pentatomomorpha: Ekblom, 1926, 1928; Ludwig, 1926; Bonhag & Wick, 1953; Leptopodomorpha: Ekblom, 1926; Jordan & Wendt, 1939;

Cobben, 1957; Nepidae: Baunacke, 1912; Larsén, 1938 *contra* Keilbach, 1935; *Mesovelia*: Ekblom, 1928; Reduviidae: Hase, 1932; Balduf, 1941; Joppeicidae: Davis & Usinger, 1970; Nabidae: Kullenberg, 1947). The available evidence suggests that all taxa with a one-sided copulatory position have asymmetric male genitalia, all taxa with a random-sided position have symmetric male genitalia (*cf.* Larsén, 1938, p. 263). Only two exceptions are known to us. (1) In *Lygaeus*, the directional asymmetry of the phallus appears related not to the mating position but to the directional asymmetry of the female receptacular duct (Ludwig, 1926, see above). Rotation of the phallus in *Lygaeus* does not simply result from rotation of the abdomen but from the expansion of a membranous portion of the phallus. These membranes are spirally folded so that their expansion rotates the phallus (Ludwig, 1926) similar to the hematodochae of spider genital bulbs (*cf.* Huber, 2004*b*). (2) In *Notonecta glauca*, only the male abdominal musculature is directionally asymmetric, but the external genitalia are apparently symmetric (Larsén, 1938).

In several species with random-sided coupling positions, an apparent male preference for one side of the female seems to exist, either for the right side (Lygaeidae: Ludwig, 1926; Ekblom, 1926; Bonhag & Wick, 1953; *Salda saltatoria*: Ekblom, 1926; *Myrmus miriformis*: Ekblom, 1928) or for the left side (*Triatoma geniculatus* and *Rhodnius pictipes*: Hase, 1932). A rare case of alternating two-sided insemination (as in most spiders!) occurs in *Embiophila africana*, a plokiophilid with symmetrical male parameres used to perforate successively the female copulatory tubes (Carayon, 1977). In Miridae (who use a one-sided position), males of most taxa seem to use the right side of the female, but in some genera like *Psallus* and *Monalocoris*, the left side is used (Kullenberg, 1944).

A female-above position without positional change during copulation occurs only in Aradidae, in the veliid *Paravelia brachialis* (Weber, 1930; Wilson, 1958; Schuh & Slater, 1995), and apparently in *Ceratocombus* (Ceratocombidae, Melber & Köhler, 1992). However, the details of coupling in species that mate in a side-by-side position (e.g. *Ranatra linearis*, Nepidae; *Joppeicus paradoxus*, Joppeicidae) suggest that this position is just a modification of a female-above position: the male places the dorsal side of the tip of his abdomen under the tip of the female abdomen (Larsén, 1938; Davis & Usinger, 1970). Similarly, males in several groups curve their abdomens underneath the tip of the female abdomen without rotation along the longitudinal axis, resulting in an overall male-above but a genital female-above position (Reduviidae: Hase, 1932; Naucoridae, Corixidae, Aphelocheiridae: Keilbach, 1935; Larsén, 1938; Rawat, 1939; Saldidae: Jordan & Wendt, 1939; Nepidae: Baunacke, 1912; Weber, 1930; Larsén, 1938; Jordan, 1972; Miridae: Stork, 1981). In other cases the male genital segment actually contacts the female genital segment from above (e.g. Gerromorpha: Ekblom, 1926; Heming-van Battum & Heming, 1989). In *Hebrus pusillus*, the male bends his genitalia ventrally 180° (but without rotation along the longitudinal axis), again resulting in an inverse correlation between male and female genitalia (Cobben, 1982, fig. 29; Heming-van Battum & Heming, 1989, fig. 20). Difficult to interpret are the data on Lygaeidae. In *Lygaeus*, the distal abdominal segments are rotated prior to genital coupling and the change to the end-to-end position reverses this rotation (Ludwig, 1926). Inverse correlation might still be present in the phallus, but Larsén (1938, p. 287) interprets Ludwig's data as showing direct correlation. In *Oncopeltus fasciatus*, 180° rotation of the genitalia occurs partly actively in the initial position, partly passively by the change to the end-to-end position (Bonhag & Wick, 1953). In *Pyrrhocoris*, the genitalia are not rotated prior to coupling but only by the positional change that results in a 180° twist of the genitalia within the unrotated 9th segment, thus maintaining inverse correlation (compare figs 39 and 40 in Ludwig, 1926). Finally, a highly derived belly-to-belly position has been reported for Prostemmatinae, a highly specialized group of Nabidae practicing traumatic insemination (Carayon, 1977).

(*d*) *Psocodea*

The large majority of Psocodea (bark lice, book lice, and parasitic lice) apparently have symmetric male and female genitalia (e.g. Qadri, 1936; Séguy, 1944; Schmutz, 1955; Klier, 1956; Lyal, 1986; Yoshizawa & Johnson, 2006). In 'Psocoptera', asymmetric genitalia are common in the subfamily Psocinae (*sensu* Lienhard & Smithers, 2002) of Psocidae (infraorder Psocetae). In males, the hypandrium is usually more or less asymmetric, sometimes combined with asymmetric apical structures of the phallosome, and in females slightly asymmetric sclerifications occur around the spermapore on the 9th sternum (e.g. Mockford, 1993; Lienhard, 1998; Yoshizawa, 2001). Symmetric and asymmetric forms frequently co-occur within a taxon, suggesting several convergent origins (Yoshizawa, 2003; Endang & New, 2005; K. Yoshizawa, personal communication, March 2006). In *Trichadenotecnum* alone, mapping asymmetric forms on the cladogram in Yoshizawa (2004) suggests three independent origins (K. Yoshizawa, personal communication, March 2006). Asymmetries of the male terminalia are also known in the families Lachesillidae and Ectopsocidae (superfamily Lachesilloidea *sensu* Yoshizawa, 2002) belonging to the infraorder Homilopsocidea. In Lachesillidae, asymmetric structures are rare, and only sclerotized hooks of epiproct and clunium (fused terminal tergites) are concerned (e.g. Garcia Aldrete, 1974; Mockford, 1993, fig. 215). In Ectopsocidae, endophallic sclerifications are always asymmetric, and occasionally the medio-apical arch of the phallosome frame is asymmetric in *Ectopsocus*; asymmetric clunial sclerifications are known in several species of *Ectopsocopsis* (e.g. Mockford, 1993; Lienhard, 1998). The statement by Badonnel (1970) that in 'Psocoptera', the radula (endophallus) may have "apophyses, hooks, or hair-like expansions forming brushes, always asymmetrical" is thus true for Ectopsocidae, but in most other cases endophallic sclerites are arranged symmetrically (C. Lienhard, K. Yoshizawa, personal communications, March 2006). Seemingly asymmetric structures illustrated in the literature for other families of 'Psocoptera' are usually artifacts due to dissection and slide mounting (e.g. Thornton & New, 1977, for *Austropsocus*; C. Lienhard, K. Yoshizawa, personal communications, March 2006) and have sometimes been erroneously interpreted as true asymmetries (e.g. Baz, 1993, for *Cerobasis*; see comment in Lienhard, 1998).

In 'Phthiraptera', male genital asymmetry has received little or no attention in general treatments (e.g. Kéler, 1969; Clay, 1970; Piotrowski, 1992) but it is apparently quite common (Lakshminarayana, 1979). It occurs in all major groups, and in some taxa, like Menoponidae (Amblycera) male genital asymmetry seems to be the rule rather than the exception. Directionally asymmetric genitalia occur, for example, in the menoponid genera *Trinoton, Eomenopon, Pacifimenopon, Heteromenopon*, and *Franciscoloa*, subgenus *Cacamenopon* (Schmutz, 1955; Clay, 1963; Price, 1966*a*, *b*, 1967, 1969; Eichler & Vasjukova, 1981). In *Goniocotes* (Ischnocera), two species (one symmetric, the other asymmetric) are considered to be closely related and the symmetric species is considered "phylogenetically older" (Emerson & Elbel, 1957; Lakshminarayana & Emerson, 1971). Symmetric and asymmetric forms also occur within the ischnoceran genus *Halipeurus* (Edwards, 1961). A similar situation was suggested for *Haematopinus* (Anoplura) by Ewing (1932): in *Haematopinus tuberculatus* (but not in *H. suis*), the parameres and endomere are directionally asymmetric (right paramere longer, endomere with hook on left side). However, Häfner (1971) notes that in *H. suis* the distal part of the aedeagus is always bent to the left side, suggesting that asymmetry *per se* may be more common in the genus. In *Pediculus humanus* (Anoplura), the male genitalia are mostly symmetric except for an asymmetric protrusion of the 'statumen penis' (mesomere) (Nuttall, 1917; Yoshizawa & Johnson, 2006).

In sum, symmetry appears to be more common than asymmetry in psocodean genitalia, and symmetry may be the plesiomorphic condition, but the polarity requires further study, both for the entire group and for specific cases like *Franciscoloa*, *Goniocotes*, and *Haematopinus*. The fact that no genital asymmetries are included in recent data matrices of Psocodea (Smith, 2000; Yoshizawa, 2002) indicates that asymmetry probably is a derived character within the group, arising at or near the terminal branches of the phylogenetic tree.

Genital coupling in 'Psocoptera' mostly occurs in a symmetric female-above position. In most cases, the male, standing in front of the female, backs underneath her until the tip of his abdomen reaches the female genitalia (Pearman, 1928; Weber, 1936; Sommerman, 1944; Badonnel, 1951; Medem, 1951; Broadhead, 1952, 1961; Klier, 1956; Eertmoed, 1966; Mockford, 1977; Betz, 1983*a*; Lienhard, 1988). In *Embidopsocus* the male reaches the same position under the female from the female's back, moving forwards (Broadhead, 1952; Weidner, 1972). *Ectopsocus* and *Trichopsocus* males also back under the female but may do so from a lateral position (Sommerman, 1943; Medem, 1951; but see Söfner, 1941). Apparently, any side can be used. In most species, the female-above position is maintained throughout copulation (Sommerman, 1944; Mockford, 1957; Weidner, 1972; Betz, 1983*a*). In *Lachesilla*, the male establishes genital contact in the female-above position, but then quickly rotates almost 360° in the vertical plane, ending up on top of the female. Since the movement is in the vertical plane, it involves no asymmetry. The resulting position reminds of an end-to-end position with the male upside down, except that the male bends his body to grasp the female with his legs (fig. 42 in Klier, 1956). In some taxa [Trogiomorpha: *Trogium, Prionoglaris, Psoquilla, Rhyopsocus,* Troctomorpha: *Liposcelis*, Psocomorpha: *Amphigerontia* and *Trichadenotecnum* (Psocidae), *Reuterella* and *Ectopsocus* (Elipsocidae)], the male turns out from under the female after genital coupling and copulation takes place in an end-to-end position where both partners have their legs on the ground (Solowiow, 1925; Weber, 1936; Sommerman, 1943; Finlayson, 1949; Klier, 1956; Broadhead, 1952, 1961; Weidner, 1972; Lienhard, 1988). In *Asiopsocus sonorensis* (Asiopsocidae) the female rather than the male turns 180° (Mockford, 1977). In *Ectopsocus briggsi*, this sideward turning of the male was interpreted to occur *after* copulation, as a process that actually terminates copulation (Söfner, 1941). The same mechanism for termination of copulation is used by certain *Archipsocus* females (Mockford, 1957). In other species, positional change occurs "almost immediately after genital contact" (Broadhead, 1961; see also Sommerman, 1956; Lienhard, 1988). In *Psoquilla marginepunctata*, the male may turn either to the left or to the right side, and this movement results in a twisting of the tip of the male abdomen through at least 90° (Broadhead, 1961). Similar rotation (though only about 40°) was reported for *Rhyopsocus bentonae* (Sommerman, 1956). In *Prionoglaris stygia,* the positional change results in a 180° rotation of the whole phallosome, while the abdomen remains in the normal untwisted position in both the male and the female (Lienhard, 1988). Indirect evidence for such a rotation comes also from the observation that *Trogium* individuals fixed in copulation rotate along their longitudinal axes until adopting an end-to-end position with one partner upside down (fig. 69 in Klier, 1956). Bearing in mind that the hypandrium plays a crucial role in genital coupling in the symmetric *T. alexanderae* (Betz, 1983*b*), it is noteworthy that in certain *Trichadenotecnum* species the hypandrium is asymmetric (see above).

Mating positions are even more variable in phthirapteran lice. Sikora & Eichler (1941) identified five positions: (1) Female-above position, common in Ischnocera and Anoplura; males often use their antennae or frontal legs to grasp the female from below (Nuttall, 1917, 1918; Florence, 1921; Séguy, 1944; Schmutz, 1955; Oniki, 1999). (2) Male above position, presumably in Menoponidae (Sikora & Eichler, 1941); males often use tibial spurs to hold on to the female. (3) Belly-to-belly position, for example in *Menopon gallinae, Trimenopon jenningsi* and *T. hispidum* (Sikora & Eichler, 1941; Schmutz, 1955). It is not clear how this position is achieved, but in *T. hispidum* the penis in the final position is twisted (inverted) 180° (Schmutz, 1955). (4) End-to-end position, for example in *Neocolpocephalum* (Menoponidae); coupling in this case is achieved in a position where the male stands behind the female (facing in the same direction) and bends his abdomen forward. Only then does the male flip back to the final end-to-end position (Sikora & Eichler, 1941). (5) Side-by-side position, for example in *Cuculicola latirostris* (Ischnocera: 'Philopteridae'). This is presumably only a slight variation of the female-above position (Sikora & Eichler, 1941). Apparently it is only the Menoponidae and

Trimenoponidae with their asymmetric male genitalia who deviate from the female-above position. Considering the derived phylogenetic position of these families (and Amblycera) in recent analyses (e.g. Johnson, Yoshizawa & Smith, 2004) it seems plausible to assume that all these menoponid positions (2-4) are derived from a female-above position.

