

The evolution of chirally dimorphic insect genitalia

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Many insect species have asymmetric (male) genitalia. A recent review of the literature (Huber et al., 2007) shows that this can be explained by structural and mechanical advantages, sometimes in association with a lateral mating position. Although asymmetry could in principle lead to antisymmetry (the occurrence of two mirror-image morphs of the same chiral shape within a species), Huber et al. report that this condition is very rare, due to yet unrevealed causes. This makes the small collection of cases where antisymmetry does occur particularly interesting from an evolutionary viewpoint. Here, I review these cases and, based on studies of antisymmetry in other organisms, I propose testable hypotheses for explaining the maintenance of antisymmetry in insect genitalia.

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Introduction

A chiral form is defined as one that, when seen in mirror-image, cannot be superimposed upon the original object. The human hand is a standard example, as left and right hands are non-identical 'enantiomorphs' of one another. Hence, for reference, the terms right-handed and left-handed or 'dextral' and 'sinistral' are normally used to indicate the two alternative forms of a chirally asymmetric structure.

Among the Eumetazoa, conspicuous whole-body asymmetry and, consequently, chirality, only occurs in the Mollusca and some derived lower-level taxa like flatfishes, verruciform barnacles, and spirorbid polychaetes (Palmer 1996; 2004). However, asymmetry of particular body-parts within an otherwise bilaterally symmetric body is a much more common phenomenon. Among the Arthropoda, claw asymmetry occurs in Crustacea, abdominal rotation in Diptera and Phasmatodea, mandible asymmetry in Thysanoptera, Orthoptera, and Coleoptera, and wing-cover asymmetry in Orthoptera (Palmer 1996; 2004).

A previously unexplored category of asymmetric body-parts among the Insecta are the genitalia. Although well-known among entomological taxonomists, who make intensive use of genital shape in identifying, describing, and classifying the objects

of their study (Schilthuizen 2003), asymmetry in insect genitalia, viewed in the light of the evolutionary biology of copulation mechanics, was systematically reviewed only recently (Huber et al. 2007).

Huber et al. list a large number of cases of genital asymmetry in insects. They conclude that asymmetry evolved independently 'a few times within Dermaptera, Neuropterida, Plecoptera, and Siphonaptera; several times within Heteroptera, Homoptera, Psocodea, Trichoptera; and many times within Coleoptera, Diptera and ditrysian Lepidoptera.' However, adopting Palmer's (2005) terminology, they point out that almost all cases of asymmetry in insect genitalia are situations of *directional asymmetry*, where only one of the two possible enantiomorphs occurs in nature. *Antisymmetry* (where both enantiomorphs occur in equal frequencies) is very rare (see below). They also notice that genital asymmetry mostly involves males, whereas female genital asymmetry is both rare and, when present, inconspicuous. When the incidences of male and female genital asymmetry are superimposed upon an evolutionary tree, it becomes clear that female asymmetry usually evolves after male asymmetry. In addition, Huber et al. show that morphological asymmetry of the genitalia is correlated with the adoption of a one-sided asymmetric mating position, in which

the male consistently enters the female from one preferred side. Based on these observations, Huber et al. propose several hypotheses for the evolution of genital asymmetry, without being able to find a single general explanation. They also acknowledge that none of their hypotheses explains the dominance of directional asymmetry over antisymmetry.

An analogy with land snails (Gastropoda: Pulmonata) may be advantageous to make further progress in understanding insect genital asymmetry. In land snails, directional asymmetry is similarly dominant: most species are dextral, few are sinistral, and only in a few rare cases does antisymmetry exist within a species. Studies have shown that, although asymmetry in Gastropoda concerns the entire body, the driving force for both directionality and antisymmetry is sexual selection and genital match (Schilthuizen & Davison 2005; Schilthuizen *et al.* 2007). Below, I will offer a closer look at those cases of genital antisymmetry in insects that are known, and attempt to use these to generate targeted research questions that may help understand the evolution of insect genital asymmetry.

