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; Alvariño 1990).

Phylum Platyhelminthes

Turbellaria: Chitinous parts of the male copulatory organ very often (strongly) asymmetric, e.g. in genera *Microstomum* and *Macrostumum* 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., *Prosorhynchus 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).

Branchiobdeliida: 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, Diplotriaenoidea, 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**: Tylodoridae) 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* (Mikhaljova & 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 (Stubbings 1936). In *Balanus* the penis, when present, is very long but has no distinct structural asymmetry (Stubbings 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 *Atheges 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 *Ctenochauliodes* 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 Acalyptratae. 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.

References

Agnarsson, I. 2006 Asymmetric female genitalia and other remarkable morphology in a new genus of cobweb spiders (Theridiidae, Araneae) from Madagascar. *Biol. J. Linn. Soc.* **87**, 211-232.

Alvariño, A. 1990 Chaetognatha. Pp. 255-282 in: (Adiyoda, K. G. & Adiyoda, R. G., eds.) Reproductive Biology of Invertebrates Vol. 4. Wiley, New York.

Anderson, R. C., Chabaud, A. G & Wilmott, S. 2009 Keys to the Nematode parasites of vertebrates: archival volume. CABI, 463 pp.

Andrassy, I. 2005. Free-living Nematodes of Hungary Vol 1. *Pedozool. Hung.* **3**, 1-518.

Anisyutkin, L. N. & Gorochov, A. V. 2004 *Haania doroshenkoi*, a new species of mantises from Cambodia (Mantina: Mantidae: Thespinae) and a case of mirror symmetry in the structure of the male genitalia of mantises. *Russ. Ent. J.* **13**, 119-122.

Arkhipkin, A. I. & Laptikhovsky, V. V. 2010 Observation of penis elongation in *Onykia ingens*: implications for spermatophore transfer in deep-water squid. *J. Moll. Stud.* **76**, 299-300.

Ax, P. & Bunke, D. 1967 Das Genitalsystem der Aeolosomatidae mit phylogenetisch ursprünglichen Organisationszügen für die Oligochaeten. *Naturwissenschaften* **54**, 222-225.

Barnard, J. L. 1969 The families and genera of marine Gammaridean Amphipoda. *Bull. US Natl. Mus.* **271**, 1-535.

Baryshnikov, G. F., Bininda-Emonds, O. R. P. & Abramov, A. V. 2003. Morphological variability and evolution of the baculum (os penis) in Mustelidae (Carnivora). *J. Mamm.* **84**, 673–690.

Bauer, R. T. & Martin, J. W. 1990 Crustacean Sexual Biology. Columbia University Press, New York.

Beddard, F. E. 1895 A Monograph of the Order of Oligochaeta. Clarendon Press, Oxford, 769 pp.

Benham, W.B. 1950. A review of certain external structures employed in the coition of earthworms. *Proceedings of the Zoological Society of London* **119**, 905-916.

Bird, A. F. 1971. The structure of nematodes. Academic Press, New York, 318 pp.

Bisazza, A., Facchin, L., Pignatti, R. & Vallortigara, G. 1998. Lateralization of detour behaviour in poeciliid fish: The effect of species, gender and sexual motivation. *Behav. Brain Res.* **91**, 157-168.

Bongers, T. 1988. De Nematoden van Nederland. KNNV Uitgeverij, 408 pp.

Breder, C.M. & Rosen, D.E. 1966 Modes of reproduction in fishes. TFH, Jersey City.

Brennan, P. L. R. & Prum, R. O. 2012 The erection mechanism of the ratite penis. *J. Zool.* **286**, 140-144.

Bronshtein, Z. S. 1988 Fresh-water Ostracoda. Balkema, Rotterdam, 470 pp.

Brüggemann, J. 1988 Ultrastructure and differentiation of the penis stylet of *Pogaina kinnei* Ax, 1970 (Plathelminthes, Rhabdocoela). *Progr. Zool.* **36**, 315-319.

Brzeski, M. W. 1998 Nematodes of Tylenchina in Poland and temperate Europe. Muzeum I Institut Zoologii Polska Akademia Nauk Warszawa, 397 pp.

Burt, W. H. 1960 Bacula of North American mammals. *Misc. Publ. Mus. Zool. Univ. Michigan* **113**, 1-76, pl. I-XXV.