(4) Holometabola

(*a*) *Neuropterida*

The vast majority of Megaloptera, Raphidioptera, and Neuroptera have symmetric male and female genitalia (e.g. Aspöck & Aspöck, 1971; Meinander, 1972; Aspöck, Aspöck & Hölzel, 1980; New, 1989; New & Theischinger, 1993; Aspöck, 2002). The only known exceptions refer to the parameres or the 'mediuncus-paramere complex' in certain taxa of Neuroptera, for example within Chrysopidae and Nymphidae (Acker, 1960, p. 45), Nemopteridae (New, 1989, p. 66), and Berothidae (Aspöck *et al.*, 1980, fig. 391; Aspöck & Aspöck, 1996, figs 7, 23, 24). In Megaloptera, the lobes of sternite 10 are often asymmetric in the genus *Ctenochauliodes* (Corydalidae) (C. K. Yang & D. Yang, 1986). Whether the asymmetries represent cases of directional asymmetry or antisymmetry is not stated. The fact that the cited families include both symmetric and asymmetric taxa, and the distribution of these families on the cladogram by Aspöck, Plant & Nemeschkal (2001) strongly suggest that genital symmetry in Neuropterida is plesiomorphic and that asymmetry evolved at least five times independently.

Mating in Raphidioptera (the putative sister taxon of Megaloptera + Neuroptera) often starts with the male putting his head under the female abdomen from posteriorly. He then curls his abdomen upward and forward to grasp the female terminal segments. This position is symmetric, and is only a slight variation of the female-above position. This position may be maintained throughout copulation (e.g. Zabel, 1941 on *Inocellia crassicornis*; Syms, 1935 on '*Raphidia*' - now *Phaeostigma – notata*; Aspöck, Aspöck & Rausch, 1994 on *Parainocellia braueri*) or the male may flip backward to a final end-to-end position (e.g. Acker, 1966 on *Agulla*; Aspöck *et al.*, 1994 on various Raphidiidae). Since no abdominal rotation around the longitudinal axis is involved, the male ends up in an inverted position, upside down (Acker, 1966; Aspöck *et al.*, 1994). Slight differences occur in the mating position in certain *Raphidia* species, where genital contact may be accomplished in a side-by-side position (Eglin, 1939; Zabel, 1941; Aspöck & Aspöck, 1971). The male bends his abdomen forward [at the left side according to Zabel (1941), but the sample size is not given; apparently at the right side according to Eglin (1939)] and rotates the tip of his abdomen 180° around the longitudinal axis. After coupling, the male again ends up in an upside-down, end-to-end position (see also Kästner, 1934), which implies that the abdominal rotation is immediately reversed. During copulation, the male may rotate back to a 'feet-on-the-ground' position (Eglin, 1939).

Mating in most Megaloptera studied is similar to that in *Inocellia* above: the male pushes his head under the female abdomen, takes a position under her abdomen and bends his abdomen forward in the vertical plane until genital contact is accomplished (Killington, 1932; DuBois & Geigy, 1935; Seitz, 1940; Azam & Anderson, 1969; Pritchard & Leischner, 1973). In *Sialis californica*, the male elevates the tip of his abdomen between the wings into the copulatory position (i.e. symmetrically; Azam & Anderson, 1969), while in other species the wings are displaced to one side. Apparently, this displacement is random-sided (DuBois & Geigy, 1935, on *Sialis lutaria*) even though Seitz's (1940) observations on the same species (under *S.* '*flavilatera*'; sample size not given) seem to suggest the opposite. In *Sialis fuliginosa*, the male changes to a final end-to-end position (Killington, 1932). In this position the male is first upside-down but then twists the abdomen and rights himself.

In Neuroptera, the mating position of *Inocellia* and *Sialis* is again realized in some Coniopterygidae. In *Parasemidalis*, *Conwentzia*, and *Semidalis*, the male pushes his head under the abdomen of the female, grasps some of her legs from posteriorly and lifts his abdomen tip dorso-anteriorly to make genital contact (Withycombe, 1923; Johnson & Morrison, 1979). No change in position occurs. It is notable in this context that Coniopterygidae were long considered an early offshoot of Neuroptera, but are now considered a highly derived taxon within 'higher Hemerobiiformia' (Aspöck *et al.*, 2001). Most other Neuroptera studied start mating in a side-by-side position (Withycombe, 1923; David, 1936; Toschi, 1965; Ickert, 1968; Henry, 1979; Tauber *et al.*, 1990; Brushwein, Culin & Hoffman, 1995; Weißmair, 1999; Tauber, Tauber & Hilton, 2006). In various taxa, early mating stages (at least until genital coupling) involve mouthpart contact (Toschi, 1965; Henry, 1983; New, 1989) and this may be directly correlated with the side-by-side position. The final position is quite variable in Chrysopidae, obviously facilitated by the highly moveable male and female abdomens (e.g. female-above in *Meleoma* and *Nothochrysa*, Toschi, 1965; end-to-end in *Anomalochrysa*, Tauber *et al.*, 2006; see also Henry, 1979).

The details of abdominal movements prior to genital contact seem to be poorly known in Neuroptera. Obviously, the male abdomen is strongly twisted and/or bent (Henry, 1979, 1983; Weißmair, 1999; Tauber *et al.*, 2006) (sometimes even the female abdomen: David, 1936; Tauber *et al.*, 1990, 2006). In certain Chrysopidae, Toschi (1965) and Tauber *et al.* (2006) observed inverse correlation (male dorsal side aligned with female ventral side). Largely unstudied is also the question of one-sided *versus* random-sided positions. The only explicit mention of a random-sided mating position we found is for *Meleoma* by Tauber (1969).

(*b*) *Siphonaptera*

Due to their strong lateral compression, fleas and flea genitalia are usually illustrated in lateral view. This, together with the fact that male fleas may have the most complicated copulatory apparatus among insects (Snodgrass, 1946; Humphries, 1967*a*) makes an evaluation of symmetry difficult in many cases. However, some illustrations of male genitalia in dorsal and/or ventral views exist (e.g. Snodgrass, 1946; Günther, 1961; Hopkins & Rothschild, 1971; Cheetham, 1988), and these show mostly perfectly symmetric structures. An apparently widespread exception are the 'endotendons' (penis rods), chitinous rods that are used to transport sperm through the bursal duct into the copulatory bursa (Snodgrass, 1946; Günther, 1961). In *Hystrichopsylla talpae*, for example, the right rod is longer, is provided with stronger muscles, and has a broader tip than the left one. The tips of the two rods are alternately pushed forward through the bursal duct, the right one first, the left one following. Together, the two tips form a 'cornet' ("Spitztüte") that fits tightly into the bursal duct and pushes the sperm forward (Günther, 1961). In *Ceratophyllus idius*, the long rod seems to enter the functional spermathecal duct, while the short rod enters a blind duct, interpreted as a vestige of the tube of the ancestral second spermatheca (Holland, 1955). In the rabbit flea *Spilopsyllus cuniculi*, a slot in the shorter rod guides the longer rod through the aperture of the spermathecal duct (Rothschild, 1975). Ontogenetically, the two rods are derived from evaginations of the lateral walls of the phallosome, but eventually they appear like upper and lower rods (Cheetham, 1988). Further slight asymmetries whose meaning remains unknown concern the lateral walls of the aedeagus in some Ethiopian species of the genus *Ctenocephalus* (Smit, 1963) and the outer hood (palliolum) in some species of, for example, *Ctenophthalmus* and *Palaeopsylla* (Smit, 1970).

Females are also mostly symmetric, with the exception of the partial or entire reduction of one spermatheca in most taxa (Snodgrass, 1946; Holland, 1955; Smit, 1970). The resulting asymmetry appears to be directional, with only the right spermatheca persisting. The presence of two spermathecae in *Hystrichopsylla talpae* (a species with asymmetric male penis rods; see above) has been thought to argue against a correlation between reduction of one spermatheca and male asymmetry (Günther, 1961). However, Snodgrass (1946) notes that in *Hystrichopsylla gigas dippei*, right and left spermathecal ducts differ in length.

Mating in fleas is usually carried out in a symmetric female-above position and involves no change in position (Lundblad, 1926; Holland, 1955; Günther, 1961; Suter, 1964; Humphries, 1967*a*, *b*). The majority of male fleas clasp the basal abdominal sternum of the female by means of their modified antennae (Mitzmain, 1910; Rothschild & Hinton, 1968), then elevate the abdominal tip and accomplish genital contact. Slight modifications occur in species where the female feeds during mating or has penetrated the host's epidermis, with only the tip of her abdomen reaching the surface (Geigy, 1953; Geigy & Suter, 1960; Suter, 1964). In the latter case, the male can obviously not position himself under the female, and copulation starts in an end-to-end position with the ventral sides of male and female facing in opposite directions.

(*c*) *Mecoptera*

Both males and females of Mecoptera have symmetric genitalia (e.g. Crampton, 1923; Setty, 1940; Grell, 1942; Kaltenbach, 1978; Mickoleit, 1976; Mickoleit & Mickoleit, 1978; Willmann, 1981). The phallosome of the relic species *Notiothauma reedi* appears asymmetric in Crampton's (1931) figure 15, but subsequent studies (Mickoleit, 1971; Willmann, 1981) have shown that this is an artefact, probably due to the fact that a single dried specimen was available to the author. As in Orthoptera (see above), symmetric morphology is maintained even though copulatory positions vary considerably, including asymmetric positions. Another parallel to Orthoptera is that all mating positions in Mecoptera can easily be derived from (or modified into) a symmetric female-above position. Closest to a typical female-above position come the Boreidae. The male usually hunts down the female or even jumps at her, grasps her with his genital claspers at any appendage he can reach, and then tries to secure the female between his modified wings and his abdomen. At this stage, where the female is in an asymmetric position towards the male (either perpendicular or oblique), he releases her appendage with his claspers and achieves genital coupling. Only then does he position the female in a symmetric, final female-above position (Carpenter, 1936; Steiner, 1937; Cooper, 1940; Crampton, 1940; Mickoleit & Mickoleit, 1976; Kaltenbach, 1978). Unfortunately, none of the publications seen considers the question of antisymmetry versus directional asymmetry at the stage when genital coupling is achieved. In the case of *Boreus* (now *Hesperoboreus*) *notoperates*, the initial position is symmetric and identical to the final position (Cooper, 1974).

The mating position of Panorpidae is superficially very different from that in Boreidae, but in principle similar. Male and female stand side by side at a varying angle, and the male lowers his abdomen under the female abdomen, recurving the tip to grasp the female's genitalia from below (Byers, 1963; Kaltenbach, 1978). The change from the boreid to the panorpid position requires no more than the female stepping down from the male (for example to get access to his nuptial gift). As for Boreidae, we found no data on side preference by males.

Finally, Bittacidae mate in a hanging position, with their anterior legs suspended from a twig or leaf. Male and female face each other, leaving the impression of a symmetric belly-to-belly position (Setty, 1940; Newkirk, 1957; Thornhill, 1977; Kaltenbach, 1978; Grassé, 1979; Iwasaki, 1996). However, the photograph of the coupled abdomens of a *Harpobittacus australis* pair (Bornemissza, 1966, pl. 3, fig. 2) clearly shows that the male abdomen is twisted and the author notes that "the ventral surface of the male abdomen ... is aligned with the dorsal surface of that of the female". In a more detailed study on *Bittacus italicus*, Mickoleit & Mickoleit (1978) confirmed that the male abdomen is rotated along its longitudinal axis for 180°. This rotation is temporary and is usually reversed immediately after copulation. The sense of twisting is random-sided, i.e. a male can twist his abdomen in either direction (Mickoleit & Mickoleit, 1978). In *H. australis*, the female eventually lowers herself, ending up in a head-downward, end-to-end position, primarily suspended by the genitalia alone (Bornemissza, 1966). A final end-to-end position is also adopted by *Nannochorista* (Tillyard, 1917; Kaltenbach, 1978).

The sexual behaviour is unknown in most of the taxa considered 'basal' in Mecoptera (Whiting, 2002): *Apteropanorpa*,Meropeidae, and *Notiothauma* (Byers & Thornhill, 1983).

(*d*) *Strepsiptera*

Mating behaviour and morphology is highly derived in Strepsiptera and appears to provide little to the analysis of genital asymmetry. Copulation involves extragenital insemination (Kirkpatrick, 1937; Silvestri, 1941*a*, *b*, 1943; Lauterbach, 1954; Kinzelbach, 1971*a*, *b*; Kathirithamby, 1989, 2000; Beani *et al.*, 2005) and this has presumably resulted in the simplification of the male copulatory organ and in the reduction or loss of the female primary copulatory organ (Kinzelbach, 1971*a*). During copulation, males use their sclerotized aedeagus to penetrate the female, either in an unspecified location of her body (in the 'basal' Mengenillidae, Silvestri, 1940*b*; however, this view may be mistaken: J. Cook, personal communication, March 2006), or in a secondary copulatory organ at the ventral side of the cephalothorax (in Stylopidia; Silvestri, 1940*a*). No asymmetry is known in either the male or female reproductive structures, and it is unknown if males in Stylopidia have to orient themselves properly relative to the female. Actually, both males and females in Stylopidia are quite consistently oriented toward each other (male facing forward on the host, female facing backward with her ventral side towards the host's tergites; Lindberg, 1939; Silvestri, 1941*b*; Kinzelbach, 1971*b*; Beani *et al.*, 2005; but see Baumert, 1959), but this might result from orientation of both relative to the host.

