

Table S1

Summary of genital asymmetry in those animal taxa that have intromittent genitalia and internal fertilization. The taxonomic classification follows Noordijk et al. (2010). Abbreviations used: AS: antisymmetric; DA: directionally asymmetric.; DA/SYM: within the same species, a directional asymmetry + pure symmetry dimorphism is present.

Please note: this list does not aim to be an exhaustive review. For many groups, the information is based on a very small number of resources only, and many cases of subtle asymmetry and/or asymmetry in less-studied, low-level taxa, will have been missed. However, it is hoped that this list can be a starting point for further, more detailed studies.

Phylum Chaetognatha

Fertilization in these hermaphrodites is internal, and sperm vesicle transfer is achieved with symmetrically arranged genital pores (Goto & Yoshida 1985; Alvariano 1990).

Phylum Platyhelminthes

Turbellaria: Chitinous parts of the male copulatory organ very often (strongly) asymmetric, e.g. in genera *Microstomum* and *Macrostomum* and in the Dalyelliini (Graff 1913; Brüggemann 1988).

Trematoda: The genital pore is often located laterally and in many species the cirrus pouch (the chamber that holds the male intromittent organ) is said to be directed towards the left side (e.g., *Proserhynchus aculeatus*, *Lepidapedon*; Dawes 1956),

Monogenea: Especially in those groups that have a completely chitinous male copulatory organ, the armature is asymmetric: "Among some forms it is almost straight and broad, in others it is thin, sometimes very long, curved, and twisted completely or partially as a spiral, etc." (Bychowsky 1957). Similarly, the (frequently chitinous) aperture of the vagina is often complicated and asymmetric in this group (Bychowsky 1957).

Phylum Acanthocephala

The vagina of at least some species of acanthocephalans (e.g., *Neoechinorhynchus buttnerae*) is coiled (Crompton & Nickol 1985), but of most species it appears to be a simple, symmetric, conical structure (Crompton & Nickol 1985).

Phylum Annelida

Polychaeta: true copulation occurs in Archiannelida: asymmetric penis present in some species of *Stratiodrilus* (Steiner & Amaral 1999).

Aphanoneura: Intromittent copulation appears to be absent in this group (Ax & Bunke 1967).

Oligochaeta: In Tubificidae, the penis sheath (of the paired penes) is asymmetric in *Limnodrilus maumeensis* and *L. cervix* (the latter DA/SYM) (Stimpson et al. 1982) and in *L. tortilipenis* (Wetzel 1987). In *Stuhlmannia*, many species have asymmetric genitalia in the males (the penis has an asymmetrically located groove, and the nature of the epithelium differs on either side; Beddard 1895), but also in the females, which are often much reduced on the left side of the body (DA) (Jamieson 1967). The paired penes in *Hyperiodrilus*, at least in those species that have them on the segment before the one that bears the male pore, are asymmetric (Beddard 1895).

Hirudinea: Genital pores are said to be "near the midline" (Govedich 2001). The cornutae in the genital atrium and the protrusible penis that it sometimes bear appear to be symmetric (e.g., Elliott & Mann 1979).

Branchiobdelliida: Female genital pore symmetrically located, but penis and bursa appear often asymmetrically arranged (Holt 1986).

Phylum Mollusca

Solenogastres: In the hermaphroditic, internally fertilizing Solenogastres, the paired, copulatory spicules are symmetric (Jones & Baxter 1987; Scheltema 1992; Scheltema pers. comm.).

Gastropoda: In Gastropoda that practise internal fertilization, the male and female genitalia are asymmetric, as a direct consequence of strong, whole-body asymmetry. Mirror-image reversals in genital asymmetry thus are always accompanied by reversal of the whole-body chirality (Schilthuizen & Davison 2005; Schilthuizen et al. 2007).

