Mating positions and the evolution of asymmetric insect genitalia

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Abstract Genital asymmetry is a recurring phenomenon in insect morphology and current data suggest that it has arisen multiple times independently in several neopteran orders. Various explanations have been proposed, including space constraints, ecological constraints, sexual selection via antagonistic coevolution, and sexual selection via changed mating positions. Each of these hypotheses may best explain individual cases, but only the last seems to account for the large majority of insect genital asymmetries. Here I summarize the basic assumptions and evolutionary steps implied in this model and review the evidence for each of them. Several components of this scenario can be easily tested, for example by including genital asymmetries and mating positions in phylogenetic analyses. Others require in-depth analyses of the function of asymmetric genital structures, targeted comparative analyses (e.g., of taxa with sex-role reversal, taxa with reversal to symmetry, etc.), and of female genital neuroanatomy.

Keywords Sexual selection · Sexual conflict · Asymmetry · Insect · Genitalia · Mating position

Introduction

Insect taxonomists have long been aware of the fact that adaptive genital asymmetries (i.e., asymmetries other than fluctuating asymmetry) are common and widespread in insects, but only recently have the relevant data been reviewed (Huber et al. 2007). In some insect orders genital

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asymmetries seem to be in the groundplan (e.g., Phasmida, Grylloblattodea, possibly also Embiidina, Mantophasmatodea), while in some orders the available data suggest several or up to dozens of independent origins (e.g., Heteroptera, Coleoptera, Diptera, Lepidoptera). The emphasis in Huber et al. (2007) was on the original data for individual insect orders, drawing information from the taxonomic, phylogenetic, ethological, and functional morphological primary literature. A relatively minor section was dedicated to evolutionary scenarios that may explain the observed patterns. About equal room was given to alternative scenarios, possibly blurring the fact that only one of them seems to best explain the majority of cases. In the present overview, I will concentrate on this scenario (which is largely built on ideas by Lamb 1922; Richards 1927; Ludwig 1932; Alexander 1964), on the evidence supporting each of its steps, and on ways in which it can be tested.

The basic idea

Figure 1 illustrates the main assumptions and evolutionary steps in the proposed scenario. The first assumption is a plesiomorphic symmetric female-above mating position. The first process involves a change of positions, in which the male moves to a position presumably giving him more control. The result is often some variant of male-above positions as shown in Fig. 1, but might also be a different position (belly-to-belly, side-by-side). At this stage, both male and female genitalia are still symmetric, and the position is individually random-sided, i.e., each individual male can mate from either side (or twist his abdomen or genitalia to either side). The inevitable and crucial consequence of most of these positional changes is asymmetric
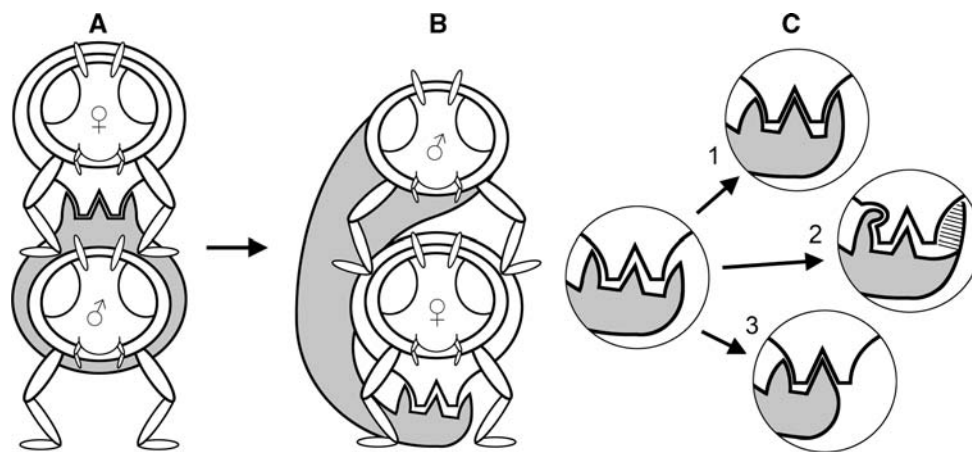
Fig. 1 Simplified scheme for the evolution of insect genital asymmetries via changed mating positions; male abdomen shown in gray. **a** Plesiomorphic female-above position with symmetric genital contact and symmetric genitalia. **b** Derived mating position as a result of selection on males for more control; the position is individually random-sided (the male can mate on either side) and the genitalia are still symmetric. **c** Morphological asymmetry, correlated with shift to fixed one-sided mating position; (1) morphological compensation for mismatch; (2) division of labor between left and right structures; (3) one-sided reduction

contact between male and female genitalia. This asymmetric contact results in different selective environments for each side, but only if an additional prerequisite is met: the position must become one-sided, i.e., an individual male must become restricted to mate from only one side. Different selective environments may then have a number of consequences, three of which are shown in Fig. 1: (1) right and left sides may change as to compensate for the mismatch resulting from asymmetric contact; (2) right and left sides may assume different functions; (3) one side may lose any function and become reduced. In some but not all of these processes, the female is expected to coevolve (not shown in Fig. 1), in rather conspicuous ways in an antagonistic coevolution scenario, in more subtle ways in a female choice scenario.