(*e*) *Coleoptera*

The general description given throughout all comprehensive studies on beetle genitalia is that of bilaterally symmetric structures (e.g. Sharp & Muir, 1912; Jeannel, 1955; Hieke, 1966; Coiffait, 1972; Crowson, 1982). However, asymmetries in the sclerotized parts of the genitalia and even more so in the membraneous compounds are common and widespread and their phylogenetic distribution suggests that asymmetries must have evolved many times independently. There is no previous comprehensive investigation of this phenomenon. Moreover, asymmetry of genitalia is rarely mentioned explicitly. As in the basic comparative study on male beetle genitalia by Sharp & Muir (1912), numerous examples of 'irregular' aedeagus shapes are reported. Sharp & Muir (1912, p. 487) even stated concisely that "a great number of the Carabids are asymmetrical, whilst the Cicindelids are generally symmetrical or nearly so", a statement corroborated by a great number of morphological descriptions for taxonomic purposes (e.g. Baehr, 2003, 2005). Normally, only the right paramere in Carabidae is used for taxonomic purposes (e.g. Koch, 1984; Angus, Brown & Bryant, 2000). Left and right parameres are dramatically different in certain species of Harpalinae (tribe Pterostichini, see Lindroth, 1956). In the subtribe Sphodrina one of the parameres – almost consistently the right one – is much longer than the left and narrower (styloid), the right paramere can be simply smaller than the left one (subtribe Agonina = Platynina), or the right (genus *Synuchus*) or left (genus *Pristosia*) paramere is reduced. The latter genus differs from all others studied up to now in that the aedeagus lies on its left side in repose. One should expect that this sharp asymmetry in the male copulatory apparatus has functional effects or/and corresponds to an asymmetry in the female abdomen. However, explicit studies on this question are missing. Similarly asymmetric parameres have been found in Mordellidae (Lu, Jackman & Johnson, 1997).

Although most male genitalia in beetles appear symmetric at first glance (see e.g. Iablokoff-Khnzorian, 1980), countless deviations from symmetry can be detected and have been reported in the literature. In some cases, these deviations are only slight, e.g. an asymmetric shape of the proximal opening (orificium) of the median lobe (e.g. Paussidae, Sharp & Muir, 1912, p. 490; Scarabaeidae, Sanmartín & Martín-Piera, 2002), or an asymmetric bending of the apex of the median lobe (*Clambus* spp., Clambidae; Endrödy-Younga, 1999). In others, the median lobe plus the parameres are slightly and irregularly curved to one side (*Megamerus grossus* – Chrysomelidae: Sagrinae; Reineck, 1913). Miller, Bergstein & Whiting (2007) state in their data matrix (their Table 5) that in the dytiscid genus *Lancetes* the median lobe is asymmetric. In a number of scarabaeid genera the 9th ventral abdominal segment is asymmetric (D. Ahrens, personal communication, July 2007). Most reported cases of asymmetry in the sclerotised parts of the male beetle genitalia pertain to unequal parameres ('lateral lobes'). Moreover, most deviations from symmetry are subtle, such as a paramedian position of the flagellum inside the median lobe of *Chrysolina terskeica* (Romantsov, 2005).

At any rate, the basic symmetry of the abdominal segments including the copulatory apparatus is not affected by the 'retournement' of the aedeagus, i.e. the rotation by 180° during ontogeny, in those families where it occurs (Silphidae, Staphylinidae, Oedemeridae, Tenebrionidae, Dytiscidae, and Chrysomelidae; Kumar & Verma, 1971; Krell, 1996).

Seemingly there are certain beetle taxa of which all species are characterised by asymmetric male genitalia, e.g. the genus *Serica* (Scarabaeidae; Ahrens, 2005) and the *fratema* species complex in the genus *Phyllophaga* (Scarabaeidae; M. Polihronakis, unpublished data; http://esa.confex.com/esa/2004/techprogram/paper_16823.htm). In the latter genus, asymmetry appears to have evolved several times independently but to be plesiomorphic for the *fratema* species complex. This is remarkable because in another scarabaeid beetle, *Melolontha melolontha*, musculature as well as the sclerotised parts of the copulatory organs in both sexes are nearly perfectly symmetric (Krell, 1996). In some lineages of the scarab beetle group Sericini (e.g. *Oxyserica, Lasioserica, Stilbolemma*), symmetric parameres appear to have evolved from asymmetric parameres (D. Ahrens, personal communication, July 2007). In his review of the family Agyrtidae, the only synapomorphy Newton (1997) could find for the family was the consistently asymmetric base of the aedeagus. But he also found that neither the male genital segment nor any part of the female genitalia are asymmetric in this family. The Cholevinae (Leiodidae) include spectacular cases of asymmetry in the male genitalia. For example, males of the oriental genus *Ptomaphaginus* have the aedeagus incised from the left side, whereas in the closely related genus *Adelopsis* from the Neotropics it is incised from the right side (Jeannel, 1936).

When a male beetle is dissected, the sclerotised copulatory apparatus appears asymmetric *in situ* in most cases, because the aedeagus is ventrally curved in nearly all species and lies inclined in the abdomen in repose (e.g. Krell, 1996). Exceptions are, e.g. the 'primitive' Staphylinidae: Xantholinini, where the aedeagus lies with its ventral face towards the abdomen wall (Coiffait, 1972). This asymmetry is only superficial and apparently without any functional role during copulation since it is "undone everytime the aedeagus is protruded for copulation" (Verma, 1994).

Conspicuous deviations from symmetry have been found in certain Galerucinae (*Lochmaea* spp., Chrysomelidae; Mohr, 1966). The asymmetries of the median lobes of the male genitalia of these beetles do not seem to follow any obvious phylogenetic patterns.

A special case of asymmetric reproductive organs worth mentioning (though outside our definition of genitalia above) occurs in the monorchid ground beetles (Carabidae) of the tribes Abacetini, Harpalini, and Platynini, i.e. those which have only one testis (of the 148 species listed explicitly by Will *et al.*, 2005, three lacked the right and 87 the left testis). This state was called absence asymmetry by Will *et al.* (2005), who discuss as a possible evolutionary cause "optimal visceral packing". In most monorchid ground beetle species the accessory glands are significantly enlarged as compared to species with two testes. Since the individuals of these species are usually found in dense populations (where sperm competition is highly probable), it might well be that sperm of another male is removed by fluid from accessory glands rather than by spermatozoa. Monorchy is also reported for featherwing beetles (Ptiliidae; Dybas & Dybas, 1987). Most likely, the loss of one testis in these minute beetles (body length normally less than 1 mm) is due to optimal visceral packing. Will *et al.* (2005) suppose that monorchy will be found in many more beetle families containing beetles of minute size that have not yet been investigated.

Another special case is the family Scirtidae. The aedeagus in this group is less sclerotised than the normal beetle organ. It is composed of a dorsal and a ventral part. The ventral part is formed by a plate with two apodemes which are reduced in several genera. In many species of several genera, this reduction resulted in a considerable asymmetry, which does not, however, correspond to an asymmetry of the female counterparts (Nyholm, 1967, 1969).

The female beetle genitalia are mostly membraneous, and therefore their shape is rarely described in detail. Distinct asymmetric female genitalia occur in certain scarab beetle genera like e.g. *Chrysoserica*, *Gastroserica*, and *Serica* (D. Ahrens, personal communication, July 2007). Sclerites in the wall of the bursa copulatrix are often irregular, tiny, and absent in many families. Usually, the only regularly sclerotised part of the female reproductive apparatus is the spermatheca. Since this organ is more or less hook- or U-shaped and unpaired, the anatomy of the female reproductive tract consequently has an asymmetric aspect as long as the spermatheca lies paramedian and/or on its curved side. In most species, no part of the male copulatory apparatus interacts with the spermatheca, and even where the flagellum is intromitted into the spermathecal duct (*Aleochara curtula*, Staphylinidae; Peschke, 1978; Gack & Peschke, 1994), the functional impact of this asymmetry is probably of minor, if any, importance.

Comparable to the case of monorchid beetles above, females of the subfamily Scarabaeinae possess obviously only a single – the left – ovary (Halffter & Matthews, 1966; Halffter & Edmonds, 1982). This phenomenon is most likely related to the low fecundity of the beetles of this subfamily that evolved in connection with enhanced brood care and a shift towards *k*-strategy life history (Halffter, 1977; Halffter & Edmonds, 1982).

In some species of the carabid tribe Platynini, the bursa copulatrix is asymmetric and mirror-image-like different in pairs of closely related species (probably sister taxa) (e.g. *Barypristus rupicola* and *B. incendarius*; Liebherr & Zimmerman, 1998). This tribe belongs to the subfamily Harpalinae, as does the above-mentioned genus *Synuchus*. Since the asymmetry described for the Platynini certainly has a hereditary basis, one would expect that it has functional consequences relevant to the fitness of these beetles. However, nothing is reported on this to date.

Verhoeff (1893) mentioned that the copulatory organs and the last visible segments of male *Carabus* beetles are asymmetric, whilst those of females are not; a similar pattern occurs in the genus *Ocypus* (Staphylinidae). He also reported that in "*Hylotrypes Gideon*" – probably the scarabaeid *Xylotrupes gideon* (Linnaeus, 1767) – the relations are opposite. Thus, there is no simple and general anatomical correspondence between the copulatory structures in the two sexes.

According to the evidence at hand, the large majority of asymmetries reported for beetle genitalia are directional asymmetries rather than antisymmetries. There are very few published examples for the co-existence of both enantiomorphs within in a population (D. Ahrens & P. K. Lago, unpublished data). Wherever several individuals of a species or individuals of several closely related species have been studied (e.g. Ahrens, 2005; Coiffait, 1972; Liebherr & Zimmerman, 1998; Lindroth, 1956; Lu *et al.*, 1997; Mohr, 1966; Miller *et al.*, 2007; Newton, 1997; Nyholm, 1969; Polihronakis, 2006), the data almost universally suggest directional asymmetry because only one enantiomorph occurs within species and higher taxa. Cases where asymmetric structures are illustrated but the asymmetry is not treated explicitly may often be examples of fluctuating asymmetry where one alternative was selected by chance for description (e.g. Reineck, 1913; Romantsov, 2005).

(*f*) *Hymenoptera*

The genitalia of Hymenoptera appear to be symmetric throughout. Explicit mention and documentation of symmetry is rare (e.g. Clausen, 1938), but none of the general texts seen, nor any of the recent morphological data matrices and detailed comparative analyses of hymenopteran genitalia include any mention of genital asymmetry (e.g. Snodgrass, 1941; Michener, 1944; Smith, 1970*a*, *b*; Berland & Bernard, 1979; Birket-Smith, 1981; Ronquist *et al.*, 1999; Vilhelmsen, 2001; Schulmeister, 2001, 2003*a*, *b*). The strong asymmetry in a drawing of the male sternum IX of the sphecid wasp *Steniolia longirostra* (Handlirsch, 1928) is either an artifact or based on a teratology (Gillaspy, 1964; Bohart & Gillaspy, 1985; W. Pulawski, personal communication, Jan. 2006).

The apparent absence of asymmetry may at first seem surprising because in certain archaic taxa males rotate their genitalia 180° along the longitudinal axis, resulting in the so-called 'strophandrous' condition (as opposed to the unrotated 'orthandrous' condition of the vast majority of taxa). The rotation may occur as early as in the pupa or shortly after emergence and be permanent, or it may occur facultatively in adults only (during copulation; Ronquist *et al.*, 1999; Schulmeister, 2001, 2003*a*). Importantly, rotation is random-sided (clockwise or counter-clockwise; Boulangé, 1924; Bischoff, 1927; D'Rozario, 1940; Togashi, 1970), and this probably explains symmetry despite rotation. Recent phylogenetic analyses suggest that facultative strophandry may be the plesiomorphic condition in Hymenoptera, with two independent changes to obligate strophandry (Xyelinae and Tenthredinoidea s.str.) and one change to (permanent) orthandry (S. Schulmeister at http://www.schulmeister.us/index.html). Internally, the rotation of the terminalia may result in an asymmetric position of the accessory glands, seminal vesicles, vasa deferentia and muscles (Bischoff, 1927; D'Rozario, 1940; Schulmeister, 2001), but none of the external structures is affected. The asymmetry of the female second valvulae (Vilhelmsen, 2000) is probably related to the ovipositor's function in penetrating the substrate for oviposition.

Correlated with the two conditions of genital rotation are two fundamentally different mating positions: strophandrous species (facultatively or obligatory) mate in an end-to-end position, orthandrous species in a male-above position (the male may 'fall off' after coupling and end up in an upside-down, end-to-end position; Enslin, 1912; Bischoff, 1927; Clausen, 1938; D'Rozario, 1940; Gordh, 1975; Weseloh, 1977; Berland & Bernard, 1979; Jänicke, 1981; Kopelke, 1981; van den Assem, 1986; Kimani & Overholt, 1995; Blösch, 2000; Schulmeister, 2001). The ichneumonid *Bathyplectes anurus* male mates in an inverted, end-to-end position, but keeps his legs on the substratum (Gordh & Hendrickson, 1976). All these positions are superficially symmetric, and there appears to be no change between initial coupling and final mating position. Slight asymmetries result from cases where the male, using the male-above position, has to bypass the female sting apparatus with his genitalia. Apparently, the male can use either the left or right side to reach the female genitalia (Bischoff, 1927).