Cephalopoda: In Cephalopoda, which have internal fertilization and a largely bilaterally symmetric bauplan, both the penis and usually also the hectocotylus (a modified arm that in many species receives the spermatophore from the penis and transfers it to the female) are located off-centre (Voight 2002; Ponder & Lindberg 2008; Arkhipkin & Laptikhovsky 2010).

Phylum Kinorhyncha

Kinorhyncha have symmetrically arranged, paired gonopores. Males have spines around the gonopores that may serve an intromittent function (Neuhaus & Higgins 2002). These spines appear to be symmetrical.

Phylum Nematoda

What follows is not even an attempt at completeness for this large group. Nonetheless, it may serve as a starting point for further explorations into the distribution and patterns of genital asymmetry in this phylum.

In male Nematoda, genital asymmetry commonly exists in the spicules. In many (mostly parasitic) taxa, e.g. *Trichostrongylus*, *Paracooperia* (**Strongylida**: Trichostrongylidae), *Victorocara* (**Spirurida**: Acuariidae), *Hoplolaimus* (**Tylenchida**: Hoplolaimidae), Heterakidae, Atractidae and Cucullanidae (**Ascaridida**), Camallanidae (**Camallanida**), Aproctidae, Diplostriaenoidea, Filarioidea, and Spiruroidea (**Spirurida**), left and right spicules are very unequal in size and shape (Anderson et al. 2009; Bird 1971; Chitwood & Chitwood 1974; Gibbons 1978). In some free-living nematodes, such as *Odontophora* (**Araeolaimida**: Axonolaimidae) and *Plectus* (**Araeolaimida**: Plectidae), unequal spicula also occur (Bongers 1988; Andrassy 2005). Although rarely mentioned explicitly, spicular asymmetry appears to be always DA. Nevertheless, chiral reversal exists across species. Chitwood & Chitwood (1974) mention that usually the left spicule is longer than the right, but in e.g. *Heterakis gallinarum* the reverse is the case. Male Enterobiinae (**Oxyurida**) have single spicules which in many species appear to be somewhat asymmetric (Hugot et al. 1996). Asymmetry in female genitalia appears to be rarer, but not nonexistent: Breszki (1998) mentions that in *Cephalenchus* (**Tylenchida**: Tyloporidae) the vulva often is displaced on the right ventrolateral side.

Phylum Onychophora

The genital openings of males and female are always in the midline. Intromittent organs are only known from *Paraperipatus*, in which they are symmetric (Ruhberg 1985).

Phylum Arthropoda: Arachnida: Acari

The Acari form a very large group with a great diversity in sperm transfer mechanisms. What follows is not a proper review, just an indication of patterns based on a very cursory reading of the acarological literature. In most cases it is not clear whether asymmetry is AS or DA.

Acari: Ixodida: genital pores as well as chelicerae are symmetric (Furman & Loomis 1984)

Acari: Mesostigmata: Rhodacaroidea: female genital pore in most genera appears to be asymmetrically located (Lee 1970, cited in Eberhard 1985).

Acari: Trombidiformes: Hydrachnidia symmetric (Wiles pers. comm.). Asymmetric (bent or sinuous) aedeagi exist in Iolinidae (Krantz & Walter 2009), many Myobiidae (Fain 1978), most Cheyletidae (Smiley 1965; Volgin 1989; Krantz & Walter 2009), Psorergatidae (Giesen 1990), Scutacaridae (Krantz & Walter 2009). Female genital asymmetry is found in the location of the insemination area in some Myobiidae (Fain 1978).

Acari: Sarcoptiformes: Anoetidae: some species with an asymmetric penis (Scheucher 1957); Proctophyllodidae, Pterodectinae (Analgoidea) and Euglycyphagidae: male genital organ often slightly asymmetric (Krantz & Walter 2009; Park & Atyeo 1971).