Bychowsky, B. E. 1957. Monogenetic trematodes; their systematics and phylogeny. English translation published by American Institute of Biological Sciences, Washington, D.C., 627 pp.

Caithness, T. A. 1971. Sexing kiwis. *Int. Zoo Yearbook*, **11**: 206-208.

Capapé, C., Quignard, J. P. & Mellinger, J. 1990 Reproduction and development of two angel sharks, *Squatina squatina* and *S. oculata* (Pisces: Squatinidae), off Tunisian coasts: semi-delayed vitellogenesis, lack of egg capsules, and lecithotrophy. *J. Fish Biol.* **37**, 347-356.

Chitwood, B. G. & Chitwood, M. B. 1974 Introduction to Nematology (2nd ed.). University Park Press, Baltimore, 334 pp.

Crompton, D. W. T. & Nickol, B. B. 1985 Biology of the Acanthocephala. Cambridge University Press, 519 pp.

Danielopol, D. L. 1969 Recherches sur la morphologie de l'organe copulateur mâle chez quelquez ostracodes du genre *Candona* Baird (Fam. Cyprididae Baird). Pp. 136-153 in (Neale, J. W., ed.) The taxonomy, morphology & ecology of recent Ostracoda. Oliver & Boyd, Edinburgh.

Dawes, B 1956 The Trematoda, with special reference to British and other European forms. Cambridge University Press, 644 pp.

Drago, L., Fusco, G., Garollo, E. & Minelli, A. 2011 Structural aspects of leg-to-gonopod metamorphosis in male helminthomorph millipedes (Diplopoda). *Front. Zool.* **8**, 19.

Dumont, H. J. 2001 Bathynellacea. Pp. 11-27 in (Day, J. A., Stewart, B. A., de Moor, I. J. & Louw, A. E., eds.) Guides to the freshwater invertebrates of Southern Africa, Volume 4. Crustacea III Bathynellacea, Amphipoda, Isopoda, Spelaeogriphacea, Tanaidacea and Decapoda. Water Research Commission, Pretoria.

Dumont, H. J. & Negrea, S. V. 2002 Introduction to the Class Branchiopoda. Backhuys, Leiden, 398 pp.

Dussart, B. H. & Defaye, D. 2001 Introduction to the Copepoda. 2nd rev. and enlarged edition. Guides to the Identification of the Microinvertebrates of the Continental Waters of the World, 16. Backhuys Publishers, Leiden, VIII, 344 pp.

Eberhard, W. G. 1985 Animal genitalia and evolution. Harvard University Press, Cambridge.

Elliott, J. M. & Mann, K. H. 1979 A key to the British freshwater leeches with notes on their life cycles and ecology. Freshwater Biological Association, 72 pp.

Enghoff, H. 2011 East African giant millipedes of the tribe Pachybolini (Diplopoda, Spirobolida, Pachybolidae). *Zootaxa* **2753**, 1-41.

Fain, A. 1978 Mites of the family Myobiidae (Acarina: Prostigmata) from mammals in the collection of the British Museum (Natural History). *Bull. British Mus. (Nat. Hist.) Zool.* **33**, 193-229.

Furman, D. P. & Loomis, E. C. 1984 The Ticks of California (Acari: Ixodida). University of California Press, Berkeley, 239 pp.

Garman, S. 1895 Sexual rights and lefts. *Am. Nat.* **29**, 1012–1014.

Gibbons, L. M. 1978 Revision of the genus *Paracooperia* Travassos, 1935 (Nematoda: Trichostrongylidae). *J. Helminthol.* **52**, 231-249.

Giesen, K. M. T. 1990 A review of the parasitic mite family Psorergatidae (Cheyletoidea: Prostigmata: Acari) with hypotheses on the phylogenetic relationships of species and species groups. *Zool. Verh. Leiden* **259**, 1-69.

Goto, T. & Yoshida, M. 1985 The mating sequence of the benthic arrowworm *Spadella schizoptera*. *Biol. Bull.* **169**, 328-333.

Govedich, F. R. 2001 A reference guide to the ecology and taxonomy of freshwater and terrestrial leeches (Euhirudinea) of Australasia and Oceania. Cooperative Research Centre for Freshwater Ecology, Thurgoona. 67 pp.