Evidence for the individual steps

Evidence for the female-above position and symmetric genitalia being plesiomorphic for Neoptera

Three types of evidence suggest that a symmetric female-above position and symmetric genitalia are plesiomorphic for neopteran insects: phylogenetic data, evidence from derived positions, and evidence from functional morphology.

A symmetric female-above position and symmetric genitalia are widespread in insects, including the Ephemeroptera (Morgan 1929; Snodgrass 1936; Despax 1949; Brinck 1957; Takemon 1990; Kluge 2003), the potential sister group of Neoptera (Ogden and Whiting 2003). I know of no formal cladistic analysis in insects including the character mating

position, but a female-above position may by plesiomorphic for several orders including Blattaria, 'Homoptera', Mecoptera, Neuropterida, Orthoptera, Psocodea, and Siphonaptera (Huber et al. 2007). On the other hand, symmetric genitalia have been shown to be plesiomorphic in several formal analyses (Nelson 1984; Asche 1985; Landry 1991; Gielis 1993; Hodges 1998; Morse and Yang 2002; Yang and Morse 2002; Hebsgaard et al. 2004; Kaila 2004; Hsu and Powell 2005; Sihvonen 2005). In other cases, character mapping strongly suggests that asymmetry is derived (Orthoptera, Plecoptera, 'Homoptera', Heteroptera, Psocodea, Neuropterida, Trichoptera, Diptera, Lepidoptera; see Huber et al. 2007 and references therein). Change in the opposite direction, from asymmetry to symmetry, has apparently occurred too (Walker 1922 on Isoptera; Carayon 1977 on certain anthocorid and plokiophilid bugs; Hoch 2006 on Hawaiian *Iolana* planthoppers; Bickel 1987 and Sinclair and Cumming 2006 on certain dolichopodine flies; Gielis 1993 and Kaila 2004 on certain pterophorine and cosmopterigine moths; D. Ahrens, pers. comm. on some Sericini beetles), but when seen in a wider systematic context, all these cases seem to represent reversals to the original condition.

Several details of derived mating positions appear best explained assuming a plesiomorphic female-above position (Alexander 1964; Alexander and Otte 1967). In the widespread 'false male-above position' (e.g., Caelifera, Phasmida, Mantodea, Thysanoptera, Plecoptera, Embiidina, Grylloblattodea, many Heteroptera, etc.), the male sits on top of the female, but his abdomen is bent around the female abdomen and his genitalia actually contact the female from below (as in a female-above position) (e.g., Baunacke 1912; Fedorov 1927; Schrader 1930; Weber 1930; Hase 1932; Friederichs 1934; Keilbach 1935; Jordan and Wendt

1938; Larsén 1938; Rawat 1939; Stefani 1953; Mika 1959; Ross 1970, 2000; Jordan 1972; Stewart and Stark 1977; Whitman and Loher 1984; Terry and Dyreson 1996). The same is usually the case in side-by-side positions (e.g., many 'Homoptera', Panorpidae, some Heteroptera, etc.) (e.g., Weber 1930; Cook 1963; Davis and Usinger, 1970; White 1970; Kaltenbach 1978). The 'circumversion' (360° rotation) of the male genitalia of cyclorrhaphan flies would seem mysterious under the assumption of a plesiomorphic male-above position, but is easily explained by hypothesizing an evolutionary 360° rotation of the male relative to the female (e.g., a horizontal rotation from female-above to end-to-end, and from there in the same direction to male-above). The same is true for end-to-end and belly-to-belly positions that usually involve rotation of the abdomen or the genitalia by 180° (e.g., Dermaptera, Heteroptera, strophandrous Hymenoptera, Bittacidae) (Kuhl 1928; Herter 1963; Popham 1965; Bornemissza 1966; Mickoleit and Mickoleit 1978; Briceño and Eberhard 1995; Schulmeister 2001; Walker and Fell 2001; Kamimura 2006). Symmetric male-above positions seem to be rare and restricted to derived taxa, and are thus considered derived (e.g., some gerromorph bugs: Ekblom 1926; Heming-van Battum and Heming 1989; Schuh and Slater 1995). They may equally (cf. cyclorrhaphan flies above) result from an evolutionary 360° rotation of the male relative to the female, in this case not horizontal but vertical. In *Lachesilla* (Psocodea) such a vertical 360° rotation happens during copulation (Klier 1956).