Phylum Arthropoda: Arachnida: Araneae, Opiliones

Araneae: Genital asymmetry very rare (Huber et al. 2007). Female genitalia in two species of *Asygyna* (Theridiidae) are AS (Agnarsson 2006), female genitalia in *Kaliana yuruani* (Pholcidae) are DA (Huber 2006). In *Metagonia* (Pholcidae), female genitalia are always AS, except in *M. mariguitarensis*, where both male and female genitalia are DA (Huber 2004). At least 7 species of *Escaphiella* (Oonopidae) have male genitalia DA (Platnick & Dupérré 2009).

Opiliones: Female genitalia always symmetric; male genitalia often asymmetric within the suborder Phalangida, especially within the Phalangioidea, the Ischiropsalidoidea, and the Troguloidea (Macías-Ordóñez et al. 2010).

Phylum Arthropoda: Myriapoda

Diplopoda: With the exception of very slight asymmetries that appear adaptations to allow the paired male gonopods to interlock (Enghoff 2011), the male and female genitalia in millipedes are always symmetric (Hopkin & Read 1992). DA/SYM variability has been recorded in *Skleroprotopus ramuliferus* (Mikhailjova & Korsós 2003), and during development, asymmetry often arises in gonopod promordia, which, however, disappears again upon maturation (Drago et al. 2011).

Phylum Arthropoda: Branchiopoda

Anostraca: males have identical, paired penes (i.e., symmetric); the vagina, which gives entry to the ovisac, is apparently also symmetrically arranged (Dumont & Negrea 2002)

Notostraca: copulation takes place, but no intromission (Dumont & Negrea, 2002)

Cladocera: copulation takes place; in certain taxa (e.g., *Diaphanosoma*, *Latona*, *Penilia*), paired penes exist; in *Leydigia*, the penis is single (Dumont & Negrea 2002). No asymmetry appears to be present in either males or females.

Phylum Arthropoda: Thecostraca

In *Baccalaureus*, the penis as described by Pyefinch (1939) is symmetric. Verrucomorph barnacles have asymmetric (AS) bodies (Palmer 2005); their penises, however, do not appear to possess structural asymmetry (Stubblings 1936). In *Balanus* the penis, when present, is very long but has no distinct structural asymmetry (Stubblings 1936).

Phylum Arthropoda: Branchiura

Gonochorists with copulation. No asymmetry visible in the figures in Yamaguti (1963).

Phylum Arthropoda: Pentastomida

Copulation is non-intromittent (Sprehn 1928)

Phylum Arthropoda: Copepoda

Last pair of legs in males (P5; used in copulation) is very often asymmetric (Neville, 1976; Huber 2004); not in cyclopoids (Dussart & Defaye 2001), where it may often be absent, as it is in gelyelloids. P5 chirality appears to be DA generally, and chiral reversals across higher taxa are common. Dussart & Defaye (2001) mention that the furca of the anal somite in male copepods is “often asymmetrical”. In females, the posterior part of the genital complex is “often asymmetric” (e.g., in *Tumeodiaptomus*, *Neutrodiaptomus*, and *Rhacodiaptomus* strongly so). They also describe the mating behaviour in calanoids, which involves directionally asymmetric use of the male antennules and legs. In Temoridae, the asymmetric male urosome is mirror-imaged in *Lamellipodia* compared with *Epischura* (Dussart & Defaye 2001).

Phylum Arthropoda: Ostracoda

Bronshtein (1988) mentions that sometimes the tube between the seminal receptacle and the ovisac is coiled. In Cytheridae, the male cirrus is coiled. The left and right members of the complex, paired copulatory organs in Cyprididae and Entocytheridae (Danielopol 1969; Hart & Hart 1969) appear identical, thus symmetric.

Phylum Arthropoda: Malacostraca

Leptostraca: Walker-Smith and Poore (2001) do not mention or figure any obvious asymmetries.

Stomatopoda: Female genitalia (paired gonopores) symmetric (Serène 1954); male paired penes subtly different in length (DA) in *Squilla ampusa* (Wortham-Neal 2002).