Gower, D. J. & Wilkinson, M. 2002 Phallus morphology in caecilians (Amphibia, Gymnophiona) and its systematic utility. *Bull. Nat. Hist. Mus. Lond. (Zool.)* **68**, 143-154.

Graff, L. von 1913 Turbellaria II. Rhabdocoelida. Friedländer, Berlin. 484 pp.

Hamlett, W. C. 1999 Sharks, skates, and rays: the biology of elasmobranch fishes. John Hopkins University Press, Baltimore, 515 pp.

Hart, C. W. & Hart, D. G. 1969 The functional morphology of endocytherid ostracod copulatory appendages, with a discussion of possible homologues in other ostracods. Pp. 154-167 in (Neale, J. W., ed.) The taxonomy, morphology & ecology of recent Ostracoda. Oliver & Boyd, Edinburgh.

Holt, P. C. 1986 Newly established families of the order Branchiobdellida (Annelida, Clitellata) with a synopsis of the genera. *Proc. Biol. Soc. Washington* **99**, 676-702.

Hopkin, S. P. & Read, H. J. 1992 The Biology of Millipedes. Oxford University Press, Oxford, UK, 233 pp.

Huber, B. A. 2004 Evidence for functional segregation in the directionally asymmetric male genitalia of the spider *Metagonia mariguitarensis* (González-Sponga) (Pholcidae: Araneae). *J. Zool.* **262**, 317-326.

Huber, B. A. 2006 Cryptic female exaggeration: the asymmetric female internal genitalia of *Kaliana yuruani* (Araneae: Pholcidae). *J. Morphol.* **267**, 705-712.

Huber, B. A., Sinclair, B. J. & Schmitt, M. 2007 The evolution of asymmetric genitalia in spiders and insects. *Biol. Rev.* **82**, 647-698.

Hugot, J.-P., Gardner, S. L. & Morand, S. 1996 The Enterobiinae Subfam. Nov. (Nematoda, Oxyurida) pinworm parasites of primates and rodents. *Int. J. Parasitol.* **26**, 147-159.

Jamieson, B.G.M. 1967 A taxonomic review of the African megadrile genus *Stuhlmannia* (Eudrilidae, Oligochaeta). *J. Zool.* **152**, 79-126.

Johnston, S. D., Smith, B., Pyne, M., Stenzel, D. & Holt, V. W. 2007 One-sided ejaculation of *Echidna* sperm bundles. *Am. Nat.* **170**, E162-E164.

Jones, F. W. 1917. The genitalia of *Tupaia*. *J. Anat.* **51**, 118-126.

Jones, A. M. & Baxter, J. M. 1987 Molluscs: Caudofoveata, Solenogastres, Polyplacophora and Scaphopoda: keys and notes for the identification of species. Brill, 123 pp.

Jones, C. J. P., Walker, T. I., Bell, J. D., Reardon, M. B., Ambrosio, C. E., Almeida, A. & Hamlett, W. C. 2005 Male genital ducts and copulatory appendages in chondrichthyans. Pp. 361-393 in (Hamlett, W. C., ed.) Reproductive Biology and Phylogeny of Chondrichthyes, Sharks, Batoids and Chimaeras. Science Publishers, Enfield, UK.

Kensley, B. 2001 Tanaidacea. Pp. 80-86 in (Day, J. A., Stewart, B. A., de Moor, I. J. & Louw, A. E., eds.) Guides to the Frehwater Invertebrates of Southern Africa, Volume 4: Crustacea III. Water Research Commission, Pretoria.

Krantz, G. W. & Walter D. E. 2009 A Manual of Acarology (3rd Edition). Texas Technical University Press.

Lee, D. C. 1970 The Rhodacaridae (Acari: Mesostigmata): classification, external morphology and distribution of genera. *Rec. South Aust. Mus.* **16**, 1-219.

Leigh-Sharpe, W. H. 1920. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. I. *J. Morphol.* **34**, 245-265.

Leigh-Sharpe, W. H. 1921. The comparative morphology of the secondary sexual characters of elasmobranch fishes. Mem. III, and V. *J. Morphol.* **36**, 191-243.

Machida, Y. 1993 Two new genera and species of the subfamily Brosmophycinae (Bythitidae, Ophidiiformes) from Northern Australia. *Jap. J. Ichthyol.* **39**, 281-286.