The evolutionary change of positions (in whatever direction) has obviously only affected internal structures but not external symmetry. Previous authors usually assumed a change from a male-above to an end-to-end position, and explained this by some advantage of the end-to-end position over the male-above position (e.g. D'Rozario, 1940; Smith, 1970*a*, *b*; Schulmeister, 2001). However, the transformation may have occurred in the opposite direction (see above), and the more appropriate question would then be about the advantage of the male-above position over the end-to-end position, and of the end-to-end position over the (as yet unknown) plesiomorphic holometabolan position. The fact that in Hymenoptera the anatomical ventral side of the male copulatory organ (the side carrying the volsellae; Schulmeister, 2001) contacts the female dorsally (e.g. Kopelke, 1981; Schulmeister, 2001) is in agreement with a derivation of the end-to-end position from an ancestral female-above position, i.e. from the position considered plesiomorphic for Neoptera (*cf.* Alexander, 1964; Alexander & Otte, 1967; see Section VI).

(*g*) *Trichoptera*

Male genital asymmetry occurs in all major subgroups of Trichoptera (Annulipalpia, 'Spicipalpia', Integripalpia), but the distribution of asymmetry among families has never been revised nor is asymmetry mentioned in some of the most fundamental general treatments (e.g. Nielsen, 1970; Malicky, 1973; Despax, 1979). Table 1 gives a certainly incomplete list of families with asymmetric representatives. Several of the genera listed contain both symmetric and asymmetric representatives (Figs. 2F, G), and cladistic analyses also suggest that asymmetry has evolved multiple times convergently close to the terminal branches. For example, male tergum X lobe asymmetry evolved within the genus *Mystacides* (Morse & Yang, 2002), and male paramere asymmetry evolved within *Glossosoma*, subgenus *Lipoglossa* (Yang & Morse, 2002). Wells (1979) considered asymmetry of paired structures to be the derived condition within the genus *Hellyethira*, but did not base this suggestion on an explicit phylogenetic hypothesis. The phylogenetic tree for the genus *Poecilopsyche* by Schmid (1968) even suggests multiple origins of asymmetry within the genus, but it is not clear how this phylogeny was constructed. The cladistic analysis of the entire order by Frania & Wiggins (1997) does not contain asymmetry at all, probably because asymmetry is not informative at this high taxonomic level of analysis.

In most cases where this detail is given, male asymmetry is directional (Mosely, 1937; Nielsen, 1957; Schmid, 1968, 1971; Flint, 1974; Weaver, 1988, 1989; Wells, 1979; Botosaneanu, 1992; Holzenthal & Harris, 1992; Weaver & Huisman, 1992*a*; Kjærandsen & Andersen, 2002; Yang & Morse, 2002). An exception occurs in *Mystacides*, where the male tergum X lobes are antisymmetric (Morse & Yang, 2002). In *Austrochorema*, symmetric and asymmetric penis sheaths occur within a species (Mosely & Kimmins, 1953).

Female asymmetry is not mentioned in most of the sources seen, even though female genitalia in Trichoptera are routinely cleared by taxonomists and comparatively well studied (Nielsen, 1970). A rare exception occurs in *Orthotrichia costalis* (Hydroptilidae), where the opening of a glandular duct on segment 8 is on the right side (Nielsen, 1980). Note that asymmetry is common in *Orthotrichia* males. In some *Phylloicus* (Calamoceratidae) species the digitate lateral pro-

Table 1. Trichoptera with asymmetric male genitalia. The systematics follows the composite phylogeny in Kjer, Blahnik & Holzenthal (2002)

Taxa	References
ANNULIPALPIA	
Hydropsychidae: *Cheumatopsyche*	Nielsen (1981)
Philopotamidae: *Wormaldia, Chimarra*	Mosely & Kimmins (1953); Botosaneanu & Marlier (1981)
Psychomyiidae: *Tinodes, Paduniella*	Schmid (1972); Malicky (2004)
‘SPICIPALPIA’[1]	
Glossosomatidae: *Agapetus, Glossosoma, Culoptila, Mastigoptila*	Nielsen (1957); Schmid (1971); Flint (1974); Yang & Morse (2002)
Hydrobiosidae: *Poecilochorema, Moruya, Austrochorema*	Mosely & Kimmins (1953); Jacquemart (1965); Schmid (1989)
Hydroptilidae: *Orthotrichia, Paroxyethira, Xuthotricha, Stactobia, Agraylea, Hydroptila, Oxyethira, Jabitrichia, Hellyethira, Mexitrichia, Loxotrichia, Dolotrichia, Guerrotrichia, Polytrichia, Orphninotrichia*	Mosely (1937, 1939); Mosely & Kimmins (1953); Nielsen (1957); Neboiss (1986); Wells (1979, 1991); Holzenthal & Harris (1992); Botosaneanu (1992); Arefina *et al.* (2002); Kjærandsen & Andersen (2002); Malicky (2004)
INTEGRIPALPIA	
Calamoceratidae: *Phylloicus*	Prather (2003)
Lepidostomatidae: *Lepidostoma, Goerodes*	Kumanski (1988); Weaver (1988, 1989); Weaver & Huisman (1992*a*, *b*)
Leptoceridae: *Poecilopsyche, Leptocerus, Mystacides, Triaenodes, Oecetis*	Mosely (1939); Mosely & Kimmins (1953); Schmid (1968, 1987); Kumanski (1988); Gibon (1992); Neboiss & Wells (1998); Morse & Yang (2002)

[1] Most recent phylogenetic studies do not recover Spicipalpia as a monophylum.

cesses of tergum X may be slightly asymmetric (Prather, 2003). Interestingly, however, symmetric and asymmetric specimens occur within species, and the same kind of subtle and varying asymmetry also occurs in males where it affects the basolateral processes of tergum X (Prather, 2003).

Mating in Trichoptera is initiated in a side-by-side position, with the male turning or flexing his abdomen sideways (without twisting it along the longitudinal axis) until genital contact is accomplished. Usually, the side-by-side position gives way to a final end-to-end position (Malicky, 1973; Erman, 1984). In certain *Himalopsyche* species the male ends up on top of the female (Schmid & Botosaneanu, 1966). Apart from these basic data, detailed information is either missing or contradictory. At present there is no evidence for precopulatory twisting of the male abdomen or genitalia, nor on the nature of positional asymmetry in asymmetric taxa (one-sided *versus* random-sided). In the final end-to-end position, there is no twisting of the abdomen, i.e. the dorsal side of the male contacts the dorsal side of the female. However, a comparison of figures 240c (phallus at rest) and 241 (genitalia during copulation) in Wiggins (1997) shows that in *Eubasilissa rahtkirani* the male endothecal sclerites are twisted 180° within the female. Other studies of genital mechanics (which equally rely on single pairs incidentally fixed during copulation) suggest that not even the phallus is twisted during copulation (Tobias, 1972; Statzner, 1974).

(*h*) *Lepidoptera*

Male genital asymmetry in Lepidoptera is a widespread phenomenon, having originated many times independently and involving a wide array of structures. Two fundamentally different kinds of asymmetry appear to exist: (1) asymmetry of the phallus and its components (especially the eversible endophallus, or vesica). This asymmetry is universal or nearly universal within the order (as already noted by Chapman, 1902), and appears to be related to asymmetries in the female internal genitalia rather than to copulatory position (see below). (2) Asymmetry of the ‘accessory’ components, especially the paired claspers (valvae). This kind of asymmetry has evolved many times independently but is by no means universal. It appears to be related not to female asymmetry but to the copulatory position (see below).

Table 2 gives a certainly incomplete list of taxa with this second kind of asymmetry. The distribution of asymmetric taxa among families and superfamilies in Table 2 suggests that asymmetry of this kind has evolved up to 30 times independently, but cladistic analyses of various taxa indicate that the actual number is even higher. For example, the analysis of Pterophoridae by Gielis (1993) suggests that symmetry is plesiomorphic for the family, and asymmetry evolved three times independently. Studies on Gelechioidea (Hodges, 1998; Kaila, 2004) also suggest that symmetry is plesiomorphic for the taxon, and that asymmetry arose three to (more probably) eight or more times [Note: Kaila (2004) used only symmetric species in several taxa where both symmetric and asymmetric species occur, like Gelechiidae and Oecophoridae]. In Scythridinae, cladistic analysis suggests at least six independent origins of valve asymmetry (Landry, 1991). An extreme case has been documented in the geometrid tribe Scopulini, where asymmetric genitalia have evolved at least ten times convergently (Sihvonen, 2005). Analysing different structures separately results in more than 20 convergent origins of asymmetry in Scopulini (Sihvonen, 2005). The 8th sternite in Scopulini is also often asymmetric and probably constitutes a copulatory organ in our sense (see Section I), but this character was not coded by Sihvonen (2005). In some cases, cladistic analysis suggests reversal to symmetry (e.g. *Singularia* in Pterophorinae, Gielis, 1993; *Macrobathra* and *Limnaecia cirrhozona* in Cosmopteriginae, Kaila, 2004). That such reversals may

Table 2. Lepidoptera with asymmetric male and/or female genitalia. Asymmetries of the phallus and the signa are excluded. The systematics follows Kristensen (1998)

Taxa	Asymmetric structures	References
ERIOCRANIOIDEA		
Eriocraniidae part	♂: median plate	Davis (1978)
HEPIALOIDEA		
Hepialidae part (e.g. *Fraus*)	♀: antrum	Nielsen & Kristensen (1989)
TINEOIDEA		
Tineidae part (e.g. *Infurcitinea*)	♂: valvae	Hannemann (1977)
GRACILLARIOIDEA		
Gracillariidae: *Phyllonorycter* part	♂: valvae, saccus, tegumen, sternite 8	Kuznetzov & Baryshnikova (2004)
GELECHIOIDEA		
Xyloryctidae: Scythridinae part (e.g. *Asymmetrura*, *Enolmis*, *Episcythris*, *Neoscythris*, *Scythris* part)	♂: valvae, gnathos, tergum 8, sternum 8 ♀: henia, sterigma, ostium, segment 6	Bengtsson (1984, 1997, 2002); Landry (1991)
Oecophoridae: Peleopodinae part (e.g. *Durrantia*)	♂: valvae	Hodges (1974, 1998)
Cosmopterigidae: Antequerinae part (e.g. *Pancalia*, *Euclemensia*, *Antequera*), Cosmopteriginae, Chrysopeleiinae part (e.g. *Calycobathra variapennata*, *Bifascicoidea leucomelanellus*, *Gisilia*)	♂: juxta, gnathos, valvae, anellus lobes, uncus lobes, brachium ♀: apophyses anteriores, ostium bursae	Hodges (1978, 1998); Scoble (1992); Koster & Sinev (2003); Kaila (2004)
Gelechiidae: Gelechiinae part (e.g. *Coleotechnites*, *Mirificarma interrupta*), Dichomeridinae part (e.g. *Dichomeris*), Pexicopiinae part	♂: vinculum, juxta, vinculum-valva complex, segment 8 ♀: bursa copulatrix, sternite 8	Scoble (1992); Hodges (1986, 1998); Huemer & Karsholt (1999)
Glyphidoceridae: *Glyphidocera asymmetricae*	♂: valvae	Adamski (2005)
ZYGAENOIDEA		
Zygaenidae: Procridinae: *Harrisina*	♂ (structure not given) ♀: antrum	Epstein *et al.* (1998)
TORTRICOIDEA		
Tortricidae: Olethreutinae: Gatesclarkeanini; Enarmoniini: *Hystrichophora*	♂: valvae	Scoble (1992); T. Gilligan (personal communication, March 2005)
PTEROPHOROIDEA		
Pterophoridae: Agdistinae, *Marasmarcha* group, Pterophorinae part	♂: valvae ♀: ostium, antrum	Gielis (1993, 1996); Kovtunovich (2003)
HESPERIOIDEA		
Hesperiidae: Pyrginae (e.g. *Erynnis*)	♂: valvae ♀: lamella	Burns (1970); Scott (1978)
PAPILIONOIDEA		
Lycaenidae: Poritiinae (e.g. *Pentila*, *Ornipholidotes*, *Mimacraea*)	♂: uncus	Stempffer (1967)
GEOMETROIDEA		
Geometridae: Larentiinae (e.g. *Eupithecia palpata* group); Sterrhinae: Scopulini part; Ennominae (e.g. *Diaprepesilla*)	♂: ventral plate (sternite 8), valvae (sacculus, valvula), socii, vinculum ♀: protuberance on bursa, lamella antevaginalis	McDunnough (1954); Stekolnikov & Kuznetzov (1982); Mikkola (1994); Ferris (2004); Sihvonen (2005)
BOMBYCOIDEA		
Saturniidae: Ceratocampinae (e.g. *Schausiella*), Subfamily? (e.g. *Scolesa*)	♂: valvae	Lemaire & Minet (1998)
Sphingidae: Sphinginae (*Dolboa*), Macroglossinae: Dilophonotini (e.g. *Enyo, Hemaris*); Philampelini (e.g. *Eumorpha*); Macroglossini (e.g. *Cautethia*)	♂: valvae, harpes, tegumen ♀: ostium bursae, base of ductus bursae	Chapman (1902); Hodges (1971); Scoble (1992)

NOCTUOIDEA		
Noctuidae: Noctuinae (e.g. *Euxoa*), Catocalinae (e.g. *Grammodes*, *Ulotrichopus*, *Crypsotidia*, *Tytroca*), Acontiinae part, Cuculliinae: *Allophyes*, unknown subfamily: *Karmanica*, Hadeninae (e.g. *Annaphila* part)	♂: valvae ♀: appendix bursae, ductus bursae, ductus seminalis	Rindge & Smith (1952); Lafontaine (1987); Hardwick (1970); Kitching & Rawlins (1998); Zilli (1999); Hacker (2001); Ebert & Hacker (2002)
Micronoctuidae	more or less marked asymmetries in the genitalia of both sexes	M. Fibiger & N. P. Kristensen (personal communication)
Arctiidae: Arctiinae part (e.g. *Vivienna*, *Ordishia*, *Melanarctia*, *Himerarctia*, *Amphelarctia*), Syntominae part	♂: juxta, valvae ♀: appendix bursae	Watson (1975); deFreina & Witt (1987)

result from simple genetic mechanisms is suggested by symmetric specimens rarely found among specimens of asymmetric species (Burns, 1970; Figs. 2H, I). A final interesting observation from Table 2 is that this kind of asymmetry is apparently restricted to the Ditrysia.

