Hypotheses

The ovotestis: an underdeveloped organ of evolution
Angus Davison

Summary
In animals that have separate sexes (gonochorists), many sperm are produced to fertilize a few eggs. As the male germline undergoes more mitoses, so the accumulated mutation frequency is elevated in sperm compared with ova, and evolution is ‘male-driven’. In contrast, in many hermaphroditic animals, a single organ—the ovotestis—produces both ova and sperm. Since self-renewing cells in the ovotestis may give rise to both cell types throughout life, ova in hermaphrodites could in theory have undergone as many cell divisions as sperm. Here, I consider some possible effects of the ovotestis on evolution. In particular, I hypothesise that the accumulated mutation frequency of nuclear genes in hermaphrodites (including species that change sex) may reach twice that compared with gonochorists. There may be an even greater increase in the mitochondrial mutation frequency. Further developmental studies and the accumulation of comparative data should allow hypothesis testing. If the prediction is correct, then it may provide the most straightforward explanation for the extraordinary diversity of mitochondrial DNA in some hermaphrodites, especially molluscs. BioEssays 28:642–650, 2006.

Introduction
Ever since Haldane’s prediction that rates of mutation should be elevated in males1,2 (mostly male) scientists have searched for evidence that evolution is ‘male-driven’. Although it took around 65 years,3–6 it is now beyond doubt that the accumulated mutation frequency in some male germ lines is elevated compared with females.4,7,8 The debate now tends to be more concerned with the magnitude of the effect (represented by \( z \), the ratio of mutations originating in males compared to females7), and whether the causes of variation between estimates are real or due to ascertainment bias.4,7,9–12

The basic rationale behind the argument for male-driven evolution is simple. In species that have separate sexes (gonochorists), there is differential investment in reproduction, since many small, inexpensive sperm attempt to fertilise few, large and costly eggs, a condition known as anisogamy. For male mammals, spermatogonia are self-renewing, so undergo mitosis throughout the reproductive life cycle whereas, in female mammals, the total number of oogonia is fixed at birth. As the male germline must in general undergo more mitoses, the accumulated mutation frequency should be elevated in sperm compared with ova, so males contribute a greater part towards the overall rate of evolution compared with females.1,2 The longer a male lives and reproduces, then the greater the accumulated mutation frequency and the greater the value of \( z \). Male-driven evolution may therefore only be of relevance in animals that are long-lived—in Drosophila, the ratio of germline cell divisions changes from a weak female bias to a weak male bias as the reproductive age increases;1,13 there is no difference in accumulated mutation frequency between the sexes.1,13,14

If male-driven evolution is real and not artefactual, then one condition is that the accumulated mutation frequency is proportional to the rate of evolution, or the rate at which mutations are fixed. Most of these mutations will be neutral or nearly neutral. There is also an implicit assumption that, while a compensatory repair mechanism could in theory evolve to counteract a high male mutation rate, it does not always do so, otherwise male-driven evolution would not have been detected in mammals,4 birds5,6 and fish.3 Finally, “male-driven evolution” is often assumed to refer to differences that are generated during mitosis rather than meiosis. This is not always the case, however, since several human sequences evolve more rapidly in males than females as a consequence of meiotic events rather than the number of germline mitoses.7

Strangely, there does not seem to be an explicit statement in the literature as to the expectation for male-driven evolution in hermaphrodites. One study on hermaphrodite plants states that it was “remarkable” to find evidence for male-driven evolution in plants, because the germ and somatic cells are shared for much of life15. Instead the main concern in previous reviews has been to discuss the theory, issues surrounding the estimation of \( z \), and explain contradictory results.7–10,16 In part, the bias in the literature towards gonochorists and male-driven evolution must result from the fact that we have viewed species predominantly as having separate sexes. The reality is somewhat different, however. Twenty of 28 animal phyla have at least some hermaphroditic species and around ten are almost exclusively hermaphroditic:
Annelida, Bryozoa, Chaetognatha, Cnidaria, Ctenophora, Entoprocta, Gastrotricha, Mollusca, Platyhelminthes, and Porifera (17, 18) (Table 1). In some phyla, hermaphroditism is ubiquitous whereas, in others, it is rarer or confined to specific groups. Although I do not consider them further here, most plants are also hermaphroditic.