Data from functional morphology also argue for a plesiomorphic female-above position. There seems to be an overwhelming dominance of 'inverse correlation' of the genitalia, i.e., the dorsal side of the male contacts the ventral side of the female (Richards 1927; Weber 1930; Hennig 1973; McAlpine 1981; Cobben 1982; Asche 1985; Heming-van Battum and Heming 1989; Sforza and Bourgoin 1998; Soulier-Perkins and Bourgoin 1998; Schulmeister 2001). This character is extremely conservative, probably due to the complex fit of male and female genitalia that does not allow the genitalia to simply rotate against each other when positions are changed. In some taxa, the external appearance suggests 'direct correlation' (i.e. dorsal side of the male contacts the dorsal side of the female) but internal structures (like the phallus) may be inverted (Lepidoptera, Heteroptera; Huber et al. 2007). A few cases of apparent direct correlation (e.g., Singh-Pruthi 1925 and Kunze 1959 on Cicadellidae; Tobias 1972 and Statzner 1974 on Trichoptera) need confirmation. In theory, both a symmetric female-above and a symmetric male-above position would imply inverse correlation, but as argued above, symmetric male-above positions are rare and almost certainly derived.

Evidence for selection on males to manipulate females and for derived mating positions being superior for this purpose

Male signals during copulation that are best explained as courtship are common and widespread in insects (Eberhard 1991, 1994). A wide range of processes are known to affect male paternity even after being accepted as a partner in copulation (Eberhard 1996), and copulatory courtship constitutes a conservative indication that selection in the form of cryptic female choice may be acting on the males (Eberhard 1991). Many of the copulatory behavior patterns listed in Eberhard (1991, 1994) involve the male legs and mouthparts, and it seems obvious that male-above positions give the male a wider range of opportunities to use these body parts as signaling devices during copulation.

Apart from signaling, male-above positions may also confer the male an advantage with respect to physically restraining the female and give him more control over the termination of copulation. In some Psocodea, the female may terminate copulation by simply turning to the side (Mockford 1957). Obviously, a male-above position will impede this female move. Male legs are usually preadapted to grasp the female, male antennae and wings are not. It is illuminating that in some groups that have retained the female-above position, male antennae and wings have indeed been modified to perform grasping and holding functions (e.g., Mitzmain 1910; Holland 1955; Rothschild and Hinton 1968 on Siphonaptera; Carpenter 1936; Steiner 1937; Crampton 1940; Cooper 1974; Mickoleit and Mickoleit 1976 on Boreidae; Séguy 1944 and Schmutz 1955 on certain Phthiraptera). Male mayflies and certain phthirapteran lice have modified front legs that are used to grasp (and/or stimulate) the female from below (Nuttall 1917; Morgan 1929; Despax 1949; Brinck 1957; Kluge 2003).

Evidence for fixed, one-sided positions being derived from individually random-sided positions

As indicated above, information on mating positions is virtually absent in phylogenetic studies. However, indirect data strongly support behavioral flexibility (individually random-sided positions) to be plesiomorphic and fixed one-sided positions to be derived. This indirect data comes from apparent strict correlations of individually random-sided positions with symmetric genitalia and one-sided positions with asymmetric genitalia. This has been particularly well studied in the Heteroptera (references in Huber et al. 2007), but supporting evidence is widespread (Caelifera, Plecoptera, Embiidina, Bittacidae, Papilionidae, Mantophasmatodea, strophandrous Hymenoptera; Huber et al. 2007). Exceptions are extremely rare (e.g., Berthélemy 1979 on Brachypterainae) and need confirmation.

This strict correlation, together with the fact that symmetry appears plesiomorphic and asymmetry derived (see above) argues for random-sided positions to be plesiomorphic and one-sided positions to be derived. What could be the advantage of a one-sided over a random-sided position? From the male's perspective, this change 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.

Evidence for selection favoring morphological asymmetry and one-sided positions

Genitalia are often considered multifunctional organs, and one way to achieve functional complexity is by specializing individual components for different tasks. Different tasks may be executed simultaneously or sequentially. In the moth *Erynnis persius*, for example, the right male valva has been observed to remain stationary, grasping the female while the left valva was used to scrape her sternum VII (Scott 1978). A similar division of labor is suggested by the terms "titillator" and "hook" for the left and right male genital structures respectively, in *Zorotypus hubbardi* (Walker 1922) but both structures may actually be derived from the same side (Walker 1922). In many other cases, conspicuous differences between left and right sides (e.g., Kuznetzov and Baryshnikova 2004 on *Phyllonorycter* moths) suggest functional segregation but no functional studies exist. In *Periplaneta* and *Blatta*, the tasks performed by right and left structures seem to be similar (to clasp the female) but one side acts during the initial phase of copulation while the other side assumes its function later (most cockroaches change position during mating) (Gupta 1947—cited in Scudder 1971; Khalifa 1950). In certain *Corixa* species and certain Miridae, one of the two parameres is used as a guide for the intromittent structure (Larsén 1938; Kullenberg 1947).