Synopsis of the known cases of antisymmetry in insect genitalia

Odonata: *Calopteryx haemorrhoidalis* (Van der Linden)

Córdoba-Aguilar (2003a) describes a population from southwestern Spain, in which the number of mechanoreceptive sensilla on the vaginal plates in females differ between the left and the right valve. These sensilla respond to the passing of an egg, and stimulate the ejection of sperm. The same happens when the (egg-shaped) penis enters the vagina, which is interpreted as an example of sexually antagonistic selection (Rice 1996), where the male 'tricks' the female physiology into dumping sperm of a previous mate. Without giving the exact numbers of sensilla on each plate, Córdoba-Aguilar reports that of 27 females, 16 had more sensilla on the left plate, five had more sensilla on the right plate, and six had similar numbers on both plates. The author performed experiments *in vivo* and showed that when an egg passes through a vagina with left-biased sensilla on the vaginal plates, the left spermathecal duct contracts, and vice versa (again, exact data are not given). The males do not show any asymmetry. Córdoba-Aguilar argues that a female with fewer sensilla on one plate may be able to retain more prior sperm during a copulation, because of understimulation of one spermathecal duct. In a comparative study of related calopterygids, Córdoba-Aguilar (2003b)

mentions asymmetry in vaginal plate sensilla number in many other species, but does not specify whether these are also cases of antisymmetry.

Orthoptera: *Locusta migratoria* (Linnaeus)

Mika (1959) describes a case of antisymmetry in the recaptaculum seminis of the female locust. In rostral direction, its entrance (the ductus receptaculi) narrows and then bends sharply right (in 35 of 47 females) or left (in 12 of 47 females) in a loop. Further rostrad, it then forms a spiral, which, after 2.5 whorls, returns on itself (forming an inner and an outer spiral) and then ends in a terminal sack (the receptaculum proper), situated within the loop. Mika only figures a situation with a left-bent ductus, which then proceeds to form a dextral spiral (twisted clockwise). From Mika's description, it remains unclear whether the spiral in a right-bent ductus is sinistral. However, in Albrecht's (1953: 71) illustration of the *Locusta migratoria* female reproductive system, the ductus is shown bent to the right, and to form a spiral that appears to be sinistral. Hence, the entire recaptaculum seminis may be chirally dimorphic, not only the loop.

Dermoptera: *Anisolabis littorea* (White), *A. maritima* (Bonelli), and *Euborellia plebeja* (Dohrn)

Giles (1961), in describing the condition of the paired penes of *A. littorea*, writes: '[O]ne or the other of the mesal lobes is bent to face forward; this is normally the longer of the two and is partly everted. It seems a matter of chance which remains straight, for of 32 males of *Anisolabis littorea* examined, 17 had the left lobe straight and 15 the right' (Fig. 1). Kamimura & Matsuo (2001; see also Schilthuizen [2001]) report similar proportions for *A. maritima* (123 versus 119 males with the left or right penis lobe folded, respectively) and *Euborellia plebeja* (16 versus 13 males with the left or right penis lobe folded, respectively). They also show that in each individual, and contrary to Giles's (1961) assertion, both lobes are functional for copulation, not just the straight one, and that the presence of two lobes possibly is maintained to have a 'spare' in case one lobe is damaged during copulation.

Mantodea: *Ciulfina baldersoni* Ginn & Holwell, *C. rentzi* Ginn & Holwell, and *C. biseriata* (Westwood)

In Australian praying mantids of the genus *Ciulfina*, several species exist with antisymmetry in the 'phallic complex' (Balderson 1978; Holwell & Herberstein, unpublished). Balderson (1978) mentioned the existence of dimorphism in one, at the time