An elevated rate of evolution in hermaphrodites

So, perhaps the question is better put as “why shouldn’t male-driven evolution occur in hermaphrodites?” (Box 1). Although it does not seem to have been generally appreciated by those that study molecular evolution, in many hermaphrodites, a single organ—the ovotestis—produces both eggs and sperm (Table 1). If self-renewing germ cells in the ovotestis continually differentiate into both sperm and eggs, then both eggs and sperm should have undergone approximately the same number of cell divisions. The expectation therefore is that the accumulated mutation frequency in male and female germ line stem cells should be about equal. Male-driven evolution should not occur in hermaphrodites. Moreover, since ova in the ovotestis of long-lived species will undergo more mitoses than in the equivalent gonochorist, then the accumulated mutation frequency in a hermaphrodite will be on average higher than the corresponding gonochorist—providing that the same conditions apply as described above (e.g. a high mutation rate is not counteracted by selection for modifiers that reduce it; \(z\) increases with increasing life-span).

If it is assumed that, in an ovotestis, the accumulated mutation frequency in ova is as high as in sperm, and if the theoretical ratio between the accumulated mutation frequency in hermaphrodites and gonochorists is \(h\), then as male-driven evolution, \(z\), tends to increase in gonochorists, \(h\) asymptotically approaches 2 in the equivalent hermaphrodite (Fig. 1). This can be expressed as:

\[
h \text{(biparenthally inherited genome)} = \frac{\text{hermaphrodite} (a^m + a^f)}{\text{gonochorist} (a^m + a^f)}
\]

where \(a^m = \) accumulated mutation frequency in the male germ line, \(a^f = \) accumulated mutation frequency in the female germ line. If twice as much evolution occurs in the male genome of a gonochorist (\(z = 2\)), then the rate of evolution in the equivalent

<table>
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<th>Occurrence of sex-change</th>
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<tr>
<td>Cnidaria</td>
<td>ubiquitous in Anthozoa absent otherwise</td>
<td>loose</td>
<td>protandrous/protogynous sex change; protogynous hermaphroditism</td>
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<tr>
<td>Ctenophora</td>
<td>ubiquitous</td>
<td>digonic</td>
<td>absent</td>
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<td>Porifera</td>
<td>ubiquitous</td>
<td>digonic</td>
<td>protandrous/protogenus sex change both common</td>
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<tr>
<td>Annelida</td>
<td>ubiquitous</td>
<td>digonic</td>
<td>protandrous/protogenus sex change; protandrous/ protogynous hermaphroditism</td>
</tr>
<tr>
<td>Bryozoa</td>
<td>ubiquitous common, perhaps ubiquitous</td>
<td>digonic</td>
<td>protandrous sex change common</td>
</tr>
<tr>
<td>Entoprocta</td>
<td>ubiquitous</td>
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<td>protandrous sex change</td>
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<tr>
<td>Gnathostomulida</td>
<td>ubiquitous; except Cephalopoda where absent</td>
<td>ovotestis</td>
<td>protandrous hermaphroditism common; protandrous sex change rarer; but common in bivalves and prosobranchs</td>
</tr>
<tr>
<td>Mollusca</td>
<td>present</td>
<td>ovotestis</td>
<td>protandrous sex change rare</td>
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<td>Platyhelminthes</td>
<td>ubiquitous</td>
<td>digonic</td>
<td>protandrous sex change</td>
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<tr>
<td>Arthropoda</td>
<td>rare in crustacean; absent or very rare otherwise</td>
<td>ovotestisb</td>
<td>protandrous sex change and protandrous hermaphroditism in crustaceans; protogynous sex change rare</td>
</tr>
<tr>
<td>Gastrotricha</td>
<td>ubiquitous</td>
<td>digonicc</td>
<td>protandrous/protogynous sex change</td>
</tr>
<tr>
<td>Nematoda</td>
<td>present</td>
<td>ovotestis</td>
<td>protandrous sex change</td>
</tr>
<tr>
<td>Tardigrada</td>
<td>parachelate heterotardigrades</td>
<td>ovotestis</td>
<td>protandrous sex change</td>
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<td>Deuterostomes</td>
<td>Chaetognatha ubiquitous</td>
<td>digonic</td>
<td>protandrous sex change</td>
</tr>
<tr>
<td>Echinodermata</td>
<td>(almost) absent</td>
<td>digonic</td>
<td>limited protandrous/protogynous hermaphroditism</td>
</tr>
<tr>
<td>Urochordata</td>
<td>ubiquitous</td>
<td>ovotestis/digonic</td>
<td>protandrous sex change common; protogynous sex change less so</td>
</tr>
<tr>
<td>Vertebrata</td>
<td>common in fish; rare or absent otherwise</td>
<td>ovotestis</td>
<td>protandrous sex change</td>
</tr>
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\(^{a}\)Sponges are said to lack gonads; instead germ cells are scattered throughout the mesohyl.