An alternative to division of labor between right and left sides is compensation for genital mismatch resulting from an asymmetric mating position. Evidence for such morphological adjustment to behavioral asymmetry is difficult to get. One prediction is correlation between the flexibility of the abdomen and the conspicuousness of the asymmetry. In taxa with less flexible abdomens the asymmetry should be more conspicuous because the abdomen cannot compensate for the mismatch. True bugs seem to support this prediction. Many true bugs have poorly flexible abdomens, and the asymmetries are often conspicuous (e.g., flat nepomorph bugs, Schuh and Slater 1995). In some taxa, however, the abdomen has secondarily acquired higher flexibility including asymmetric muscles, and their genitalia are symmetric (e.g., Keilbach 1935 and Larsén 1938 on *Notonecta glauca*).

A fixed, one sided position may result in one side of the male genitalia losing its function. If that is the case, it may either adopt a new function, be modified as to be able to continue perform the original function, or disappear. In the latter case one would expect to find secondarily unpaired male genital structures. Cimicidae and relatives may exemplify this route to morphological asymmetry (Carayon 1977). Other examples are the Eudermaptera where the left penis lobe is completely reduced (Hincks and Popham 1970; Haas 1995; Haas and Kukalova-Peck 2001), and the Ochteroidea where the left paramere is reduced or absent (Schuh and Slater 1995).

Evidence for female asymmetry appearing after male asymmetry

The taxonomic literature seems to strongly suggest that genital asymmetries are much rarer in female that in male insects. In many groups there is no evidence for female asymmetry even though the male genitalia are strongly asymmetric (e.g., Phasmida, Grylloblattodea, Mantophasmatodea, Psocodea, references in Huber et al. 2007). In some taxa this may simply be due to the fact that female genitalia are barely studied (e.g. Embiidina, Zoraptera, Dermaptera), but in most taxa this seems to be a real trend. For example, morphological analyses of the female genitalia of *Timema* (Vickery 1993; Tilgner et al. 1999) revealed no asymmetry while the male genitalia are strongly asymmetric (Snodgrass 1937; Vickery 1993; Tilgner et al. 1999; Bradler 1999). Comparable in-depth studies are rare, but in several groups male and female genitalia are routinely illustrated by taxonomists (e.g. Trichoptera, Heteroptera, Lepidoptera, Diptera), and in these, character mapping generally resolves female asymmetry as being nested within taxa showing male asymmetry (Huber et al. 2007).

Testing the scenario

In contrast to the processes leading to asymmetry, the patterns resulting from the above scenario appear easy to test. Taxonomic studies need to be specific about the direction of asymmetry (directed, i.e., all males within a species are same-sided, versus bidirected); ethological studies need to be specific about the direction of mating positions (random sided versus one-sided); phylogenetic studies need to include both male and female asymmetries, as well as mating positions in the character matrix (provided there is variation within the studied taxon). Formal cladistic analyses including genital asymmetries are still rare (Nelson 1984; Asche 1985; Landry 1991; Gielis 1993; Hodges 1998; Morse and Yang 2002; Yang and Morse

2002; Hebsgaard et al. 2004; Kaila 2004; Ahrens 2005; Hsu and Powell 2005; Sihvonen 2005; Hoch 2006). One reason may be that asymmetries often evolve many times independently at or near terminal branches. Thus, they introduce noise rather than resolution, and excluding them from the analysis may result in a 'better' tree (or at least better tree statistics).

One field that appears in particular need of new data is functional morphology. In many groups, our understanding of functional details continues to be "almost unbelievably rudimentary" (Alexander and Otte 1967). Traditional studies tended to be not only typological but often relied on specimens that were by chance fixed during copulation. Only detailed observations of the positions and movements of right and left structures in asymmetric species may show if division of labor is a common phenomenon or not. In general, division of labor predicts a higher degree of specialization for different functions in asymmetric versus symmetric genitalia.

The case of termites suggests a possible test for the causal correlation between sexual selection and genital asymmetry. Termites have secondarily simple and symmetric genitalia, and this may be a result of relaxed sexual selection due to female monogamy (Eberhard 1985; Huber et al. 2007). Several further cases of reversal to symmetry have been reported (see above), and these might be correlated with similar changes in mating systems. On a similar line, one might predict changes to female-controlled positions in taxa with sex-role reversal. A possible example is *Paravelia brachialis* (Heteroptera, Veliidae), where the female mounts the male and stimulates him to copulate (Wilson 1958—cited in Heming-van Battum and Heming 1989). Depending on the mating position of the outgroup taxon, this might even select for female asymmetry.

At least in taxa with strongly asymmetric male genitalia, sexual selection theory would seem to predict certain levels of asymmetry in female genitalia. I propose that in an antagonistic coevolution scenario, where traits are supposed to evolve to overcome or defeat the other sexes' resistance or manipulation, females should be expected to respond to conspicuous male asymmetries with similar (i.e., often conspicuous) morphological changes. In a female choice scenario, females are less expected to react conspicuously but to at least adapt their sensory system to male asymmetries. In general, the rareness of conspicuous female asymmetries does not seem to support antagonistic coevolution as being a widespread selective force shaping insect genitalia. Detailed studies of the female genital sensory system in species with strongly asymmetric male genitalia are largely missing but might shed light on the importance of cryptic female choice.