Machida, Y. 1994 Descriptions of three new and one resurrected species of the bythitid genus *Dinematichthys* (Ophidiiformes). *Jap. J. Ichthyol.* **40**, 451-464.

Macías-Ordoñez, R., Machado, G., Pérez-González, A. & Shultz, J. W. 2010 Genitalic evolution in Opiliones. Pp. 285-306 in (Leonard, J. L. & Córdoba-Aguilar, A., eds.) The Evolution of Primary Sexual Characters in Animals. Oxford University Press, Oxford.

McLaughlin, P. A. 2003 Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. *Mem. Mus. Victoria* **60**, 111-144.

Meyer, A. & Lydeard C. 1993 The evolution of copulatory organs, internal fertilization, placentae and viviparity in killifishes (Cyprinodontiformes) inferred from a DNA phylogeny of the tyrosine kinase gene X-src. *Proc. R. Soc. Lond. B* **254**, 153-162.

Mikhaljova, E. V. & Korsós, Z. 2003 Millipedes (Diplopoda) from Korea, the Russian Far East, and China in the collection of the Hungarian natural history museum. *Acta Zool. Acad. Scient. Hung.* **49**, 215–242

Møller P. R., Schwarzhans W., Iliffe, T. M. & Nielsen J. G. 2006 Revision of the Bahamian cave-fishes of the genus *Lucifuga* (Ophidiiformes, Bythitidae), with description of a new species from islands of the little Bahama bank. *Zootaxa* **1223**, 23-46.

Montgomerie, R. 2010. Sexual conflicts and the intromittent organs of male birds. Pp. 453-470 in: (Leonard, J. L. & Córdoba-Aguilar, A., eds.) The Evolution of Primary Sexual Characters in Animals. Oxford University Press.

Mueller, J. F. 1925 Some new features in nematode morphology in Proleptus obtusus Dujardin. Journal of Parasitology **12**, 84-90.

Nelson, J. S. 1994 Fishes of the World. Wiley, New York.

Neuhaus, B. & Higgins, R. P. 2002 Ultrastructure, biology, and phylogenetic relationships of Kinorhyncha. *Integr. Comp. Biol.* **42**, 619-632.

Neville, A. C. 1976 Animal Asymmetry. Edward Arnold, London, 60 pp.

Nicholls, G. E. 1938 Australasian Antarctic Expedition 1911-14 under the leadership of Sir Douglas Mawson, O.B.E., B.E., D.Sc., F.R.S.; Scientific Reports Series C—Zoology and Botany (Ed. by Professor T. Harvey Johnson, University of Adelaide), Vol. II, Part 4: Amphipoda Gammaridea, 145 pp.

Noordijk, J., Kleukers, R. M. J. C., Nieukerken, E. J. van & Loon, A. J. van (ed.) 2010 *De Nederlandse Biodiversiteit; Nederlandse Fauna 10*. NCB Naturalis and EIS Nederland, Leiden. 510 pp.

Nupponen, K. 2009. *Scythris antisymmetrica* Nupponen, sp. n. from Central Spain, an example of antisymmetric male genitalia in the order Lepidoptera (Lepidoptera: Scythrididae). *SHILAP Revta. Lepid.* **37**, 439-444.

Oliveira, C. A. & Mahecha, G. A. B. 2000. Morphology of the copulatory apparatus of the spotted tinamou *Nothura maculosa* (Aves, Tinamiformes). *Annls. Anat.* **182**, 161-169.

Palmer, A. R. 1996. From symmetry to asymmetry: phylogenetic patterns of asymmetry variation in animals and their evolutionary significance. *Proc. Natl. Acad. Sci. USA* **93**, 14279-14286.

Palmer, A. R. 2004 Symmetry breaking and the evolution of development. *Science* **306**, 828-833.

Palmer, A. R. 2005 Antisymmetry. Pp. 359-397 in: *Variation* (Hallgrimmson, B. & Hall, B. K., eds.) Elsevier.

Parenti, L. R. 1986 Bilateral asymmetry in phallostethid fishes (Atherinomorpha) with description of a new species from Sarawak. *Proc. Cal. Acad. Sci.* **44**, 225-236.

Parenti, L. R. 1989 A phylogenetic revision of the phallostethid fishes (Atherinomorpha, Phallostethidae). Proc. Cal. Acad. Sci. **46**, 243–277.