\(^{b}\)In Phyllopoda and Decapoda.

\(^{c}\)In Remipedia and Cirripedia.
h (maternally inherited genome) = $\frac{\text{hermaphrodite} \ (a')}{\text{gonochorist} \ (a')}$

If $a = 5$ in a gonochorist, then $h = 5/1$ for maternally inherited organelles.

There is one further consideration: in hermaphrodites, the effective population size of organelles is in theory twice that of normal (all else being equal), since all individuals in a population can potentially contribute to the next generation. Under equivalent circumstances as described above ($a = 2$ or 5), the expectation therefore is that the neutral variation of organelles should be 4 or 10 times as great in a hermaphrodite compared with an equivalent gonochorist (by “equivalent” I mean a gonochoristic species that does not differ substantially from a closely related hermaphroditic species, except for the defining difference in their reproduction).

Together, these theoretical calculations give rise to several hypotheses for the patterns expected if female germ cells
Box 2

1. In hermaphrodites, the mutation rate in ova may approach that in sperm, unlike in gonochorists. 2. Since ova in an ovotestis potentially undergo almost as many mitoses as sperm, then the rate of evolution of nuclear genes in hermaphrodites may reach twice that compared with gonochorists. 3. There will be a much greater amplification of the relative mutation rate in maternally-inherited cytoplasmic organelles. 4. Providing that both kinds of germ cell develop from a common, self-renewing stem cell, those species that change sex from male to female (protandrous sex change) or male to hermaphrodite (protandrous hermaphroditism) may have a greater rate of molecular evolution than those that change from female to male (protogynous sex change) or female to hermaphrodite (protogynous hermaphroditism).

As with male-driven evolution in gonochorists, the above predictions are also dependent upon much the same assumptions: the accumulated mutation frequency should be proportional to the rate of evolution; a lack of a compensatory repair mechanism in response to a higher mutation rate; most mutation taking place during mitosis rather than meiosis.

Germ cell development in hermaphrodites

About half of all hermaphrodite animal phyla contain species that have an ovotestis (Table 1); the other hermaphrodite animal groups are digonic (Box 1). I needed further precise information on ovotestis development to determine absolutely whether male and female germ cells develop from a common progenitor or stem cell. Unfortunately, except for some model organisms, hermaphrodites are a neglected group, so detailed histological and developmental information is lacking for most. Moreover, for several organisms, the later stages of the developmental path of the male and female germ cells have been determined but the precise origins of the cells remain unknown. A complete review is therefore not yet possible.

Nematodes

Undoubtedly, the most-detailed information on germ cell development in hermaphrodites comes from studies of the nematode Caenorhabitis elegans. In hermaphroditic C. elegans, the germline is organised in a linear fashion: the most distal cells in the ovotestis undergo mitosis, those in the middle enter meiosis and proximal cells differentiate to sperm or ova. The mitotic region of the germline thus renews the supply of mitotic cells, as well as supplying meiotic cells for oogenesis or spermatogenesis; whether a particular cell becomes a sperm or ovum is dependent upon an interaction between several key genes. Over a lifetime, each worm generates about 2000 germ cells, of which more than 1000 undergo apoptosis, so that around 300 sperm and a slightly larger number of oocytes finally mature. Although there have been few comparative studies on nematodes, the mode of germ cell development in C. elegans (and sex determination?) may be common, as a similar path has also been found in a distantly related species, Pristionchus pacificus.

Fish

Perhaps the next-best-studied group are fish. Many fish are hermaphrodites and able to change sex, usually from female to male, but occasionally from male to female. In simultaneously hermaphroditic fish species, the ovotestis is divided into separate male and female regions, so it is reasonable to suppose (though not proven) that different sets of primordial germ cells differentiate into sperm or oocytes (the same is true of ascidians). In sequentially sex-changing fish, however, adult sex change involves the degeneration of functional gonadal tissue of the first sex, then the growth and maturation of the gonadal tissue of the opposite sex. Presently, in most if not all species, it is unknown whether the proliferating tissue of the second sex differentiates at the same time as the first sex, then becomes dormant, or else whether it differentiates at a later stage from a common and self-renewing primordial germ cell. In at least some cases, the latter may be correct: in Epinephelus microdon, sex change takes place within ex-ovarian lamellae, as bipotential primordial germ cells begin to differentiate.