Finally, comparative evidence may come from groups with similar trends towards asymmetric genitalia. In crustaceans, for example, asymmetric genitalia are common in certain groups (e.g., Copepoda) but absent in others (Ludwig 1932). No recent review on asymmetric genitalia in crustaceans seems to exist.

Conclusion

The single most important first step towards insect genital asymmetry appears to be a switch of mating position from a symmetric female-above to an asymmetric male-above position. The driving force behind this switch is presumed to be selection on the male for more control over the female and over details of copulation. Once an asymmetric position is established, left and right genital structures may experience different selective environments and thus become asymmetric. The fact that genital asymmetries have evolved many times independently in a variety of insect orders opens the possibility to test this scenario and its components.

References

Ahrens D (2005) A taxonomic review on the *Serica* (s.str.) MacLeay, 1819 species of Asian mainland (Coleoptera, Scarabaeidae, Sericini). Nova Suppl Entomol 18:1–163

Alexander RD (1964) The evolution of mating behavior in arthropods. R entomol Soc London Symp 2:78–94

Alexander RD, Otte D (1967) The evolution of genitalia and mating behavior in crickets (Gryllidae) and other Orthoptera. Misc Publ Mus Zool Univ Mich 133:1–62

Asche M (1985) Zur Phylogenie der Delphacidae Leach, 1815 (Homoptera Cicadina Fulgoromorpha). Marburger entomol Publ 2(1):1–910

Baunacke W (1912) Statische Sinnesorgane bei den Nepiden. Zool Jb Abt Anat Ontog Tiere 34:179–346 (pl. 10–13)

Berthélemy C (1979) Accouplement, période d'incubation et premiers stades larvaires de *Brachyptera braueri* et de *Perlodes microcephalus* (Plecoptera). Ann Limnol 15:317–335

Bickel DJ (1987) Babindellinae, a new subfamily of Dolichopodidae (Diptera) from Australia, with a description of symmetry in the dipteran male postabdomen. Entomol Scand 18:97–113

Bornemissza GF (1966) Observations on the hunting and mating behaviour of two species of scorpion flies (Bittacidae: Mecoptera). Aust J Zool 14:371–382. doi:10.1071/ZO9660371

Bradler S (1999) The vomer of *Timema* Scudder, 1895 (Insecta: Phasmatodea) and its significance for phasmatodean phylogeny. Courier Forschungsinstitut Senckenberg 215:43–47

Briceño RD, Eberhard WG (1995) The functional morphology of male cerci and associated characters in 13 species of tropical earwigs (Dermaptera: Forficulidae, Labiidae, Carcinophoridae, Pygidicranidae). Smithson Contrib Zool 555:1–64

Brinck P (1957) Reproductive system and mating in Ephemeroptera. Opusc Entomol 22:1–37

Carayon J (1977) Insémination extra-genitale traumatique. Traite Zool 8:351–390

Carpenter FM (1936) Descriptions and records of Nearctic Mecoptera. Psyche 43:56–64

Cobben RH (1982) The hebrid fauna of the Ethiopian Kaffa Province, with considerations on species grouping (Hebridae, Heteroptera). Tijdschr Entomol 125:1–24

Cook PP (1963) Mating behaviour of *Psylla pyricola* Forster (Hom. Psyllidae). Pan-Pac Entomol 39:175

Cooper KW (1974) Sexual biology, chromosomes, development, life histories and parasites of *Boreus*, especially of *B. notoperates*, a southern Californian *Boreus*, II. (Mecoptera: Boreidae). Psyche 81:84–120

Crampton GC (1940) The mating habits of the winter mecopteron, *Boreus brumalis* Fitch. Psyche 47:125–128

Davis NT, Usinger RL (1970) The biology and relationships of the Joppeicidae (Heteroptera). Ann Entomol Soc Am 63:577–586

Despax R (1949) Ordre des éphéméroptères. Traite Zool 9:279–309

Eberhard WG (1985) Sexual selection and animal genitalia. Harvard University Press, Cambridge, Massachusetts

Eberhard WG (1991) Copulatory courtship and cryptic female choice in insects. Biol Rev Camb Philos Soc 66:1–31. doi:10.1111/j.1469-185X.1991.tb01133.x

Eberhard WG (1994) Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. Evolution Int J Org Evolution 48:711–733. doi:10.2307/2410481

Eberhard WG (1996) Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton, NJ

Ekblom T (1926) Morphological and biological studies of the Swedish families of Hemiptera–Heteroptera. Part I. The families Saldidae, Nabidae, Lygaeidae, Hydrometridae, Veliidae and Gerridae. Zool bidrag Uppsala 10:31–180