Bathynellacea: no asymmetry apparent in the genitalia as described and figured in Dumont (2001)

Mysida: penes paired; individual species descriptions of Mysida (e.g., San Vicente 2007; Wittmann 1992) normally only show one member of the pair, suggesting that symmetry is the rule.

Amphipoda: Genitalia, where they occur, appear to be symmetric (Barnard 1969; Thomas 1993; Vonk 2003; Nicholls 1938; Vonk, pers. comm.).

Isopoda: Whole-body asymmetry (incl. genitalia) in female *Bopyrus*, *Phryxus*, and *Athebes paguri* (Neville 1976). Genitalia are very diverse in the isopods; males have paired or fused penile papillae or penes and sometimes highly modified pleopods, either or both of which may be involved in sperm(atophore) transfer to the female paired oopores or cuticular organs (Wilson 1991). Besides the whole-body-asymmetric groups mentioned, genitalia in all other Isopoda appear to be symmetric.

Tanaidacea: With the exception of the mandibles, body organisation (incl. genitalia) apparently strictly symmetric (Kensley 2001; Sieg 1980).

Cumacea: Apparently strictly symmetric, including the genital papillae (Radha Devi & Kurian 1989).

Euphausiacea: Male copulatory organ and female gonopores and thelycum are apparently symmetric (Spiridonov & Casanova 2010).

Decapoda: Males have symmetric, paired, penes, gonopods and other structures for sperm transfer (Fransen, pers. comm. Bauer & Martin 1990). The only exceptions are hermit crabs, which have, due to their asymmetric body shape (forced by the fact that they live in gastropod shells) genitalia that are usually slightly to strongly asymmetric (Neville 1976; McLaughlin 2003; Tudge & Lemaitre 2006).

Phylum Arthropoda: Hexapoda

For the orders within the Insecta (except the Coleoptera), I refer only to the recent review paper by Huber et al. (2007) and the references therein.

Orthoptera: Genitalia mostly symmetric. Asymmetry, possibly AS in *Acanthacris* (Acrididae) male genitalia. Potential cases of DA in male genitalia in a small number of other genera. (Huber et al. 2007.)

Phasmida: Male genitalia always DA. (Huber et al. 2007.)

Embiidina: Male genitalia (and terminal abdominal segments) always subtly (Clothodidae) or strongly (all other families) DA. Female genitalia symmetric. (Huber et al. 2007.)

Grylloblattoidea: Male genitalia always DA, female genitalia symmetric. (Huber et al. 2007.)

Mantophasmatodea: Male genitalia DA, except *Tanzaniophasma subsolana*, which is nearly symmetric. Female genitalia symmetric. (Huber et al. 2007.)

Plectoptera: Male genitalia DA in Brachypterainae, in some genera of the Nemouridae, and in some species of the Capniidae. (Huber et al. 2007.)

Dermaptera: Male genitalia DA in Eudermaptera (Forficulidae, Chelisochidae, Spongiphoridae) and convergently in the archaic Karschiellidae. In a small number of taxa (nested within the groups with male genital DA), DA exists in the female genitalia. (Huber et al. 2007.)

Zoraptera: Some, if not all, species have DA in male genitalia. Female genitalia may also be DA in at least some species. (Huber et al. 2007.)

Dictyoptera (Blattaria+Isoptera+Mantodea): Male genitalia are DA in all Blattaria and Mantodea, with AS in a few species (see Table 1 and Anisyutkin & Gorochov 2004). Isoptera have symmetric genitalia. (Huber et al. 2007.)

Thysanoptera: Symmetric genitalia (Huber et al. 2007.)

Homoptera: Male genitalia DA in many Cicadellidae (Cicadomorpha). In Fulgomorpha, male genitalia are symmetric in certain families, but commonly DA in Achilidae, Derbidae, and Tropiduchidae, and in almost all Cixiidae and Delphacidae. AS in some Delphacidae (see Table 1). Female genitalia always symmetric. (Huber et al. 2007.)