There are several other salient features in fish. First, gonadal maturation does not begin until rather late in development. Even in gonochoristic species, such as zebrafish, it is not possible to determine sex until after several weeks of development. Second, it has been argued that the ‘default’ fish sex is female, because, even in protandrous species, development of male cells is both preceded and followed by ovarian development (the first set of female gametes never mature, and are absorbed, so can easily be missed). Thus, in some gonochoristic species, the developing gonads differentiate into ovaries in the female and, much later, into testes in the male. In zebrafish, gonads first develop into ovary-like gonads. In half of the individuals, the ovary-like gonads become ovaries and produce oocytes. In the other half, they develop into testes and the fish become male.
**Molluscs**
In hermaphroditic molluscs, the consensus is that, in most species, both types of gamete originate from indeterminate germ cells in every part of the ovotestis, and that this occurs throughout the life cycle.\(^{(42)}\) Gametes arise by proliferation of germinal cells that line the follicle wall. In species where reproduction is seasonal, the ovotestis degenerates at the end of each year, then regenerates again during spring.\(^{(42)}\) Unfortunately, it is presently unknown whether ova and sperm arise from the same self-renewing germ cells during ordinary development, or over the seasonal cycles.

Many molluscs are also long-lived—land snails live for five or more years, so go through several reproductive seasons; some clams live for up to 150 years and produce large quantities of sperm, which is linked evolutionarily to multiple mating and fierce sperm competition.\(^{(17)}\) Both of these factors could also increase the number of germine mitoses.\(^{(7,12)}\) Many molluscs also have a period in which they are male before becoming hermaphrodite, or else change sex entirely.\(^{(31,43)}\) In addition, just as in fish, gonadal differentiation (and thus sex determination in gonochoristic species) does not occur until rather late in the development of many molluscs. In gonochoristic marine bivalves, in particular, sex is not determined until the germ cells are differentiated, whether in the larva or in the juvenile.\(^{(42)}\) The cell types present in the testis, ovary or ovotestis are apparently identical until a late stage of development.

**Other groups**
In the remaining groups, even less is known about development. In hermaphroditic tardigrades such as *Macrobiotus* and *Amphibolus*, mature gametes of both types are never separated by physical barriers, and there are at least two cycles of egg production.\(^{(44,45)}\) In some groups of crustaceans, specifically the phyllopods, decapods and isopods, both protandrous hermaphroditism and sex change are relatively common, with protogynous hermaphroditism/sex change less so.\(^{(31,48)}\) In the clam shrimp *Eulimnadia*, the anterior portion of the hermaphroditic ovotestis is ovarian tissue and the smaller posterior portion is testis.\(^{(47)}\) Thus, while in this species and other branchiopods,\(^{(48)}\) there is an apparent functional separation, it remains unclear whether the separation occurs early or late in development. In the tadpole shrimp *Triops*, the separation is less—male germ cells originate along both the longitudinal tubules and the lateral branches at whose tips female germ cells differentiate\(^{(49)}\)—so it is conceivable that both germ cell types derive from the same stem cells.\(^{(49)}\) Finally, while most hermaphroditic echinoderms have separate ovaries and testes,\(^{(18)}\) in those that change sex the male secondary structures degenerate very rapidly with increasing size, sperm production ceases and the gonad becomes a developing ovary filled with large yolk-filled oocytes. Transitional gonads with previtellogenic oocytes and mature spermatozoa have been observed, suggesting that sex change could be initiated from a common germ cell.\(^{(50)}\)

What then are the expectations for molecular evolution and diversity in the above-mentioned hermaphrodites? There are several clear predictions (Box 3). Since both male and female germ cells undergo around the same number of cell divisions in *C. elegans*, then the rate of evolution through the male and female germline should be about equal (providing that the potential and unquantified contribution of males is ignored). However, the overall rate of evolution will be relatively low (including mitochondria), since the number of cell divisions to generate egg and sperm are rather few: hermaphrodite nematodes produce few sperm, a probable consequence of lowered reproductive effort due to a high degree of selfing and lessened sperm competition (the effects of inbreeding on evolution have been reviewed elsewhere\(^{(51–53)}\)).