Fedorov SM (1927) Studies in the copulation and oviposition of *Anacridium aegyptium*, L. (Orthoptera, Acrididae). Trans entomol Soc Lond 75:53–61

Friederichs K (1934) Das Gemeinschaftsleben der Embiiden und Näheres zur Kenntnis der Arten. Arch Naturgesch NF 3:405–444

Gielis C (1993) Generic revision of the superfamily Pterophoroidea (Lepidoptera). Zool Verh 290:1–139

Haas F (1995) The phylogeny of the Forficulina, a suborder of the Dermaptera. Syst Entomol 20:85–98. doi:10.1111/j.1365-3113.1995.tb00085.x

Haas F, Kukalova-Peck J (2001) Dermaptera hindwing structure and folding: new evidence for familial, ordinal and superordinal relationships within Neoptera (Insecta). Eur J Entomol 98:445–509

Hase A (1932) Beobachtungen an venezolanischen *Triatoma*-Arten, sowie zur allgemeinen Kenntnis der Familie der Triatomidae (Hemipt.–Heteropt.). Zeitschr Parasitenk 4:585–652 (pl. 4)

Hebsgaard MB, Andersen NM, Damgaard J (2004) Phylogeny of the true water bugs (Nepomorpha: Hemiptera–Heteroptera) based on 16S and 28S rDNA and morphology. Syst Entomol 29:488–508. doi:10.1111/j.0307-6970.2004.00254.x

Heming-van Battum KE, Heming BS (1989) Structure, function, and evolutionary significance of the reproductive system in males of *Hebrus ruficeps* and *H. pusillus* (Heteroptera, Gerromorpha, Hebridae). J Morphol 202:281–323. doi:10.1002/jmor.1052020302

Hennig W (1973) Ordnung Diptera (Zweiflügler). Handb Zool 4(2) 2/31:1–337

Herter K (1963) Zur Fortpflanzungsbiologie des Sand- oder Uferrohrwurms *Labidura riparia* Pall. Zool Beitr NF 8:297–329

Hincks WD, Popham EJ (1970) Dermaptera. In: Tuxen SL (ed) Taxonomists's glossary of genitalia in insects. Munksgaard, Copenhagen, pp 75–80

Hoch H (2006) Systematics and evolution of *Iolania* (Hemiptera: Fulgoromorpha: Cixiidae) from Hawai'i. Syst Entomol 31:302–320. doi:10.1111/j.1365-3113.2005.00312.x

Hodges RW (1998) The Gelechioidea. Handb Zool 4(35):131–158

Holland GP (1955) Primary and secondary sexual characteristics of some Ceratophyllinae, with notes on the mechanism of copulation (Siphonaptera). Trans R entomol Soc Lond 107:233–248

Hsu Y-F, Powell JA (2005) Phylogenetic relationships within Heliodinidae and systematics of moths formerly assigned to *Heliodines* Stainton (Lepidoptera: Yponomeutoidea). Univ California Publ 124:1–158 (Figs. 26–220)

Huber BA, Sinclair B, Schmitt M (2007) The evolution of asymmetric genitalia in spiders and insects. Biol Rev Camb Philos Soc 82:647–698. doi:10.1111/j.1469-185X.2007.00029.x

Jordan KHC (1972) Heteroptera (Wanzen). Handb Zool, IV Arthropoda, 2 Insecta 20:1–113

Jordan KHC, Wendt A (1938) Zur Biologie von *Salda litoralis* L. (Hem. Het.). Stettiner entomol Z 99:273–292

Kaila L (2004) Phylogeny of the superfamily Gelechioidea (Lepidoptera: Ditrysia): an exemplar approach. Cladistics 20:303–340. doi:10.1111/j.1096-0031.2004.00027.x

Kaltenbach A (1978) Mecoptera (Schnabelkerfe, Schnabelfliegen). Handb Zool, IV Arthropoda, 2 Insecta 28:1–111

Kamimura Y (2006) Right-handed penises of the earwig *Labidura riparia* (Insecta, Dermaptera, Labiduridae): evolutionary relationships between structural and behavioral asymmetries. J Morphol 267:1381–1389. doi:10.1002/jmor.10484

Keilbach R (1935) Über asymmetrische Flügellage bei Insekten und ihre Beziehungen zu anderen Asymmetrien. Z Morphol Oekol Tiere 29:1–44. doi:10.1007/BF00407463

Khalifa A (1950) Spermatophore production in *Blatella germanica* L. (Orthoptera: Blattidae). Proc R entomol Soc Lond (A) 25:53–61

Klier E (1956) Zur Konstruktionsmorphologie des männlichen Geschlechtsapparates der Psocopteren. Zool Jb Abt Anat Ontog Tiere 75:207–286

Kluge NY (2003) Trudi Russkogo Entomologicheckogo Obshchestva. Ob evolyutsii i homologii genitalinich pridatkov nacekomich 74:3–16 (in Russian)