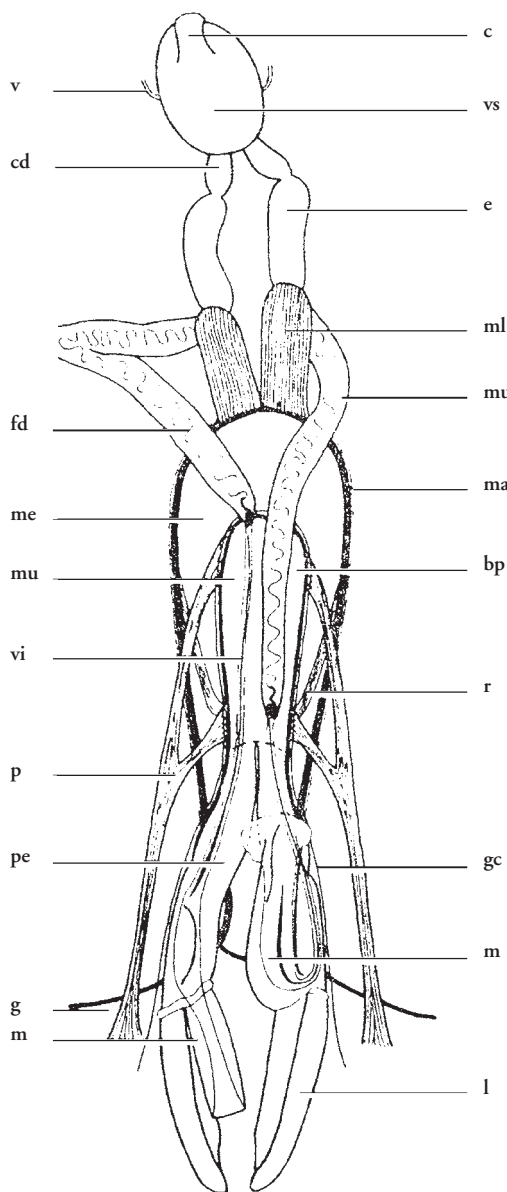


Fig. 1. Male genitalia of the earwig *Anisolabis littorea*, showing the paired penis lobes (m), of which, in this individual, the right is bent rostrad, whereas the left points caudad. In other individuals of the same species, it is the left lobe that is bent. (After Giles 1961.)

undescribed, species of *Ciulfina* ('*C. sp. 7*'). He reports 35 sinistral against 22 dextral males. Holwell & Herberstein found both dextral and sinistral forms of the male genitalia in populations of *C. baldersoni* and *C. rentzi* (14 dextral: 16 sinistral; 7 dextral:

16 sinistral, respectively); one or both of these species are presumably conspecific with Balderson's *C. sp. 7*, but the taxonomic paper on these species (Holwell et al., in press) is not yet available. They also found antisymmetry in one out of three populations of *C. biseriata*, but do not give numbers of individuals for each morph.

Hemiptera: *Stiroma affinis* Fieber

De Jong (1985) described a sample of this species from the vicinity of The Hague (Netherlands), containing 11 males. Based on the positioning of combs of teeth on the aedeagus, De Jong distinguishes two mirror-image forms, which he called l-type and r-type. Six males were of the l-type and five of the r-type. In some of the individuals of the one type he found rudiments of rows of teeth expected for the other type, and vice versa. He speculates that these individuals may be heterozygotes. He also points out that in the genus *Ribautodelphax*, mirror image dimorphism exists in the non-genitalic 'appendages of the tubus analis', and suggests that the same may be true for genitalic characters in species of this genus.

Hemiptera: *Xylastodoris luteolus* Barber

Cassis et al. (1999) mention a case of antisymmetry in the Thaumastocoridae. These bugs have extremely asymmetric male genitalia, with the genital opening shifted strongly to either the left or the right side of the eighth abdominal sternite. Usually in this family, intraspecific asymmetry is directional, but one New World species exists in which antisymmetry is found: *Xylastodoris luteolus*. Baranowski (1958) describes the biology of this species and records 746 'right-sided' and 649 'left-sided' males (while also showing that these proportions are not significantly different from a 1:1 ratio). The author explains the presence of two male morphs as an adaptation to the fact that females usually position themselves against the midrib of the palm leaf they feed on. This means that usually only one side of a female can be approached. In the case of male directional asymmetry, half of the females would be inaccessible for mating at any one time. Hence, Baranowski writes, 'the occurrence of two types of males asymmetry does appear to have a definite advantage over only one type'.

Trichoptera: *Mystacides*

Huber et al. (2007) state that Morse & Yang (2002) report on antisymmetry in the genus *Mystacides*. The antisymmetry concerns the lobes on the 10th tergum of the male. I have not seen this paper, and it is not clear whether the antisymmetry concerns one or all species in this genus, and what the proportions of dextrals and sinistrals are within each population.

Evolutionary considerations

Why is antisymmetry so rare?