By contrast, asymmetry of the phallus also occurs among monotrysian moths, as for example in Nepticulidae (Nieukerken, 1985; Johansson *et al.*, 1990; Puplesis, 1994). However, the literature on this kind of asymmetry is difficult to evaluate, for several reasons: first, this asymmetry is rarely mentioned explicitly in the text; second, figures of the phallus are not consistently shown in dorsal or ventral views, and usually this information is not provided; third, mounting techniques may have led to a bias in that asymmetry is interpreted as artificial (Chapman, 1902). The asymmetry of the phallus appears to result primarily from twisting of the structure along the longitudinal axis rather than from different structural development of right and left sides (Chapman, 1902; see also Porter & Shapiro, 1990). The fact that muscle attachment is only rarely asymmetric (Stekolnikov & Kuznetzov, 1982) suggests that in most cases the twisting involves only the terminal parts of the phallus.

Both kinds of male asymmetry in Lepidoptera represent cases of directional asymmetry rather than antisymmetry. This detail is often not mentioned explicitly, but whenever it is mentioned (usually without sample size), the asymmetry is directional (e.g. Chapman, 1902; Rindge & Smith, 1952; Hannemann, 1977; Scott, 1978; Gielis, 1996; Nieukerken, 1985; Hodges, 1986, 1998; Landry, 1991; Mikkola, 1994; Arenberger, 1995; Ebert & Hacker, 2002; Koster & Sinev, 2003; Kuznetzov & Baryshnikova, 2004). In the strongly asymmetric *Erynnis persius*, the left valva was observed to scrape the female while the right valva remained relatively stationary (Scott, 1978), suggesting functional segregation between right and left sides. The same is suggested by the extreme differences between right and left valvae in certain *Phyllonorycter* species, where even genital muscles may become highly asymmetric (Kuznetzov & Baryshnikova, 2004).

A unique case of male genital asymmetry among the usually symmetric Pyralidae occurs in *Syntonarcha iriastis*. Directionally asymmetric structures at the bases of the valves and on the 8th sternite are used for stridulation, with the left side providing file and scraper, the right side a complicated "tracer and groove" system (Gwynne & Edwards, 1986).

Female asymmetry usually affects only internal structures, like ostium bursae and sterigma, ductus bursae and antrum, corpus bursae, signa, etc. Note that these are all structures traversed or contacted by the aedeagus and/or vesica and/or spermatophore. This, together with a tight morphological correlation of the male and female structures involved (e.g. Mikkola, 1992; Callahan, 1958*b*; Ferro & Acre, 1975), suggests a causal correlation between male phallus asymmetry and female internal asymmetry. The evolutionary origin (male or female) of these asymmetries is unclear, as is the direction of the correlation. Female asymmetry has been included in a few cladistic analyses, but in one case only ostium and antrum were considered (Gielis, 1993), in the other cases only the signa were coded (Kaila, 2004; Hsu & Powell, 2005). This certainly underestimates the incidence of female asymmetry in the taxa studied. As in males, female asymmetry is directional in at least the majority of cases (e.g. Rindge & Smith, 1952; McDunnough, 1954; Emsley, 1963; Hodges, 1971, 1986; Watson, 1975; Arenberger, 1995; Munroe & Solis, 1998; Bengtsson, 2002; Koster & Sinev, 2003). In the noctuid genus *Euxoa*, the orifice of the ductus seminalis is either on the right (subgenus *Orosagrotis*) or on the left side (subgenera *Euxoa* and *Pleonectopoda*). Interestingly, the vesica in each case is bent to the opposite side (Hardwick, 1970). In exceptional cases, female asymmetry may involve externally visible structures, like the 8th sternite in *Mirificarma interrupta* (Huemer & Karsholt, 1999), the 7th sternite in *Eupithecia* (Mikkola, 1994), or the 6th segment in *Enolmis jemenensis* (Bengtsson, 2002). These external asymmetries are possibly all correlated with asymmetric male structures other than the phallus (in *Eupithecia* with modifications of the male 8th sternite; Mikkola, 1994).

The mating position in Lepidoptera is relatively homogenous. The male usually initiates contact in a side-by-side position, bending his highly moveable abdomen up to 180° towards the female until the tip of her abdomen can be grasped by the claspers (Titschak, 1922; Hannemann, 1957; Callahan, 1958*a*; Scott, 1973, 1986; Kozlov, 1985). Depending on the substratum, this side-by-side position may continuously pass into a belly-to-belly position, for example on grass blades or twigs (e.g. Mallet, 1984). In lower Lepidoptera, the side-by-side position may be facultatively maintained throughout copulation (Kozlov, 1985), but in the majority of taxa, the male moves to an end-to-end position immediately or shortly after establishing genital contact (Titschak, 1922; Khalifa, 1950*b*; Hannemann, 1957; Callahan, 1958*a*; Powell, 1968; Ackery & Vane-Wright, 1984; Kozlov, 1985; Scott, 1986; Krebs, 1988; Fänger & Naumann, 1998). In the pyralid *Galleria*, the male mounts the female to initiate copulation (Khalifa, 1950*b*); a similar male-above position occurs in *Eucheira socialis* (Pieridae), a species that is also unusual for other morphological and behavioural traits (Shapiro, 1989). In '*Laspeyresia*' (now *Cydia*) *pomonella*, copulation is initiated in the end-to-end position (Ferro & Acre, 1975). One crucial piece of information seems to be largely missing: is the lateral position (in symmetrical and asymmetrical taxa, respectively) one-sided or random-sided? The only explicit mentions we are aware of are by Scott (1973, 1986) for the morphologically symmetric papilionoids, where the position is random-sided.

Numerous accounts of genital functional morphology indicate that there is no inversion of the accessory components of the male genitalia in Lepidoptera. In all published accounts available to us, the dorsal side of the male abdomen contacts the dorsal side of the female abdomen (Michael, 1923; Hewer, 1934; Bayard, 1944; Khalifa, 1950*b*; Hannemann, 1954; Emsley, 1963; deJong, 1978; Chovet, 1982; Fänger & Naumann, 1998; Miller, 1988). In particular, the male uncus (a process of the 8th tergite) often was found to interact with the female 8th tergite (Norris, 1932; Hannemann, 1957; Arnold & Fischer, 1977; Miller, 1988). This unusual direct correlation was already noted as "difficult to reconcile" with information on other insects by Richards (1927). However, if the asymmetry of the phallus indeed results primarily from twisting of the structure along the longitudinal axis (see above) then this suggests that inverse genitalic correlation also occurs in Lepidoptera, even though it is restricted to the phallus. Asymmetric attachment of muscles to the phallus would support this idea, but such asymmetry seems to be the exception rather than the rule (Stekolnikov & Kuznetzov, 1982).

(*i*) *Diptera*

Male genital asymmetry occurs mostly sporadically within the Diptera (Table 3), with nearly all cases occurring in the Eremoneura, either uniquely derived in some species, species groups, genera, or even families. This list is intended only to demonstrate the distribution of asymmetry in the Diptera and many more examples certainly exist. Only in a few families is asymmetry much more extensive and it has evolved independently numerous times. The extent of asymmetry can also vary from only slight asymmetry to grossly derived forms (see below). This survey does not include examples of asymmetry of the apex of the phallus, which is quite widespread among Acalyptratae, although not often discussed (e.g. *Syringogaster*: Prado, 1969; Agromyzidae: Spencer & Steyskal, 1986; Diopsidae: Kotrba, 1993; Dryomyzidae: Falk, 2005; Tephritidae: Eberhard & Pereira, 1995). In addition, the phallus is coiled to one side (often the right side) in Tephritidae and some related families (Griffiths, 1972; Eberhard, 2005). Asymmetry was not discussed in reviews of the homologies of the male terminalia in Diptera (Wood, 1991; Sinclair, Cumming & Wood, 1994; Cumming, Sinclair & Wood, 1995).

Male genital asymmetry is not common in nematocerous Diptera (or lower Diptera), with only a few species known in the Mycetophilidae (Vockeroth, 1981) and asymmetric parameres (right side enlarged and left side reduced) in the genus *Dasyhelea* (Ceratopogonidae; Downes & Wirth, 1981). In the Scatopsidae, a clade of four genera within the Colobostematini is defined by asymmetric terminalia (including a species from Dominican amber), and genital asymmetry is strongly pronounced in the genus *Borneoscatopse* (Amorim, 1998). In Tipulidae, one example is known where the aedeagus is arched to the left side (Theischinger, 1993).

In the lower Brachycera, no examples of male genital asymmetry are known. In the subfamily Anthracinae (Bombyliidae), pregenital intersegmental muscles are asymmetric, which enables obligate 180° rotation, with segment 8 rotated partially (Yeates, 1994). In this subfamily rotation is known in either direction, but assumed to be directional within lower taxa, with species or genera rotated either clockwise or counter clockwise. The male pursues the female and makes genital contact in a venter-to-venter position in the air, then the pair alights and sits end-to-end (Yeates, 1994; Stubbs & Drake, 2001).

The Eremoneura comprise two monophyletic groups: Empidoidea and Cyclorrhapha (Sinclair & Cumming, 2006). Symmetric male terminalia is the ground plan

Table 3. Examples of genera with species possessing asymmetric male terminalia in Diptera (not including aedeagus or phallus) († - fossil taxon). Classification follows McAlpine (1989)

Taxa	Asymmetric structures	References
NEMATOCEROUS DIPTERA		
Mycetophilidae: (e.g. *Acnemia*)		Vockeroth (1981)
Scatopsidae: Colobostematini (e.g. *Borneoscatopse, Lumpuria*), Rhegmoclematini (e.g. *Neorhegmoclemina*), Scatopsini (e.g. *Apiloscatopse*), Swammerdamellini *(Coboldia)*	paramere, gonocoxite, gonstylus	Cook (1955); Amorim (1998); D. Amorim (personal communication)
Thaumaleidae: (e.g. *Androprosopa tridanta*)	paramere	Schmid (1970)
Ceratopogonidae: (e.g. *Dasyhelea*)	paramere	Downes & Wirth (1981, figs 100, 101)
BRACHYCERA – EREMONEURA		
EMPIDOIDEA		
Atelestidae: Nemedininae (e.g. *Neoturonius*†)	most structures (e.g. surstylus, hypandrium, epandrium)	Grimaldi & Cumming (1999)
Hybotidae: Tachydromiinae (e.g. *Symballophthalmus, Platypalpus, Stilpon*), Ocydromiinae (e.g. *Ocydromia*), Hybotinae (e.g. *Hybos, Syndyas*), Oedaleinae (*Oedalea*, *Anthalia*), Trichininae (e.g. *Trichina*)	most structures (e.g. epandrium, surstylus, hypandrium)	Chvála (1975, 1983); Cumming & Cooper (1992); Sinclair & Cumming (2006)
Empididae: [e.g. *Rhamphomyia* (*Pararhamphomyia*) unpubl. species group]		B. J. Sinclair (unpublished data)
Brachystomatidae: (e.g. *Ephydrempis, Sabroskyella, Trichopeza*)	anus and cerci slightly to left of centre and phallus and surstyli to right	Chvála (1983); Sinclair & Cumming (2006)
Dolichopodidae *s.lat.*: Microphorinae (e.g. *Microphor, Schistostoma*) Parathalassiinae (e.g. *Chimerothalassius*, *Eothalassius*, *Microphorella*, *Parathalassius*, *Thalassophorus*)	most structures (e.g. surstylus, postgonite, epandrium)	Chvála (1986, 1987, 1988); Ulrich (1988); Sinclair & Cumming (2006)
Dolichopodidae *s.str.*: (e.g. most genera, except *Plagioneurus*, Badindellinae)	base of epandrium	Ulrich (1974); Bickel (1987); Sinclair & Cumming (2006)
LOWER CYCLORRHAPHA		
Phoridae Sciadocerinae (e.g. *Sciadocera*), Hypocerinaae (*Burmophora*, *Hypocera*), Phorinae (e.g. *Spiniphora*), Metopininae (e.g. *Metopina*)	surstylus (*Sciadocera*), epandrium, hypandrium	Brown (1992); Sinclair & Cumming (2006)
Pipunculidae: Chalarinae (e.g. *Chalarus, Verrallia*), Nephrocerinae (e.g. *Nephrocerus*), Pipunculinae (e.g. *Claraeomorpha, Dorylomorpha, Eudorylas, Tomosvaryella*)	epandrium, hypandrium, surstylus	Albrecht (1990); Jervis (1992); Rafael & De Meyer (1992); Sinclair (2000: fig. 36)
Syrphidae: Eristalinae (e.g. *Blera, Cheilosia, Chrysogaster, Sericomyia, Sphegina, Teuchocnemis, Xylota*), Microdontinae (e.g. *Microdon*), Syrphinae (e.g. *Citrogramma,. Eosphaerophoria, Giluwea, Simosyrphus, Sphaerophoria*)	all combinations: epandrium, hypandrium, surstylus, gonostylus, phallus	Metcalf (1921); Vockeroth (1969, 1992); Dušek & Láska (1987)
CYCLORRHAPHA – ACALYPTRATAE		
NERIOIDEA		
Micropezidae: (e.g. *Micropeza*)	surstylus	M. Buck (personal communication)
TEPHRITOIDEA		
Lonchaeidae: (e.g. *Lonchaea impressifrons* group)	pregonite, surstylus	McAlpine (1960); MacGowan (2005)
OPOMYZOIDEA		
Periscelididae: (e.g. *Stenomicra*)	pregonite, postgonite	Merz & Roháček (2005)
Asteiidae: (e.g. *Asteia*)	surstylus	Merz (1996)
SCIOMYZOIDEA		
Sepsidae: (e.g. *Saltella sphondylii, Microsepsis, Palaeosepsis*)	surstylus	Silva (1993); Eberhard (2001); Pont & Meier (2002)
LAUXANIOIDEA		
Lauxaniidae: (e.g. *Calliopum*, *Lauxania*, *Minettia*, *Mycterella, Sapromyza*)	postgonite	Shewell (1987);Yarom *et al.* (1986); Freidberg & Yarom (1990); Shatalkin (2000); Merz (2001)