In most *simultaneously* hermaphroditic fish, the expectation is arguably for unequal rates of evolution, because the oocytes and sperm are produced within different regions of the ovotestis. In *sequentially* hermaphroditic fish, however, it seems more likely that male and female germ cells develop from a common self-renewing germline stem cell. If so, then equal and high rates of molecular evolution are expected, with particularly high rates of mitochondrial evolution, especially in the few species that are protandrous and sex-changing.

As for the other animal groups, the expectations are much the same as in fish. The main difference is that, unlike in fish where protogyny is most common, in most invertebrates protandry is more common. It is therefore even more likely that some long-lived invertebrates may have an accelerated rate of molecular evolution.

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**Box 3**
Some general predictions for the impact of the ovotestis effect. **(1)** Male-driven evolution in gonochorists; male-driven evolution absent or much reduced in ovotestis-bearing hermaphrodites. **(2)** Male-driven evolution reduced in gonochorists with late-developing gonads. **(3)** Elevated rate of molecular evolution of nuclear genes in ovotestis-bearing hermaphrodites. **(4)** A highly elevated rate of evolution of maternally-inherited organelles (e.g. mitochondria); no effect on the evolution of paternally-inherited factors. **(5)** More rapid molecular evolution in protandrous species compared with protogynous species; simultaneous hermaphrodites intermediate. **(6)** Lower rate of evolution and reduced male-driven evolution in self-fertilizing hermaphrodites. **(7)** Paternal inheritance of organelles more common in some hermaphrodites.
Analysis of molluscs and the ovotestis

It has been noted frequently that molluscs may have exceptionally high rates of molecular evolution, especially of mitochondrial DNA (54–99) but probably also at some nuclear loci. (60–64) Within species, mitochondrial divergence in many land snails is of the order of 5 to 30%, depending upon the species and gene fragment used. In *Mandarina* land snails, the rate of evolution has been estimated to be 10% per million years at a gene that is normally slowly evolving. (55) Strikingly, it has also been found that two species of protandrously hermaphroditic littorinid snails have a remarkably elevated rate of evolution compared with their gonochoristic relatives. (65,66) There are no other significant differences between the species, except for their hermaphroditism. (66)

Several authors have previously tried to explain the high molecular diversity in land snails. (54,62) The main explanations have been (1) unusually structured or exceptionally large populations, (2) ancient isolation of populations that consequently diverged, (3) selection acting to generate and maintain variability, and (4) an exceptionally high mutation rate. (54) There is some evidence that population structure helps promote or maintain genetic diversity with molluscs, (67) but it is doubtful that it is the whole explanation. I am not aware of any satisfactory data on (2) or (3), except the special case of doubly uniparental inheritance (68,69) (see below). A high mutation rate (4) is by itself an unsatisfactory explanation, because it begs the question of why the mutation rate should be so high? The ovotestis effect could therefore provide the most-straightforward explanation for the high genetic diversity and high rates of molecular evolution in molluscs.

Doubly uniparental inheritance in bivalve molluscs

Species in three families of bivalves are exceptional because the sexes contain two separate types of mitochondrial DNA (F and M), which are transmitted through the female and male line, hence the term doubly uniparental inheritance (DUI). (68,69) Since F and M genomes are transmitted unparentally, evolve rapidly and do not usually recombine, they are markedly divergent. Mussels also have a characteristic sex ratio bias—individual females tend to give birth to offspring that are (1) mostly one sex or the other, (2) about equal proportions of male and female, or (3) hermaphroditic. (70,71)

One explanation for the rapid evolution of both M and F mitochondria that has not been considered is the ovotestis effect. F mitochondria are in cells that could undergo almost as many cell divisions as the M types, because the gonad—a functional ovotestis—does not differentiate into an ovary or testis until late in development, when the germline stem cells have already proliferated (the M genome evolves more rapidly than the F, due to a relaxation in selective constraints (72) and/or because there are still more mitotic divisions in differentiated males).