The short enumeration of all known cases of antisymmetry in insect genitalia given above, appears to show that antisymmetry is a rare exception, and that directional asymmetry is the rule, as it is in most other situations of asymmetry in animal body form. However, we should heed the caveat that the literature may be biased. A priori, genitalia are often (and probably wrongly; Eberhard 1985; Kawano 2004) considered morphologically less variable than the rest of the body. Consequently, taxonomists are inclined to study and picture only a single or a very few individuals of a given species. Due to this, cases of antisymmetry may remain undiscovered (Huber 2003). Even so, the conclusion appears inescapable that antisymmetry in genital shape is relatively rare in insects.

Recently, the genetic basis for genital chirality in *Drosophila melanogaster* has become known. Spéder et al. (2006) described a gene (*Myo31DF*) that controls dextrality in the rotation of the genital plate and the consequent coiling of the spermiduct. A mutation in this gene can, in homozygous state, override dextrality and produce an individual with sinistral genital development (i.e., dextrality is dominant). Hence, if this genetic-developmental system is universal in insects, symmetry reversal may be a genetically simple event (as it is in Gastropoda, where also a single locus with full dominance of one of the two alleles is involved). Given the widespread occurrence of genital asymmetry in insects, and the indication that reversal may in principle be a common event, it is worthwhile to ask the question, why is antisymmetry so rare?

The first possibility is that, even though chirality reversal may be possible, and mutant genotypes may drift to appreciable frequencies, it may be subjected to both internal and external selection. Internal selection may be expected if developmental constraints exist that require one particular chiral morph, and result in developmental problems if they function in a reverse-chirality context. Similar cases have recently been reported in snails: mutant sinistral individuals in snail species that are normally dextral show delayed development, morphological shell differences, and reduced egg hatch rate (Schilthuisen & Davison 2005; Shibazaki et al. 2004; Asami, pers. comm.). If the same applies to mutant insects with reversed genital chirality (and this could be studied in *Myo31DF* mutants), the establishment of an antisymmetric population may be impeded by the reduced fitness of the mutant individuals.

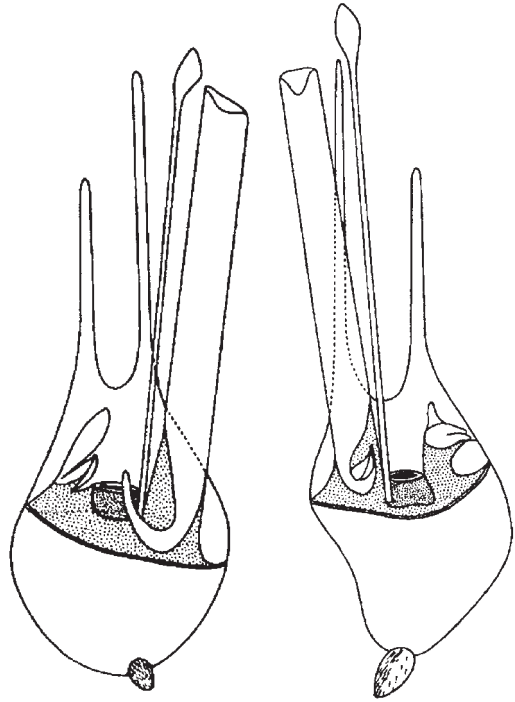


Fig. 2. Male genitalia in the cockroaches *Ectobius panzeri* (left) and *E. lapponicus* (right), after Brown (1975). In *Ectobius*, species differ in the chirality of their male genitalia. Cases of genital antisymmetry (the co-occurrence of both dextral and sinistral forms in the same species) are the expected intermediate stages that represent the reversal from one chiral form to another.

In addition, 'external' frequency-dependent selection may take place. The review by Huber, Sinclair & Schmitt (2007) suggests that male genital asymmetry evolves first, occasionally followed by female genital symmetry, and that it is often associated with a one-sided mating position. This may mean that a reverse-chirality male may not be able to mate with a 'normal' female (or vice versa) as easily as a male and a female of the same chirality. Hence, as in snails with internal fertilisation, the rare morph will always be at a disadvantage and there may thus exist a frequency dependent selection that maintains directional asymmetry.