Table 3 *(cont.)*

Taxa	Asymmetric structures	References
SPHAEROCEROIDEA		
Sphaeroceridae: [e.g. *Aluligera*, *Copromyza*, *Gonioneura*, *Kabaria*, *Minilimosina* (*Amputella*)]	postgonite, surstylus	Marshall (1982, 1985); S. A. Marshall (personal communication); Roháček (1992)
EPHYDROIDEA		
Drosophilidae: Steganinae (e.g. *Stegana*, *Amiota*), Drosophilinae (e.g. *Cladochaeta*)	paraphyses, postgonites	Grimaldi & Nguyen (1999); Chen & Wang (2004); Chen *et al.* (2005)
Ephydridae: Hydrelliinae (e.g. *Hydrellia*), Discomyzinae (e.g. *Discomyza*, *Mimapsilopa*), Gymnomyzinae (e.g. *Orasiopa*)	surstylus, phallus, epandrium, hypandrium, cercus	Papp (1983); Zatwarnicki (2002)
CYCLORRHAPHA – CALYPTRATAE		
Anthomyiidae: (e.g. *Coenosopsia*, *Phorbia*)	cercus, pregonite, surstylus	Suwa (1974); Michelsen (1991)
Tachinidae: (e.g. *Ginglymia*)	cercus, surstylus	J. O'Hara (personal communication)

condition of the superfamily Empidoidea, but asymmetric male terminalia have evolved numerous times (Sinclair & Cumming, 2006). Asymmetry is rather rare in the most plesiomorphic family, Empididae (Table 3) and the unique asymmetry of the male terminalia defines the *Trichopeza* clade in the Brachystomatidae (Sinclair & Cumming, 2006). In this latter clade the anus and cerci are displaced to the left side, while the phallus, apex of the hypandrium and surstyli extend to the right. No information on mating position is available for this family. The Hybotidae are also well known for male genital asymmetry. In the subfamily Tachydromiinae all taxa bear asymmetric male terminalia, with the right side enlarged compared to the left side (Chvála, 1975; Cumming & Cooper, 1992). In the genus *Stilpon*, the epandrium is divided with a small left lamella fused to the hypandrium (Cumming & Cooper, 1992). Although widespread in the family, asymmetry does not appear to be a ground plan feature, whereas permanent rotation of up to 90° involving normally only the genitalia is interpreted as being synapomorphic (Sinclair & Cumming, 2006). The terminalia are symmetric in *Trichinomyia* (Trichininae), whereas the terminalia of *Bicellaria*, *Syneches* and *Lamachella* are only very slightly asymmetric. Although there is very little information on mating positions in the Hybotidae, photographs of pairs in copula indicate that they mate in the false male-above position, with the apex of the abdomen passing over the left side of the female abdomen (i.e. one-sided).

In Dolichopodidae *s.str.* (Empidoidea), the hypopygium is attached laterally to the abdomen, with sternite 8 forming a cap over the hypopygial foramen on the left lateral or laterodorsal side (Ulrich, 1974; Bickel, 1987). The asymmetry of the male hypopygium in Dolichopodidae is interpreted as the result of rotation and flexion, where segment 8 is rotated clockwise 90°, the genitalia rotated 90° and then lateroflexed beneath the abdomen (same result as circumversion with the ejaculatory duct arched over the gut) (Ulrich, 1974; McAlpine, 1981). This modified circumversion permits mating in the male above position (Richards, 1927). Although the epandrium (sternite 9) is asymmetric due to the position of the foramen, the apical 'appendages' (e.g. cerci, surstyli, postgonites, hypandrium, etc.) are normally developed symmetrically (Bickel, 1987). Secondary symmetry of the epandrium with the foramen in the median sagittal plane (i.e. abdomen attached apically) characterises the Babindellinae (Bickel, 1987) and *Plagioneurus* (Sinclair & Cumming, 2006). Secondarily asymmetric apical 'appendages' have also evolved independently on numerous occasions [e.g. *Viridigona asymmetrica* and other species of the same species group (Naglis, 2002), *Parentia asymmetrica* (Grichanov, 2000) and within the Dolichopodinae (Brooks, 2005)].

In Cyclorrhapha, characterized by its hypopygium circumversion (see explanation below), sclerites of segment 6 are often asymmetric in addition to segments 7 and 8 and this has led to the conclusion that the asymmetry of the pregenital sclerites (including spiracles) is not due to rotation (since rotation begins between segments 7 and 8), but has developed *in situ* (Emmert, 1972; Griffiths, 1972). Although segment 6 is not directly rotated, the distortion and drag caused by different muscle reduction, contraction and rotation certainly also affects the symmetry of segment 6. Asymmetry in the pregenital sclerites occurs in the archaic families of the Cyclorrhapha and has been interpreted as a ground plan autapomorphy of the higher flies (McAlpine, 1989). In nematocerous Diptera which undergo 180° inversion, asymmetry of the sclerites of segments 6 and 7 is due to random-sided torsion of the abdomen through the contraction of specialized muscles, but only occurs in highly specialized marine midges (Dordel, 1973).

Within the archaic families of the Cyclorrhapha, the Sciadocerinae is the sister group to the remaining Phoridae (Brown, 1992) and has distinctively asymmetric male terminalia, with the left surstylus greatly enlarged (Cumming *et al.*, 1995; Sinclair & Cumming, 2006, fig. 360). The outgroups to the Phoridae (Platypezidae and Ironomyiidae) both have symmetric male terminalia. There appear to be various states of asymmetry in the remaining Phoridae, only slightly asymmetric in the primitive *Burmophora* and markedly asymmetric with a portion of the hypandrium displaced to the right side in some Metopininae (Brown, 1992).

In both Syrphidae and Pipunculidae the terminalia are circumverted and at the same time flexed or deflexed forward to the right side of the abdomen (asymmetric position below tergite 4 or 5) and involve an asymmetric configuration of segments 6-8 (Vockeroth & Thompson, 1987; Cumming *et al.*, 1995). This position and asymmetry is apomorphic for the Syrphoidea (Griffiths, 1972; Cumming *et al.*, 1995). Male genital asymmetry is widespread in the Syrphidae, yet sporadic with various structures involved and normally the left side or left appendage shortened or towards which the parts are bent (Metcalf, 1921). Perhaps given the asymmetric resting position of the genitalia this is to be expected. In recent phylogenies of the Syrphidae, the Microdontinae has been assigned as the sister group to the remaining Syrphidae (Skevington & Yeates, 2000; Ståhls *et al.*, 2003), but asymmetry in the Microdontinae is apparently not common.

In the Pipunculidae, male genital asymmetry is widespread, with slightly to highly asymmetric structures. Only distinctive asymmetry has been utilized in phylogenetic analyses (Rafael & De Meyer, 1992; e.g. synapomorphy of *Claraeomorpha* and *Dorylomorpha*) and arises independently numerous times. In the 'basal' subfamily (Chalarinae), genital asymmetry is associated with the asymmetric attachment of segment 8 (positioned and fused mostly to right side of epandrium), and consequently the base of the epandrium and possibly also the hypandrium is asymmetric (Jervis, 1992). In more derived lineages, the surstyli are slightly to highly asymmetric (Dempewolf, 1998; Skevington & Yeates, 2001), with the right or left surstylus enlarged or reduced in size compared to its partner. Like all other cyclorrhaphans, the Pipunculidae mate in the male-above position (Morakote & Yang, 1988).

Asymmetry in the Acalyptratae is scattered and rather rare in most groups (Table 3). When present, it is often restricted to single species or species groups. Asymmetric postgonites occur often in the family Lauxaniidae, with the right (as viewed in unrotated, non-flexed position) postgonite greatly lengthened. Within the Calyptratae, very few examples of male genital asymmetry are known.

Only a single case of female genital asymmetry has been identified. The apex of the apical sclerite of the ovipositor of *Apocephalus asymmetrica* (Brown, 1997) is asymmetric. Internally, the spermathecal number varies from one to three in Diptera (rarely four), with the ducts of one pair often fused, especially in the Acalyptratae (Sturtevant, 1925). For example, the ducts of the right pair were fused in nearly all individuals of *Cyrtodiopsis whitei* examined (Kotrba, 1993). During mating, the surstyli and epandrial lobes of *Dryomyza anilis* are used to tap the female abdomen, where mechanoreceptors are located (Otronen, 1998). Male tapping affects sperm distribution in the spermathecae, with more sperm located in the single, isolated spermatheca during tapping sequences (Otronen, 1998). It remains to be studied whether asymmetric epandrial lobes (although likely representing fluctuating asymmetry) are related to sperm distribution in the female's spermathecae (Otronen, 1998).

Apart from the spermathecae, there are very few investigations that we know of that have studied the symmetry of the internal female genital tract in great detail and most studies illustrate the tract in lateral view (e.g. Kotrba, 1993; Eberhard & Pereira, 1995). Asymmetric vagina and vaginal sclerites are likely widespread in the Phoridae (Buck, 2001; Buck & Disney, 2001) and are probably associated with the asymmetric male distiphallus (M. Buck, personal communication, 2006). The asymmetric apex of the phallus in certain acalyptrate families (e.g. Tephritidae), is possibly related to the asymmetric position of the spermathecal ducts (see Solinas & Nuzzaci, 1984, fig. 7a). The symmetry of the female vagina requires further study.

The symmetry in Dipteran spermatophores has also not been investigated and the shape is quite variable among and within families (Kotrba, 1993, 1996). In higher Diptera, the shape is especially variable and dependent on the form of the vaginal cavity where they are moulded (M. Kotrba, personal communication). In Simuliidae, the spermatophore is preformed, appears to possess a definitive shape and is mostly symmetric (Davies, 1965).

The Diptera have received greater attention than most other orders of insects in the discussion of mating or copulatory positions and were used as the primary examples of insect mating positions in the initial reviews by Lamb (1922) and Richards (1927), and the later discussions of Hardy (1935, 1944). There is a wider range of mating positions in Diptera than any other insect group, with at least eight recorded positions (Richards, 1927; Hardy, 1935, 1944; Alexander, 1964; Dordel, 1973; McAlpine, 1981; Bickel, 1990) (see illustrations of positions in McAlpine, 1981, figs 142-146). All Diptera mating positions maintain inverse correlation (or inverse coupling) of genital contact (Richards, 1927), where the ventral side of the male aedeagus or phallus is fitted against the dorsal surface of the female bursa or oviduct (Hennig, 1973; McAlpine, 1981) (i.e. the terminalia of the male is inverted with respect to the female).

The initial coupling position is considered to involve both male and female facing in the same direction, but for the final stages of mating the partners may assume a specific final mating position (McAlpine, 1981). Aerial swarming and the initial coupling in-flight are the plesiomorphic conditions in Diptera (McAlpine & Munroe, 1968). Swarming is most common in nematocerous Diptera, but is also found throughout more derived lineages (McAlpine & Munroe, 1968; Headrick & Goeden, 1994; Wilkinson & Johns, 2005). The final stage of mating (ejaculation and sperm transfer) usually occurs while the pair rests on the substratum and the final mating position is believed to result from the awkwardness of the initial position required to establish the inverse interlock. There are only a few families where all stages of mating occur in flight (e.g. Deuterophlebiidae, Nymphomyiidae: Courtney, 1991, 1994; some Syrphidae: Dušek & Láska, 1987).