Park, C. K. & Atyeo, W. T. 1971 A generic revision of the Pterodectinae, a new subfamily of feather mites (Sarcoptiformes: Analgoidea). *Bull. Univ. Nebraska State Mus.* **9**, 39-88.

Pinto, R. M., Vicente, J. J. 1995 *Tetrameres (Tetrameres) spirospiculum* n. sp. (Nematoda, Tetrameridae) from the buff-necked ibis, *Theristicus caudatus caudatus* (Boddaert) (Aves, Threskiornithidae). *Mem. Inst. Oswaldo Cruz* 90, 615-618.

Platnick, N. I. & Dupérré, N. 2009 The American goblin spiders of the new genus *Escaphiella* (Araneae, Oonopidae). *Bull. Am. Mus. Nat Hist.* **328**, 1-151.

Ponder, W. & Lindberg D. R. 2008 Phylogeny and evolution of the Mollusca. University of California Press, 488 pp.

Prasad, M. R. N. 1974. Männliche Geslechtsorgane. *Handb. Zool.* **8 (51)**, 1-150.

Puigcerver, M., Gallego, S., Rodrígo-Teijeiro, J. D. & Rodrigo-Rueda, F. J. 1994. Presence of penis in the European quail, *Coturnix c. coturnix*. *Misc. Zool.* **17**, 288-291.

Pyefinch, K. A. 1939 Ascothoracica (Crustacea, Cirripedia). *John Murray Exped. 1933-34* **5**, 247-262.

Radha Devi, A. & Kurian, C. V. 1989 A collection of Cumacea from the South West and South East coasts of India. *Rec. Zool. Surv. India Occas. Pap.* **121**, 1-37.

Rosen, D. E. & Bailey, R. M. 1963 The Poeciliid fish (Cyprinodontiformes), their structure, zoogeography, and systematics. *Bull. Am. Mus. Nat. Hist.* **126**, 1–176.

Ruhberg, H. 1985 Die Peripatopsidae (Onychophora). *Zoologica* **137**, 1-184.

San Vicente, C. 2007 A new species of *Marumomysis* (Mysidacea: Mysidae: Erythropini) from the benthos of the Bellingshausen Sea (Southern Ocean). *Sci. Mar.* **71**, 683-690.

Scheltema, A. H. 1992. The Aplacophora: history, taxonomy, phylogeny, biogeography, and ecology. Unpublished doctoral dissertation, University of Oslo, Norway, 370 pp.

Scheucher, R. 1957 Systematik und Ökologie der deutschen Anoetinen. *Beitr. Syst. Ökol. mitteleurop. Acarina* **1**, 233-384.

Schilthuizen, M. & Davison, A. 2005 The convoluted evolution of snail chirality. *Naturwissenschaften* **92**, 504-515.

Schilthuizen, M., Craze, P. G., Cabanban, A. S., Davison, A., Gittenberger, E., Stone, J. & Scott, B. J. 2007 Sexual selection maintains whole-body chiral dimorphism. *J. Evol. Biol.* **20**, 1941-1949.

Serène R. 1954 Observations biologiques sur les Stomatopodes. *Mém. Inst. Océanogr. Nhatrang* **8**, 1-93, pl. i-x.

Shelley, R. W. 1981 Revision of the milliped genus *Sigmoria* (Polydesmida: Xystodesmidae). *Memoirs of the American entomological Society* **33**, 1-139.

Shine, R., Olsson, M. M., LeMaster, M. P., Moore, I. T. & Mason, R. T. 2000 Are snakes right-handed? Asymmetry in hemipenis size and usage in gartersnakes (*Thamnophis sirtalis*). *Behav. Ecol.* **11**, 411-415.

Sieg, J. 1980 Taxonomische Monographie der Tanaidae Dana 1849 (Crustacea: Tanaidacea). *Abhandl. Senckenb. Naturf. Gesellsch.* **537**, 1-267.

Smiley, R. L. 1965 Two new species of the genus *Cheyletiella* (Acarina : Cheyletidae). *Proc. Ent. Soc. Washington* **67**, 75-79.