Kuhl W (1928) Die Variabilität der abdominalen Körperanhänge von *Forficula auricularia* L. unter Berücksichtigung ihrer normalen und abnormen Entwicklung, nebst einem Anhang über die Geschlechtsbiologie. Z Morphol Oekol Tiere 12:299–532. doi:10.1007/BF00403121

Kullenberg B (1947) Über Morphologie und Funktion des Kopulationsapparates der Capsiden und Nabiden. Zool bidrag Uppsala 24:217–418

Kunze L (1959) Die funktionsanatomischen Grundlagen der Kopulation der Zwergzikaden, untersucht an *Euscelis plebejus* (Fall.) und einigen Typhlocybinen. D entomol Z (NF) 4:322–387

Kuznetzov VI, Baryshnikova SV (2004) Evolutionary-morphological approach to the systematics of leafmining moths of the genus *Phyllonorycter* Hbn. (Lepidoptera, Gracillariidae) with account of species feeding specialization. Entomol Rev Wash 84:588–599

Lamb CG (1922) The geometry of insect pairing. Proc R Soc Lond B Biol Sci 94:1–11

Landry J-F (1991) Systematics of Nearctic Scythrididae (Lepidoptera: Gelechioidea): phylogeny and classification of supraspecific taxa, with a review of described species. Mem Entomol Soc Can 160:1–341

Larsén O (1938) Untersuchungen über den Geschlechtsapparat der aquatilen Wanzen. Opusc Entomol Suppl 1:1–388

Ludwig W (1932) Das Rechts-Links-Problem im Tierreich und beim Menschen. Springer, Berlin

McAlpine JF (1981) Morphology and terminology—adults. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth

JR, Wood DM (eds) Manual of Nearctic Diptera, vol 1, Agriculture Canada Monograph 27:9–63

Mickoleit G, Mickoleit E (1976) Über die funktionelle Bedeutung der Tergalapophysen von *Boreus westwoodi* (Hagen) (Insecta, Mecoptera). Zoomorph 85:157–164. doi:10.1007/BF00995409

Mickoleit G, Mickoleit E (1978) Zum Kopulationsverhalten des Mückenhaftes *Bittacus italicus* (Mecopetra: Bittacidae). Entomol Gen 5:1–15

Mika G (1959) Über das Paarungsverhalten der Wanderheuschrecke *Locusta migratoria* R. und F. und deren Abhängigkeit vom Zustand der inneren Geschlechtsorgane. Zool Beitr 4:153–203

Mitzmain MB (1910) Some new facts on the bionomics of the California rodent fleas. Ann Entomol Soc Am 3:61–82

Mockford EL (1957) Life history studies on some Florida insects on the genus *Archipsocus* (Psocoptera). Bull Fla State Mus Biol Sci 1:253–274

Morgan AH (1929) The mating flight and the vestigial structures of the stump-legged mayfly, *Campsurus segnis* Needham. Ann entomol Soc America 22:61–68 (pl. 1)

Morse JC, Yang L (2002) Phylogeny, classification, and historical biogeography of world species of *Mystacides* (Trichoptera: Leptoceridae), with a new species from Sri Lanka. Nova Suppl Entomol 15:173–186

Nelson CH (1984) Numerical cladistic analysis of phylogenetic relationships in Plecoptera. Ann Entomol Soc Am 77:466–473

Nuttall GHF (1917) Studies on *Pediculus* I. The copulatory apparatus and the process of copulation in *Pediculus humanus*. Parasitology 9:293–324 (pl. 3, 4)

Ogden TH, Whiting MF (2003) The problem with "the Paleoptera problem:" sense and sensitivity. Cladistics 19:432–442

Popham EJ (1965) The functional morphology of the reproductive organs of the common earwig (*Forficula auricularia*) and other Dermaptera with reference to the natural classification of the order. J Zool 146:1–43

Rawat BL (1939) On the habits, metamorphosis and reproductive organs of *Naucoris cimicoides* L. (Hemiptera–Heteroptera). Trans R entomol Soc Lond 88:119–138

Richards OW (1927) Sexual selection and allied problems in the insects. Biol Rev Camb Philos Soc 11:298–364. doi:10.1111/j.1469-185X.1927.tb01401.x

Ross ES (1970) Biosystematics of the Embioptera. Annu Rev Entomol 15:157–172. doi:10.1146/annurev.en.15.010170.001105

Ross ES (2000) A review of the biology of Embiidina. Occas Pap Calif Acad Sci 149(2):1–36

Rothschild M, Hinton HE (1968) Holding organs on the antennae of male fleas. Proc R entomol Soc Lond (A) 43:105–107

Schmutz W (1955) Zur Konstruktionsmorphologie des männlichen Geschlechtsapparates der Mallophagen. Zool Jb Abt Anat Ontog Tiere 74:189–338

Schrader F (1930) Observations on the biology of *Protortonia primitiva* (Coccidae). Ann Entomol Soc Am 23:126–132