The male-above position predominates most initial coupling positions and is thought to be more suited for performance in flight. To facilitate coupling, genitalic rotation and flexion is often required to accommodate this mating position. Flexion occurs when the genitalia or apical portion of the abdomen is bent or folded ventrally, dorsally or laterally and is either facultative (voluntary and temporary) or obligatory (fixed and permanent) (McAlpine, 1981).

In nematocerous Diptera and lower Brachycera, there are often several mating positions. In the male-above position, the male flexes the tip of its abdomen forward, making contact with the female terminalia. This is known to occur in some Tipulidae (e.g. *Limonia*), Bibionidae (Leppla, Carlysle & Guy, 1975), Tabanidae (Richards, 1927), Ceratopogonidae (e.g. *Atrichopogon*; Downes, 1978) and Asilidae (Melin, 1923; Reichardt, 1929). The male finally assumes the male-inverted end-to-end mating position in Simuliidae, Tabanidae (McAlpine, 1981) and Thaumaleidae (B. Sinclair, unpublished data).

In the false male-above position the male abdomen passes on either the right or left side of the female abdomen (Richards, 1927). In some Tipulidae, the position is random-sided, with the abdomen passing to either the female's right or left side (Sellke, 1936). In the final mating position in Tipulidae, the male abdomen twists through 180° when the end-to-end position is taken up (Richards, 1927; Sellke, 1936). This twisting also occurs in Ptychopteridae (Tonnoir, 1919; Just, 1973) and Bibionidae (Leppla *et al.*, 1975). The Blephariceridae also mate in the false male-above position (Mannheims, 1935; Zwick, 1977).

In Culicidae and many Ceratopogonidae, males and females couple in flight and a venter-to-venter position is assumed, which often leads to an end-to-end final position (Downes, 1978; Clements, 1999). In these cases the male terminalia are inverted 180°.

Another strategy for achieving inverse coupling is genitalic inversion or rotation of 180°, either obligatory or facultative. Inversion has occurred independently throughout nematocerous Diptera, involving various pregenital segments. For example, within the Culicomorpha, segment 8 and the terminalia are inverted in Culicidae and Corethrellidae (Clements, 1999; McKeever, 1985), segment 7 is partially rotated, segment 8 is rotated 90° and the terminalia a final 90° in some Ceratopogonidae (Downes, 1978), segments 5-7 are partially twisted and segment 8 and the terminalia are inverted in Dixidae (Peters & Cook, 1966), and inversion is obligate or facultative, occurring between segments 7 and 8 in Chironomidae (Dordel, 1973). The inversion is random-sided in Culicidae, with rotation occurring either clockwise or counter clockwise. In Anisopodidae up to three segments are involved (Abul-Nasr, 1950) and twisted up to 180°. In some Psychodidae only the terminalia are inverted, with rotation being random-sided (Just, 1973), whereas in Phlebotominae tergite 7 is rotated 90° and sternite 8 and the terminalia are rotated 180°. Again rotation is known to be random-sided in Phlebotominae (Just, 1973).

In Asilidae (lower Brachycera), the terminalia are often in the hypopygium inversum position (180°), with rotation initiated between segments 7 and 8 and final rotation between 8 and the terminalia. Consequently, the sclerites of segment 8 are in an asymmetric position, rotated up to 90° (Karl, 1959). It is mostly facultative occurring in either direction (random-sided), but often only clockwise. Mostly rotation occurs during mating, except in Laphriinae where rotation occurs just after eclosion.

Mating positions and courtship behaviour in the Asilidae were reviewed by Lavigne (2002). Several positions have been documented: male-above position (either true or false), end-to-end position (in the final stages in some cases, the male releases and swings with head downward and facing in the opposite direction), and side-by-side position (male & female resting side by side, but genitalia angled) (Melin, 1923; Reichardt, 1929; Lavigne, 2002). The pendant position is a variation of the false male-above position, where the male releases himself from the above position and swings down below the female, both facing in the same direction (Melin, 1923). The end-to-end position has been observed in most Laphriinae and Stenopogoninae, where the terminalia are rotated to the hypopygium inversum position (Karl, 1959; Lavigne, 2002). For the side-by-side mating position, the male initiates mating in the male-above position (at least in *Heteropogon*) (Lavigne & Bullington, 1999). In a recent molecular phylogeny of the Asilidae (Bybee *et al.*, 2004), the family was divided into three groups, with the Leptogastrinae as the sister-taxon to the remaining asilids. Based on this phylogeny, the male-above position appears to be primitive; it is quite common in the second grouping, which includes the Asilinae and Apocleinae. The third group includes Dasypogoninae, Laphriinae and Stenopogoninae, which exhibit an end-to-end position.

The Cyclorrhapha all mate in the male-above position with the male terminalia hooked around the female terminalia from above (e.g. Thomas, 1950; Morakote & Yang, 1988; Kotrba, 1993; Headrick & Goeden, 1994). However, this coupling position is only possible due to genitalic rotation, where the Cyclorrhapha are characterized by a dextral genitalic rotation through 360° (with the asymmetric looping of the vasa deferentia + ejaculatory ducts and post-abdominal nervous system around the hind gut), and is termed circumversion (Feuerborn, 1922). The first 180° rotation occurs between sclerites of segments 7 and 8, whereas the remaining 180° occurs between segment 8 and the hypopygium. This rotation is followed by ventral flexion of the hypopygium (Emmert, 1972; Griffiths, 1972; Cumming *et al.*, 1995). A gene has been identified in

Drosophila (presumable *melanogaster*) that controls looping morphogenesis (Ádám, Perrimon & Noselli, 2003).

As stated above, all Cyclorrhapha mate in the male-above position and normally remain in this position, except in Opetiidae and Platypezidae (most archaic families, see Cumming *et al.*, 1995), where in the final position the pair are upright end-to-end (i.e. unwinding of terminalia) (Cumming *et al.*, 1995; Chandler, 1998, 2001). Several examples of end-to-end final position are known in Syrphidae (e.g. Waldbauer, 1984) and the bat fly family, Mystacinobiidae (Holloway, 1976). In Tephritidae, disengagement of the coupling occurs as the male dismounts and moves away end-to-end, pulling the phallus from the female aculeus (Headrick & Goeden, 1994). Ablation experiments of sensilla on the clasping structures of *Drosophila melanogaster* resulted in asymmetric male mating postures (Acebes, Cobb & Ferveur, 2003).

VI. DISCUSSION

(1) Multiple origins of genital asymmetry

We have demonstrated that genital asymmetry has evolved multiple times in insects. It originated a few times within Dermaptera, Neuropterida, Plecoptera, and Siphonaptera; several times within Heteroptera, Homoptera, Psocodea, Trichoptera; and many times within Coleoptera, Diptera and ditrysian Lepidoptera. Genital asymmetry tends to define entire orders or superorders in lower Neoptera (Dictypotera, Mantophasmatodea, Grylloblattodea, Embiidina), while originating closer to the terminal branches (and much more often) in eumetabolous insects. More detailed estimates of the numbers of independent origins must await stable phylogenetic hypotheses on the ordinal relationships among lower Neoptera and of the lower-level relationships among eumetabolous taxa that include both symmetric and asymmetric representatives. By contrast, only four independent origins of genital asymmetry are known in spiders: two in Pholcidae, two in Theridiidae.

The published information suggests that male insects are much more prone to have genital asymmetries than females. Female asymmetry is not only rare but often inconspicuous, and in at least some cases it evolved after male asymmetry (e.g. Heteroptera, Lepidoptera: the rarer conspicuous external asymmetries). Exceptions to this sequence occur rarely, for example in *Lygaeus* and in Lepidoptera (female internal genitalia and phallus). The evidence from taxa like Trichoptera, where female genitalia are routinely cleared and studied in great detail, support the idea that male asymmetry usually appeared first (or appeared exclusively). However, in some groups female genitalia are barely used in taxonomy (e.g. Embiidina, Dermaptera), and inconspicuous internal asymmetries may simply remain undiscovered. In spiders, the same pattern (males only) occurs in *Tidarren*, but it is clearly reversed in the other three cases (females are the first or only asymmetric sex).

Morphologically asymmetric insect genitalia are overwhelmingly directionally asymmetric, i.e. the side is fixed within a species. By contrast, morphological antisymmetry is very rare and is probably derived from directional asymmetry in each of the four cases known to us (*Ciulfina* praying mantids, the thaumastocorid bug *Xylastodoris luteolus*, *Mystacides* caddis flies, a *Stiroma* plant-hopper population). Asymmetric spider genitalia, on the other hand, are mostly antisymmetric (most *Metagonia* females, *Asygyna* females, *Tidarren* males). Only *Metagonia mariguitarensis* males have evolved directionally asymmetric genitalia, and females of the same species are the only case in this entire review where an unambiguous change occurred from antisymmetry to directional asymmetry. Whether genital asymmetry in *Kaliana* females is directed or bidirected remains unknown.

Reversals to symmetry occurred at least a few times (Isoptera, certain anthocorid and plokiophilid bugs, Hawaiian *Iolana* planthoppers, dolichopodine flies, certain pterophorine and cosmopterigine moths, some Sericini beetles). Occasional (probably non-functional) duplications of one side in Embiidina and *Erynnis* moths (Figs 2H, I) suggest that the genetics behind such reversals may be quite simple and need not depend on continuous selection and gradual evolution back to symmetry.

(2) The evolution of mating positions in insects

An intimate relationship between mating positions and morphological asymmetry has long been suspected (e.g. Ludwig, 1932; Snodgrass, 1937), and this explains our emphasis of this aspect of insect biology. The available data strongly corroborate a correlation between morphological asymmetry and one-sided mating position/twisting, whereas random-sided positions are correlated with symmetric genitalia (see e.g. Heteroptera). Here we summarize the evolution of mating positions in insects as a basis for the explanation of genital asymmetry below. We treat only insects here because we see no corresponding correlation in spiders. For a review of spider mating positions see von Helversen (1976).

As already argued by Alexander (1964), all evidence suggests that a symmetric female-above position is plesiomorphic for Neoptera (Fig. 1). This is the position of Ephemeroptera, and probably the plesiomorphic position of Blattaria, 'Homoptera', Mecoptera, Neuropterida, Orthoptera, Psocodea, and Siphonaptera (see above). According to this view, the false male-above position, where the male sits on top of the female but bends his abdomen around the female to insert the genitalia from below, has evolved several times convergently (Mantodea, Embiidina, Grylloblattodea, Mantophasmatodea, Heteroptera, 'Homoptera', Orthoptera, Phasmida, Plecoptera, Thysanoptera, Diptera). An intermediate position that presents a plausible evolutionary link between the female-above and the false male-above positions is the side-by-side (or V-shaped) position, common in 'Homoptera', Lepidoptera, Trichoptera, and Mecoptera. End-to-end positions result from the male turning 180° away from the female, either in a horizontal or vertical plane. Without twisting of the abdomen or the genitalia, this results in an inverted (upside-down) position of the male (as in certain Diptera, Hymenoptera, Neuropterida, Orthoptera, Zoraptera). In most insects that mate in this position, however, the male twists the abdomen or the genitalia so that his legs remain on the ground (Dermaptera, Diptera, Heteroptera, strophandrous Hymenoptera, Lepidoptera). Twisting of the abdomen (or genitalia) is also involved in the change from the female-above to the belly-to-belly position (e.g. Bittacidae, a few Heteroptera, Psocodea, and Lepidoptera). Symmetrical or seemingly symmetrical male-above positions have apparently evolved *via* several routes. First, *via* the end-to-end position with one partner upside-down, by a further 180° rotation of the male along the vertical plane. This involves no abdominal twisting and no positional asymmetry at any time, and may explain the positions of gerromorph bugs and orthandrous Hymenoptera. Second, *via* the end-to-end position with both partners standing upright, by a further 180° rotation of the male along the horizontal plane. Assuming that the male genitalia cannot freely rotate within the female (see below) this involves twisting of the abdomen or genitalia and may result in a total twist of 360° (as in higher Diptera with a 'hypopygium circumversion'). Circumversion thus permits mating in the male-above position. Third, *via* the false male-above position by flexion of the abdomen as in certain Diptera. All other positions are rare and obviously highly derived.

Rotation of 360° would appear odd, but there must be some advantages to such a condition, especially since it is a defining feature of higher Diptera. There is little doubt that it evolved to accommodate changes in mating behaviour (Bickel, 1990). Rotation permits rapid mating, it is less awkward and allows mating on a substratum. Flexion and rotation are also considered to be adaptations for mating and storing the terminalia when not in use and permit both sexes to mate in an upright unidirectional position (McAlpine, 1981, 1989). Bickel (1990) suggests that female sexual selection pressure has facilitated mating on a substratum, encouraging coupling in the male-above position and circumversion of the terminalia. Ultimately, genitalic rotation (either inversion or circumversion) in Diptera, which enables the male-above final position, has likely evolved due to selection for greater control over mating by the male (see below).

We argue that the most reasonable driving force behind most of these multiply convergent positional changes invokes sexual conflict about the control of mating (*cf.* Richards, 1927; Alexander, 1964). A male on top of the female may not only grasp his mate more securely and control the timing of disengagement, but he may also be better able to fend off intruding males or to stimulate the female using his legs and mouthparts (*cf.* Eberhard, 1991, 1994). Males in species that have retained the female-above position have often reverted to other mechanisms that suggest the same function. Examples include manipulation of the female by male glandular products in cockroaches; grasping of the female with modified wings in Boreidae, with modified antennae in fleas, or with front legs that have an extra joint in Ephemeroptera. Even the end-to-end position may be best explained as a male strategy against female disengagement by turning away, as occurs for example in certain *Archipsocus* booklice.