Heteroptera: Male genitalia DA in many groups, suggesting numerous independent evolutions, even within families. AS in a few species (see Table 1). Female genitalia DA in a smaller group of taxa, fully nested in those in which there is male genital DA. (Huber et al. 2007.)

Psocodea: DA widespread in male and female genitalia in Psocinae and in male genitalia in some Lachesillidae and Ectoptocidae. In Phthiraptera, male genitalia are commonly DA. (Huber et al. 2007.)

Neuropterida (Raphidioptera+Megaloptera+Neuroptera): (Subtle) asymmetry in male genitalia in several families in Neuroptera, e.g., Chrysopidae, Nymphidae, Nemopteridae, and Berothidae, and in the genus *Ctenochauiodes* of Megaloptera. It is not clear whether these are DA or AS. (Huber et al. 2007.)

Siphonaptera: DA in many species for one particular part of the male genitalia, the endotendon, which is related for functional segregation of left and right. A few species have additional asymmetries in the male genitalia. (Huber et al. 2007.)

Mecoptera: Genitalia symmetric (Huber et al. 2007.)

Strepsiptera: Genitalia symmetric (Huber et al., 2007.)

Coleoptera: DA very widespread. Among 177 coleopteran families, 100 appear to have fully symmetric male and female genitalia. In all other families (including very speciose ones like Scarabaeidae, Staphylinidae, and Carabidae) asymmetry occurs, sometimes in the female (e.g., in dorcine Lucanidae), but usually in the male genitalia. This may involve the midpiece and/or the parameres, sometimes only the endophallus or internal sac. Within these families, asymmetry may be fixed at any taxonomic level: in individual species (*Agathidium pilosum* is the only asymmetric species within Leiodinae), in genera (e.g., *Bibloporus*, *Euplectus* within Pselaphinae), or in entire tribes (e.g., Leiodidae: Ptomaphagini), subfamilies (e.g., Scarabaeidae: Glaphyrinae) or families (e.g., Mordellidae). AS is present in a few species (see Table 1). (Schilthuizen, unpublished.)

Hymenoptera: Genitalia symmetric (Huber et al. 2007.)

Trichoptera: Asymmetric male genitalia occur in all major subgroups, but symmetry also occurs at all taxonomic levels, even within some asymmetric genera. Mostly DA, but in *Mystacides*, AS occurs (Table 1), and in *Austrochorema* symmetry and asymmetry occur within a species (Table 2). Little is known of female genital asymmetry, except for *Orthotrichia costalis*, and some *Phylloicus* species, which may be DA/SYM (symmetric and asymmetric within the same species, both for male and female). (Huber et al. 2007.)

Lepidoptera: Phallus asymmetry is almost universal. Clasper (valve) asymmetry is common but not widespread (restricted to Ditrysia)—and has evolved up to 30 times independently (Huber et al. 2007). Asymmetry is always DA except in *Scythris antsymmetrica* (Nupponen 2009; see Table 1).

Diptera: Male DA occurs sporadically, at the level of families, genera, or individual species, but almost only in the Eremoneura. The apex of the phallus, however, is asymmetric in most Acalypratae. Phallus is coiled to one side in Tephritidae s.l. Asymmetry is uncommon in Nematocera. No asymmetry in the lower Brachycera. (Huber et al. 2007.)

Phylum Chordata: Chondrichthyes

It appears that the claspers in Squalomorphii, Rajomorphii, and Holocephalii are always symmetric (Capapé et al. 1990; Hamlett 1999; Jones et al. 2005; Leigh-Sharpe 1920, 1921).

Phylum Chordata: Actinopterygii

Atheriniformes: In Phallostethidae DA or (more frequently) AS in male priapum and female genital opening (Parenti 1986, 1989; Palmer 1996, 2004).