Schuh RT, Slater JA (1995) True bugs of the world (Hemiptera: Heteroptera). Classification and natural history. Cornell University Press, Ithaca and London

Schulmeister S (2001) Functional morphology of the male genitalia and copulation in lower Hymenoptera, with special emphasis on the Tenthredinoidea s. str. (Insecta, Hymenoptera, 'Symphyta'). Acta Zool 82:331–349. doi:10.1046/j.1463-6395.2001.00094.x

Scott JA (1978) Mid-valval flexion in the left valva of asymmetric genitalia of *Erynnis* (Hesperiidae). J Lepid Soc 32:304–305

Scudder GGE (1971) Comparative morphology of insect genitalia. Annu Rev Entomol 16:379–406. doi:10.1146/annurev.en.16.010171.002115

Séguy E (1944) Insectes ectoparasites (Mallophages). Faune Fr 43:23–407

Sforza R, Bourgoin T (1998) Female genitalia and copulation of the planthopper *Hyalesthes obsoletus* Signoret (Hemiptera: Fulgoromorpha: Cixiidae). Ann Soc entomol France (NS) 34:63–70

Sihvonen P (2005) Phylogeny and classification of the Scopulini moths (Lepidoptera: Geometridae, Sterrhinae). Zool J Linn Soc 143:473–530. doi:10.1111/j.1096-3642.2005.00153.x

Sinclair BJ, Cumming JM (2006) The morphology, higher-level phylogeny and classification of the Empidoidea (Diptera). Zootaxa 1180:1–172

Singh-Pruthi H (1925) The morphology of the male genitalia in Rhynchota. Trans entomol Soc London (1925):127–267

Snodgrass RE (1936) Morphology of the insect abdomen. Part III. The male genitalia. Smiths Misc Coll 95:1–96

Snodgrass RE (1937) The male genitalia of orthopteroid insects. Smiths Misc Coll 96:1–107

Soulier-Perkins A, Bourgoin T (1998) Copulatory mechanisms and sexual selection in the Lophopidae (Hemiptera: Fulgoromorpha). Ann Soc entomol France (NS) 34:149–162

Statzner B (1974) Funktionsmorphologische Studien am Genitalapparat von drei neuen *Cheumatopsyche*-Arten (Trichoptera, Hydropsychidae). Zool Anz 193:382–398

Stefani R (1953) Un particolare modo di accoppiamento negli Insetti Embioterri. Rend Accad Naz Lincei (sci fis mat nat) ser 8(14):544–549

Steiner P (1937) Beitrag zur Fortpflanzungsbiologie und Morphologie des Genitalapparates von *Boreus hiemalis* L. Z Morph Ökol Tiere 32:276–288

Stewart KW, Stark BP (1977) Reproductive system and mating of *Hydroperla crosbyi*: a newly discovered method of sperm transfer in Insecta. Oikos 28:84–89. doi:10.2307/3543326

Takemon Y (1990) Functional morphology of the genitalia in *Epeorus ikanonis* (Ephemeroptera, Heptageniidae). Jap J Entomol 58:115–124

Terry LI, Dyreson E (1996) Behavior of *Frakliniella occidentalis* (Thysanoptera: Thripidae) within aggregations, and morphometric correlates of fighting. Ann Entomol Soc Am 89:589–602

Tilgner EH, Kiselyova TG, McHugh JV (1999) A morphological study of *Timema cristinae* Vickery with implications for the phylogenetics of Phasmida. Entomol Z 46:149–162

Tobias W (1972) Zur Kenntnis europäischer Hydropsychidae (Insecta: Trichoptera), I. Senckenb Biol 53:59–89

Vickery VR (1993) Revision of *Timema* Scudder (Phasmatoptera: Timematodea) including three new species. Can Entomol 125:657–692

Walker EM (1922) The terminal structures of orthopteroid insects: a phylogenetic study. Ann Entomol Soc Am 15:1–87

Walker KA, Fell RD (2001) Courtship roles of male and female European earwigs, *Forficula auricularia* L. (Dermaptera: Forficulidae), and sexual use of forceps. J Insect Behav 14:1–17. doi:10.1023/A:1007843227591

Weber H (1930) Die Biologie der Hemipteren. Biol Studienb Berl 11:1–537

White TCR (1970) Some aspects of the life history, host selection, dispersal and oviposition of adult *Cardiaspina densitexta* (Homoptera: Psyllidae). Aust J Zool 18:105–117. doi:10.1071/ZO9700105

Whitman DW, Loher W (1984) Morphology of the male sex organs and insemination in the grasshopper *Taeniopoda eques* (Burmeister). J Morphol 179:1–12. doi:10.1002/jmor.1051790102

Yang L, Morse JC (2002) *Glossosoma* subgenus *Lipoglossa* (Trichoptera: Glossosomatidae) of China. Nova Suppl Entomol 15:253–276