Nevertheless, data on genital asymmetry in insects do suggest that reversals from all-dextral to all-sinistral lineages have taken place regularly. For example, in the cockroach genus *Ectobius* some species have dextral male genitalia, whereas other species have sinistral ones (Brown 1975; Bohn 1987; Fig. 2). In the praying mantids *Ciulfina* and *Stenomantis*

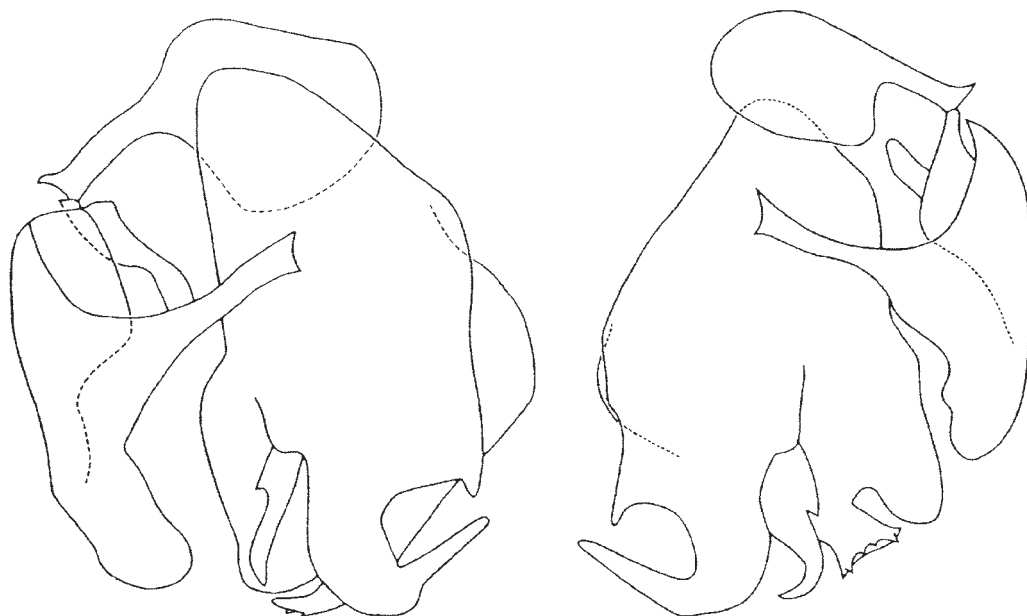


Fig. 3. Male genitalia in the praying mantid genus *Ciulfina*. Left, '*C. sp. 7*', in which both dextral (figured) and sinistral genitalia occur. The sinistral genitalia of a related (unidirectionally asymmetric) species ('*C. sp. 3*') are shown on the right (after Balderson 1978).

six species are of dextral male genital type, ten species are of the sinistral type (Balderson 1978; Fig. 3), and three *Ciulfina* species (see above) are dimorphic. In the Heteropteran genera *Nabis* and *Corixa* the male genital segments and the parameres, respectively, are dextral in some species, sinistral in others (Ekblom 1926; Keilbach 1935; Larsén 1938; Kullenberg 1947). And, finally, in the Thaumastocoridae, the aedeagus is bent to the left or right, depending on the species (Cassis et al. 1999). Only one thaumastocorid species is antisymmetric in this respect (see above). In addition, many examples exist where higher-level sister taxa have opposite chirality in the genitalia.

It goes without saying that in evolution, such reversals, even if they rapidly go to fixation, must pass through an antisymmetric stage. In fact, three of the examples given above occur in groups in which antisymmetric species are also known. This suggests that, despite the selection pressure that normally may prevent symmetry reversal, conditions may arise that facilitate or even encourage the appearance of antisymmetry. Given the rarity of antisymmetry, however, it would appear that these conditions are of relatively brief duration. I will now provide some suggestions as to what these conditions might entail, and how this may be tested experimentally.

Antisymmetry as a result of sexual selection

Animal genitalia in general, and male insect genitalia in particular, are under strong pressure from sexual selection (Cordero & Eberhard 2003; Eberhard 1985, 1996; Schilthuizen 2003). Given the likelihood of natural selection against symmetry reversal per se (see above), it is unlikely that symmetry reversal could come about by genetic drift, even in small populations. Consequently, sexual selection may be the only evolutionary force strong enough to drive it.