Any asymmetric position (and any abdominal twisting) may in principle exist in two fundamentally different versions: one-sided and random-sided (for terminology see Section I). All the evidence suggests that behavioural flexibility (random-sided positions) pre-dates fixed, one-sided positions. From the male's perspective, this change from a random-sided to a one-sided mating position seems disadvantageous, as it reduces his options. The negative effect must be outweighed by some advantage of morphological asymmetry (see below), as the latter is always correlated with one-sided mating positions. However, the fact that some apparently symmetric Heteroptera and Dermaptera have a preference for one side seems to suggest that behavioural asymmetry pre-dates morphological asymmetry.

(3) The evolutionary stability of inverse genital correlation

Since insect genitalia are often complex three-dimensional structures, the mechanical mesh between male and female genitalia may usually not allow free twisting against each other. This probably explains the evolutionary stability and hence overwhelming dominance of inverse genital correlation documented above (male dorsal side contacts female ventral side, see Section I and Fig. 1). Inverse correlation follows inevitably from a plesiomorphic female-above position. Even in cases where the external appearance suggests direct correlation, the internal structures like the phallus may be inverted (see Lepidoptera, Heteroptera). Some rare exceptions may exist but need confirmation (e.g. Cicadellidae, certain Trichoptera). An analogous case exists in entelegyne spiders, where ipsilateral insertion (right palp inseminates right female spermatheca) is an extremely conservative character (von Helversen, 1976). However, changes to contralateral or random-sided copulation have occurred a few times, apparently always correlated with a secondary simplification of the intromittent organs (Huber & Senglet, 1997; Knoflach, 1998; Knoflach & van Harten, 2000*a*, *b*).

If the male genitalia could freely rotate within the female genitalia, positional changes would not require twisting of the abdomen or genitalia. It is only for the stability of inverse correlation that males often have to perform fantastical twists and flexions in order to adopt new mating positions (e.g. abdomen twists of up to 180° in Dermaptera, lower Diptera, Bittacidae, Psocoptera; highly flexible abdomens in taxa with false male-above position: nepomorph bugs, Orthoptera). In some cases, these abdominal twists have become permanent (strophandrous Hymenoptera; certain flies, e.g. Culicidae). An important potential consequence of twisting or asymmetrical flexing of the abdomen is that male and female genitalia do not contact symmetrically any more. We will argue that compensation for such asymmetric contact may be one of the major selective forces driving the evolution of genital asymmetry.

(4) The evolution of genital asymmetry: six hypotheses

Numerous studies suggest that asymmetry is often discriminated against by sexual selection, both in vertebrates and invertebrates (reviews: Møller & Pomiankowski, 1993; Watson & Thornhill, 1994; Møller & Swaddle, 1997). This implies that some factor must at least initially offset the disadvantage of sexual discrimination against asymmetry. This could be either an advantage of asymmetry *per se*, or an advantage conferred by an additional factor that favours or requires asymmetric morphology. We will here list a number of hypotheses that appear supported by the available evidence, some of them potentially widely applicable (the first two), some apparently more restricted to special cases. They are not thought to be mutually exclusive. What most hypotheses have in common is that they are at some point intimately related to sexual selection.

(*a*) *Compensation*

This hypothesis explains morphological asymmetry as a mechanical compensation to evolutionary and behavioural changes of mating position. The asymmetry *per se* is not advantageous, but the newly adopted mating position is. Asymmetries evolve as adjustments to the newly adopted positions or to the change of positions. Potential examples are flat nepomorph bugs where the false male-above position requires the male to make a deep indentation on one side of his body or to perform complex folding of the abdomen in order to access the female genitalia. A similar adaptation occurs in certain hybotine flies, where the right side is much enlarged compared to the left, or cockroaches, where males change position during copulation, holding on to the female with asymmetric hooks that are missing in those taxa that do not change position during mating.

(*b*) *Functional segregation*

This hypothesis implies a split of functions, or division of labour, between right and left sides. Genitalia are multifunctional organs (grasp, transfer sperm, stimulate, etc.), and some of the functions performed simultaneously or at different stages of copulation might favour specialized morphologies that do not perform equally well at all functions. In contrast to the *Compensation hypothesis*, asymmetry *per se* is advantageous. A recently proposed example is the spider *Metagonia mariguitarensis*, where the large right pedipalp appears to specialise in stimulation, the smaller left pedipalp (which has the larger sperm reservoir) in sperm transfer (Huber, 2004*a*). Functional segregation between grasping and stimulating may occur in the moth *Erynnis persius*, where the left valva scrapes the female while the right valva remains relatively stationary (Scott, 1978). Similar functional segregation is strongly suggested by extreme differences in muscles and external morphology between right and left sides, as for example in *Phyllonorycter* (subgenus *Asymmetrivalva*) moths (Kuznetzov & Baryshnikova, 2004). An analogous case exists in certain asymmetric copepods, where a leg of one side is used to hold the female, the opposite leg for transferring the spermatophore (Ludwig, 1932, p. 198). In the acalyptrate fly *Dryomyza anilis*, the surstyli and epandrial lobes are used during mating to tap the female abdomen, where mechanoreceptors are located (Otronen, 1998). Tapping with asymmetric epandrial lobes (= small claspers) results in higher fertilization success than tapping with symmetric lobes. Otronen (1998) suggested that since male tapping affects sperm distribution in the spermathecae, the higher fertilization success of males with asymmetric epandrial lobes could have a functional relationship with the asymmetric position of the spermathecae.

(*c*) *One-sided reduction*

Asymmetry may result from complete reduction of one side. Examples are cimicoid bugs, Eudermaptera, and possibly Zoraptera and *Tidarren* spiders. Asymmetry *per se* may not be advantageous, or it may be disadvantageous, but material, energy, and development time may be saved.

(*d*) *Functional constraint*

This hypothesis may explain cases such as the penis rods in fleas, where right and left sides form a functional unit that pushes sperm through the narrow female insemination duct. As in the functional segregation hypothesis, right and left structures perform different functions (one rod leads and guides, the other pushes the sperm), but from the female perspective they perform a single function, which is sperm transfer. In asymmetric Plecoptera, the left paraproct may function as a guide for a flagellum on the right paraproct. An exceptional case in this category is the pyralid moth *Syntonarcha iriastis* with its stridulating genitalia (Gwynne & Edwards, 1986; see Section V.4*h*). Analogous asymmetries occur in non-genital structures like the female second valvulae in Hymenoptera that are used to penetrate the substratum.

(*e*) *Space constraint*

In contrast to all other hypotheses listed here, genital asymmetry according to this hypothesis usually originates in the female, and male asymmetry may evolve later as a response to female asymmetry. Space constraints within the insect body are probably responsible for common internal asymmetries like digestive tract asymmetries, and such asymmetries may also affect the internal genitalia. In spiders, the asymmetric female internal genitalia of *Metagonia* and *Kaliana* have been interpreted as the result of space constraints (Huber, 2004*a*, 2006). Lepidoptera (the female internal genitalia and the male phallus, not the external genitalia; see above) and certain Coleoptera may be further examples. The available evidence suggests that female asymmetries are rare, but we may have overlooked some published examples, and in many taxa the internal female genitalia remain virtually unstudied.

(*f*) *Intersexual arms race*

This hypothesis covers the very specific and currently unique case of certain Odonata, where an arms race over the control of sperm transport within females may have led to morphological asymmetry. Males induce females to eject sperm by stimulating sensilla on vaginal plates that control the ejection of spermathecal sperm during fertilization. Females may evolve asymmetric numbers of sensilla in order to gain independent lateral control over each spermatheca (Córdoba-Aguilar, 2003*b*).

(5) The difference between insects and spiders

The most obvious difference we wish to explain is the rarity of asymmetry in spiders as opposed to insects. Apart from this, we have identified a number of further differences that appear significant in the present context, even though the small sample in spiders makes these contrasts preliminary. Most insect asymmetry originates in males, most spider asymmetry originates in females. Most insect asymmetry originates as directional asymmetry, most or all spider asymmetry originates as antisymmetry. Given the list of potential routes to asymmetry above, we anticipate that there need not be a single explanation for these differences. However, one single and simple fact seems largely to explain why certain evolutionary routes can be travelled by insects rather than by spiders: the paired *versus* unpaired sperm transfer organ.

Spiders carry two independent sperm reservoirs in their palps, each typically destined to fill one of the paired female spermathecae. To transfer the full amount of sperm, a male must use both palps, i.e. copulate either in a symmetric position with simultaneous intromission or in alternating two-sided positions. In fact, with the exception of *Tidarren*, all male spiders do, or at least try to, inseminate both sides of the female. This precludes the adoption of a one-sided mating position. By contrast, most Neoptera have a single unpaired sperm transfer organ and may thus copulate from one side only and still transfer the full amount of sperm. This means that the change to a one-sided asymmetric position does not inevitably result in a 50% decrease of sperm transferred. Whenever this positional change conveys some advantage the arena is set for the evolution of morphological asymmetry according to three of the hypotheses outlined above (compensation, functional segregation, one-sided reduction). For the other three hypotheses we see no reason to assume that they explain insect but not spider asymmetry, or *vice versa*. This is additional evidence for the idea that the three former hypotheses best explain the majority of insect genital asymmetries.

(6) Open questions

Almost every one of the descriptive chapters above identifies specific open questions related to individual taxa. More generally, the functional significance of individual genital structures continues to be one of the large poorly explored fields in insect and spider morphology. Experiments carefully designed specifically to test the hypotheses outlined above will be incomparably more fruitful than the scattered collection of chance data based on pairs collected *in copula*. A more systematic approach is also necessary to properly address questions of directional asymmetry *versus* antisymmetry, one-sided *versus* random-sided mating position, or direct *versus* inverse genital correlation. Numerous insect taxa contain both symmetric and asymmetric species and might serve as model groups to test the correlations proposed herein.

Other animals may provide independent tests for some of the ideas presented herein. Among crustaceans, for example, genital asymmetry is common in some taxa (e.g. Copepoda) but absent in others (Ludwig, 1932). Like in insects and spiders, the data have not been reviewed since Ludwig (1932) as far as we know. A recent review on snail chirality (Schilthuizen & Davison, 2005) has identified a series of parallel and additional questions related to reproductive isolation, speciation, and developmental genetics. Although the focus of that review is on a different system, some of the evolutionary forces driving the origin and maintenance of snail chirality seem to be analogous to those proposed herein.

Reversals to symmetry suggest a number of exciting questions relating to mating strategies and sexual conflict. Is there a relationship between monogamy and reduced sexual conflict and secondary symmetry? Isoptera suggest such a correlation, but no data on reproductive biology are available for the other cases cited above (certain anthocorid and plokiophilid bugs, Hawaiian *Iolana* planthoppers, dolichopodine flies, certain pterophorine and cosmopterigine moths). A related question refers to sex role reversals. Have such reversals ever led to changes of mating position initiated by the female and if yes, has this ever resulted in female asymmetry?

All of the hypotheses proposed above may explain why asymmetry evolved, but none of them explains why directional asymmetry is so dominant over antisymmetry in insect genitalia.

Finally, it is a mystery to us why females do not seem to respond to male directional asymmetry. If females are under selection to choose among males, they should optimise their receptors on the respective side. Such female asymmetry does not need to be conspicuous but may be confined to numbers and densities of sensilla. Discovery of such details will again require a specific search strategy.

VII. CONCLUSIONS

(1) Even though our effort to summarise the huge and scattered literature on insect genital asymmetries is necessarily incomplete, it is clear that insect genital asymmetries are widespread and have evolved many times independently within Neoptera. By contrast, genital asymmetry is an extremely rare phenomenon in spiders.

(2) Insect genital asymmetries are predominantly directional and limited to the male. Antisymmetric insect genitalia are apparently very rare and always derived from directionally asymmetric genitalia. By contrast, spider genital asymmetries are predominantly antisymmetries and limited to the female. The only unambiguous transition from morphological antisymmetry to directional asymmetry occurs in the spider genus *Metagonia*.

(3) In neopteran insects, multiple convergent changes from the presumably plesiomorphic female-above copulatory position to positions where males are in greater control may be the single most important aspect in the explanation of insect genital asymmetry. While the plesiomorphic mating position is symmetric, most derived positions require asymmetrical flexing, rotating, or bending of the male abdomen or genitalia. Even in superficially symmetric male-above positions, the complex fit of male and female genitalia apparently prevented free rotation of these organs against each other, resulting in complex twists and flexures.

(4) Once the contact between male and female genitalia is asymmetric, various selective pressures may favour morphological asymmetry, directly or indirectly. Such asymmetry is always correlated with one-sided mating positions (or abdominal twists). Compared to random-sided positions that are plesiomorphic among asymmetric positions, one-sided mating positions imply reduced options from the male perspective, suggesting direct or indirect benefits from asymmetric morphology.

(5) Spiders with their paired male copulatory organs (pedipalps) do not have the option to assume one-sided mating positions. Thus, there is no selective pressure on males to evolve asymmetric genitalia. Of the few spider genital asymmetries known, some appear best explained as a result of space constraints in females. Such a space constraint explanation may also explain some insect genital asymmetries, but it appears to be rare in insects just as it is in spiders.

(6) It is our hope that this review will stimulate more systematic research into the phenomenon of insect genital asymmetry. While most of the existing information is anecdotal, numerous insect orders contain both symmetric and asymmetric species, providing the opportunity for multiple independent tests of many of the correlations we hypothesize.

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