Sonntag, C. F. 1925 A monograph of *Orycteropus afer.* I. Anatomy except the nervous system, skin, and skeleton. *Proc. Zool. Soc. Lond.* **95,** 331–437**.**

Spiridonov, V. & Casanova, B. 2010 Order Euphausiacea Dana, 1852. Pp. 1-82 in (Schram, F. R. & Vaupel Klein, J. C. von, eds.) Treatise on Zoology—Anatomy, Taxonomy, Biology; The Crustacea; complementary to the volumes translated from the French of the Traité de Zoologie Vol. 9, Part A Eucarida: Euphausiacea, Amphionidacea, and Decapoda (partim). Brill, Leiden.

Sprehn, C. 1928 Pentastomida (Linguatulida), Zungenwürmer. Pp 84-94 in (Dahl, F. ed.) Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach inhren Merkmalen und nach ihrer Lebensweise. 8. Teil Spinnentiere oder Arachnoidea II: Opiliones—Pseudoscorionida—Pantopoda—Pentastomida. Fischer, Jena.

Steiner, T. M. & Amaral, A. C. Z. 1999 The family Histriobdellidae (Annelida, Polychaeta) including descriptions of two new species from Brazil and a new genus. *Contr. Zool.* **68**, 95-108.

Stephenson, J. 1930 The Oligochaeta. Clarendon Press, Oxford, 978 pp.

Stimpson, K. S., Klemm, D. J. & Hiltunen, J. K. 1982 A guide to the freshwater Tubificidae (Annelida: Clitellata: Oligochaeta) of North America. US Environmental Protection Agency, Cincinnati. 61 pp.

Stubbings, H. G. 1936 Cirripedia. *John Murray Exped. 1933-34* **4**, 1-70.

Thomas, J. D. 1993 Identification manual for marine Amphipoda (Gammaridea). I. Common coral reef and rocky bottom amphipods of South Florida. Department Environmental Protection, Tallahassee.

Tudge, C. C. & Lemaitre, R. 2006 Studies of male sexual tubes in hermit crabs (Crustacea, Decapoda, Anomura, Paguroidea). II. Morphology of the sexual tube in the land hermit crabs, *Coenobita perlatus* and *C. clypeatus* (Coenobitidae). *Crust. Res. S. N.* **6**, 121-131.

Voight, J. R. 2002 Morphometric analysis of male reproductive features of octopodids (Mollusca: Cephalopoda). *Biol. Bull.* **202**, 148-155.

Volgin, V. I. 1989 Acarina of the Family Cheyletidae of the World. Brill, Leiden, 532 pp.

Vonk, R. 2003 Explorations of the systematics and deep history of stygobiont amphipods. PhD Thesis, University of Amsterdam, 189 pp.

Walker-Smith, G. K. & Poore, G. C. B. 2001 A phylogeny of the Leptostraca (Crustacea) with keys to families and genera. *Mem. Mus. Victoria*, **58**, 383-410.

Walton, W. 1960 Copulation and natural insemination. In (Parkes, A. S., ed.) Marshall's Physiology of Reproduction Vol. 2. Longman's, London.

Wetzel, M. J. 1987 *Limnodrilus tortilipenis*, a new North American species of freshwater Tubificidae (Annelida: Clitellata: Oligochaeta). *Proc. Biol. Soc. Wash.* **100**, 182-185.

Wilkinson, R. & Birkhead, T. R. 1995 Copulation behaviour in the vasa parrots *Coracopsis vasa* and *C. nigra*. *Ibis* **137**, 117-119.

Wilson, G. D. F. 1991 Functional morphology and evolution of isopod genitalia. Pp. 228-245 in (Bauer, R. T. & Martin, J. W., eds.) Crustacean Sexual Biology. Columbia University Press, New York.

Wittmann, K. J. 1992 Morphogeographic variations in the genus *Mesopodopsis* Czerniavsky with descriptions of three new species (Crustacea, Mysidacea). *Hydrobiologia* **241**, 71-89.

Woodall, P. F. 1995. The penis of elephant shrews (Mammalia: Macroscelididae). *J. Zool.* **237**, 399-410.

Wortham-Neal, J. L. 2002 Reproductive morphology and biology of male and female mantis shrimp (Stomatopoda: Squillidae). *J. Crust. Biol.* **22**, 728-741.

Yamaguti, S. 1963 Parasitic Copepoda and Branchiura of fishes. Interscience, New York, 1104 pp.