It is not difficult to imagine a hypothetical situation in which mirror-image genitalia may be favoured in a population. In polygamous species, females will be selected for increased control over sperm reception, storage, and usage. Indications exist that her reproductive morphology is adapted to this end (Eberhard 1996). In a species with directionally asymmetric male genitalia, the female reproductive anatomy (and perhaps also her external behaviour) will be adapted to a one-sided intromission of the male organ. However, if a new male morph appears in the population that has chirally reversed genitalia, upon mating his genitalia will not be matched by co-adapted female genitalia. Consequently, some of the 'security measures' of the female may be circumvented, leading to this male siring more offspring.

Unfortunately, the exact interaction between male and female reproductive systems during copulation is unknown for many insect species with asymmetric genitalia. This is partly due to the fact that in most taxa, the genitalia of only one sex are species-specific and/or sufficiently sclerotised for mounting and study. Only in a few groups, most notably certain Lepidoptera, are male and female genital structures studied simultaneously in genitally asymmetric species (Huber et al. 2007).

If sexual selection would indeed favour reverse-chirality males in a population, then one may expect this new morph to spread rapidly to fixation, soon followed by an evolutionary response in the females' genitalia to adapt to the new type of males. The antisymmetric stage would thus only exist during the relatively brief period of spread of the new chirally-reversed morph. This would explain the rarity of antisymmetry, but it would also suggest that dextral-sinistral proportions in antisymmetric species would range broadly, from predominantly dextral, via 1:1, to predominantly sinistral. However, inspection of the examples given above suggest that this may not be the case. In six out of the eight species in which exact proportions for dextrals and sinistrals are available, the proportions do not deviate significantly from 1:1 (2-test; $P > 0.05$). Interestingly, all these cases concern male antisymmetry, whereas the two cases where proportions do deviate significantly from 1:1 (i.e., *Calopteryx haemorrhoidalis* and *Locusta migratoria*), involve female antisymmetry. This suggests that, at least where antisymmetry in the male genitalia is concerned, balanced dimorphism persists for a long time, and the reversed condition does not automatically go to fixation.

An alternative explanation that would lead to balanced dimorphism is the so-called 'rare-male advantage' (Partridge & Halliday 1984; Kokko et al. 2007). Eberhard (1985; 1994) has argued that the male genitalia act as an 'internal courtship device' and that male genital shape is driven primarily by female choice. Some studies indicate that females may prefer novel features in male courtship (e.g., in *Drosophila*; Singh & Sisodia 2000). If such 'rare male advantage' would apply to the newly-appeared reverse-chirality male genitalia in a population, the novel morph would initially spread slowly, impeded by the natural selection due to developmental constraints. However, purging selection may remove or assuage these constraints, after which the new morph may spread faster until its frequency reaches 50% and it will no longer benefit from the advantage.

Testing the hypotheses

The above scenarios are little more than a few

thought-experiments on how genetal antisymmetry in insects may come about, and alternative hypotheses may be suggested. What little information we have on genetal antisymmetry at the moment unfortunately provides very few clues. This is because the examples include both male and female genitalia, and a diverse array of insect orders with very different reproductive anatomy and mechanics. Therefore, it is impossible to draw any general conclusions from them. However, the fact that male and female genetal antisymmetry differ in their proportions of dextral versus sinistral suggests that both are governed by different processes. It may be worthwhile to select a species from each of those groups (e.g., *Locusta migratoria* and *Xylastodoris luteolus*) and carry out a number of studies, e.g.: (a) detailed anatomical studies to investigate the fate of sperm in all four possible copulation combinations; (b) genetic studies to determine the genetic basis for male and female sinistrality/dextrality; (c) population genetic studies to introduce a reverse-chirality individual into a line fixed for the alternative morph and monitor its spread over generations. In addition, comparative studies may be helpful. For example, chirality reversals may be mapped in both polygamous and monogamous sister taxa, with the expectation (under the sexual selection hypothesis) that the former have a higher proportion of reversals.

Given its rarity, it is easy to be led to consider genetal antisymmetry in insects irrelevant. However, as I have pointed out above, antisymmetry is an unavoidable transition state in evolutionary chirality reversal. And chirality reversal is currently a much studied phenomenon in evolutionary developmental biology, partly because of medical geneticists' interest in understanding congenital defects that arise from it. Consequently, studies of antisymmetry may lead to a better understanding of how developmental constraints can be breached.

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