In addition, DUI may have originally evolved in a simultaneously hermaphroditic species, or else one in which sex is determined late and by the development of the gonad. The reasoning is that, if mitochondrial DNA is always inherited maternally, and males are heterogametic, then mitochondria can never evolve a function that directly benefits the male, unless the same function simultaneously benefits the female. (73,74) Therefore, with paternal inheritance of mitochondrial DNA in a species with separate sexes, it is not in the interests of maternally expressed sex-linked genes to “allow” paternal inheritance to persist, since sex-linked genes and maternally inherited mitochondria should be co-adapted. In contrast, in simultaneous hermaphrodites, especially those with an ovotestis, no such conflicts exist. Instead, the nuclear genome will tend to be associated with the mitochondrial genome that gives the greatest inclusive fitness, irrespective of whether it is inherited maternally or paternally.

As selection should be weak against paternally inherited mitochondria in hermaphrodites, they could be retained for some time in the ovotestis, just as occurs in mussels. (75) However, for paternally inherited mitochondria to persist in the long term, then they must ensure their own transmission. One way would be to masculinise the ovotestis (as is believed to occur (70,71,76)), so that paternal transmission and sex changing would become associated together.

Hypothesis testing

Except for encouraging further studies on the development of gonadal stem cells, especially in the ovotestis, the approach to determining whether the ovotestis effect is real or not must depend upon the comparative method. (77–80) If mutation is equal in both types of germ cell in a hermaphrodite, then one consequence is that the latter should evolve more rapidly at a molecular level. The molecular evolution of mitochondrial DNA will be even faster compared with nuclear sequences. Protandrous species may evolve more rapidly than protogynous species.

From a purely practical perspective, it would be unwise to use a gonochorist-calibrated molecular clock in a hermaphroditic lineage, at least not without a corrective factor. Fortunately, most authors already use and interpret the data from molecular clocks with caution, and are increasingly using a ‘local’ clock method, (81) where possible. All of the usual precautions must be extra-rigorously applied when dealing with hermaphrodites.

Does the ovotestis effect contribute to long-term molecular evolution?

While I have hypothesised as to the potential evolutionary effects of the ovotestis in hermaphroditic organisms, some of the underlying assumptions may not apply, or be relevant, in all circumstances. The ovotestis effect is only appropriate when all else is equal between comparable gonochorists and
hermaphrodites, species that have similar life histories and levels of sexual selection.

The longevity of the organism, in particular, may be a key factor in determining whether male-driven evolution is important in both hermaphrodites and gonochorists. Generation time is also a confounding factor. In Drosophila, male-driven evolution is lacking; the best explanation is that, because individuals are short-lived, male germline stem cells undergo around the same number of mitoses as female stem cells. There is therefore no expectation that short-lived hermaphrodites should have an elevated rate of mutation compared with their equivalent short-lived, gonochorist relatives. In terms of long-term molecular evolution, other factors such as effective population size and generation time may be much more important.

Another consideration is that mutation rate is likely to evolve. The ovotestis effect might not be relevant since a high mutation rate may lead to selection for modifiers that reduce the mutation rate. On the one hand, the physiological cost of reducing mutation may be the most important factor in setting the genomic mutation rate, regardless of the benefits of mutation in producing new adaptive variation. On the other hand, as the vast majority of mutations that have a phenotypic effect are likely to be individually deleterious, then this may maintain persistent selection in favour of lower mutation rates. Most likely, both factors have a role in maintaining low rates of mutation. Presently, the high rate of mitochondrial mutation is thought to reflect high rates of DNA damage, coupled with more limited DNA repair; it is also clear that the rate of mitochondrial DNA can evolve, at least in plants.

Finally, the degree of sexual selection may be important. If hermaphrodites self-fertilise more frequently than they outcross (e.g., C. elegans), then selection should lead them to reduce their investment in the male function. If there are fewer sperm, then there should be fewer mitoses and fewer mutations. With a high degree of selfing, then the expectation is that male-driven evolution should be lacking. There could even be slight bias towards female-driven evolution.

**Conclusion**

Although considerable effort is and has been devoted to estimating and understanding male-driven evolution, there have been few investigations of the corollary, a rapid though equal male- and female-driven evolution. Moreover, the evolutionary significance of having a single ovotestis, compared with the ‘normal’ situation, has rarely been considered. As the bias is due to an overemphasis of the research effort on a few, model gonochorists, then this may lessen as more genome sequences accumulate from diverse groups, including that of the first molluscs. Direct evidence for a heightened rate of evolution in hermaphrodites is currently lacking, so I would like to encourage research that complements the valuable work that has already been done. It remains to be determined whether the ovotestis effect is general, or may only apply under limited circumstances.

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**References**

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