Cyprinodontiformes: In Poeciliidae: two genera DA (sinistral), one genus DA (dextral), one genus AS, one genus DA/SYM (Rosen & Bailey 1963; Bisazza et al., 1998). In Anablepidae: DA, AS (or biased AS; Garman 1895) in *Anableps* and *Jenynsia* in side of gonopodium bend as well as female genital opening (Bisazza et al. 1998; Breder & Rosen 1966; Neville 1976; Nelson 1994; Palmer 1996). In Goodeidae and all other Cyprinodontiformes with internal fertilization, the andropodium or gonopodium is apparently symmetric (Meyer & Lydeard 1993).

Ophidiiformes: Male intromittent organ in Bythitidae appears symmetric (Machida 1993, 1994; Møller et al. 2006).

Intromittent organs exist in several other families (**Beloniformes:** Adrianichthidae, Hemiramphidae; **Siluriformes:** Auchenipteridae; **Characiformes:** Characidae; **Perciformes:** Clinidae, Embiotocidae, Zoarcidae; **Scorpaeniformes:** Comephoridae, Scorpaenidae), but I have been unable to check these for (a)symmetry.

Phylum Chordata: Lissamphibia

Gymnophiona: The intromittent organ in caecilians, the only amphibians that transfer sperm internally, appears symmetric (Gower & Wilkinson 2002).

Phylum Chordata: Mammalia

Monotremata: In *Tachyglossus aculeatus*, the bifid penis is anatomically symmetric, but in erection, one half is retracted, making it functionally asymmetric (Johnston et al. 2007)

Marsupialia: Symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Edentata: Symmetric (Prasad 1974)

Pholidota: Symmetric (Prasad 1974)

Rodentia: Distinctly asymmetric bacula in all Sciuridae (Burt 1960; Prasad 1974); usually DA (but see Table 1; Burt 1960)

Lagomorpha: Symmetric (Prasad 1974)

Macroscelidea: Symmetric (Prasad 1974; Woodall 1995; Van Beek, Hoogenboom & De Jong pers. comm.)

Primates: Symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Scandentia: Symmetric (Prasad 1974; Jones 1917)

Chiroptera: Symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Dermoptera: Symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Insectivora: Symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Carnivora: Slight asymmetry in the baculum of most families (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm. Baryshnikov et al. 2003)

Artiodactyla: DA in all families except Cervidae (Walton 1960; Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Cetacea: Externally symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Tubulidentata: Symmetric (Sonntag 1925)

Perissodactyla: Symmetric (Prasad 1974; Van Beek, Hoogenboom & De Jong pers. comm.)

Hyracoidea: Symmetric (Prasad 1974)

Sirenia: Symmetric (Prasad 1974)

Proboscidea: Symmetric (Prasad 1974)

Phylum Chordata: Reptilia

Squamata: all snakes have unequal hemipenes. In gartersnakes, Shine et al. (2000) found that the right hemipenis was slightly wider than the left.

Testudines: no data

Aves: Although all birds have internal fertilization, only a few taxa have retained intromittent organs (Montgomerie 2010). The following list is limited to those taxa. Palaeognathae: DA in the penis of Ostrich and Emu (Brennan & Prum 2012; M.F. Cardoso, pers. comm.). DA/SYM in Rhea (Brennan & Plum 2012 and references therein). DA (sinistral spiral) in *Nothura maculosa* (Oliveira & Mahecha 2000). Anseriformes: The penis is always asymmetric in the sense that it lies to the left of the cloacal aperture (Caithness 1971). Clear DA in the morphology of both penis (sinistral spirals) and vagina (dextral spirals and invaginations) is seen in at least 16 (perhaps all) species of duck and goose (Brennan et al. 2007; M.F. Cardoso, pers. comm.). Galliformes: In those species in which an intromittent organ occurs, it appears to be symmetric (e.g., *Coturnix coturnix*; Puigcerver et al. 1994). Neoaves: The pseudophallus in *Coracopsis* (Wilkinson & Birkhead 1995) is apparently symmetric.

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