

is a difficult one as there is much at stake and it is not easy to get the balance right. For instance, some have argued that fishermen should be 'let off the hook' because some stock collapses appear to be related to climatic changes [10], even though most scientists agree that overfishing is an overwhelmingly dominant force driving stock collapse [11]. Although the mechanisms that drive stock collapse can be difficult to unravel, the cascading effects shown by Frank *et al.* imply that we should look beyond the stock collapse itself. Their work also suggests two important questions for future research:

#### *Where should we expect cascading effects of stock decline?*

Do the findings of Frank *et al.* highlight an exceptional case or would similar cascading effects occur in other open ocean systems? It is important to keep in mind that fishing is already known to be a major driver of change in many coastal ecosystems [7]. A particularly striking example is the role of fishing in the collapse of Caribbean coral reef ecosystems [6,12]. Depletion of herbivorous fish left sea urchins as the only grazer to control macro algae. When a disease affected the sea urchins during the early 1980s, brown fleshy algae rapidly encrusted the reefs, replacing the corals and inducing radical change of the ecosystem at all levels.

#### *When may marine ecosystem shifts be irreversible?*

In both the Scotian shelf and the coral example, there are indications that the changes observed might not be easy to reverse. Although sea urchins have recolonized the Caribbean coral reefs in small numbers, the algae remain dominant. Similarly, the Scotian shelf system shows no signs of recovery despite the near-elimination of cod exploitation and the return to normal seawater temperatures. Although the question of reversibility remains open, the persistence of the new state is striking.

#### **Conclusions**

Overall, the observations on the Scotian shelf and the Caribbean reefs are in line with the emerging view that marine communities are characterized by strong nonlinearities [13,14]. Such an ecosystem view [15] suggests that there is a need to look differently at management of marine ecosystems. It implies that sharp irreversible

change can sometimes result from gradually increasing fishery pressure, and that the critical threshold for such change will vary with climatic conditions. Although the task of unraveling the functioning of ocean ecosystems is daunting, many will agree that a true ecosystem approach is needed if we want to predict, and eventually avoid, adverse shifts in marine communities.

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## The darting game in snails and slugs

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**Love darts are hard 'needles' that many snails and slugs use to pierce their partner during mating. In a few**

**species, darts have been shown to play a role in sperm competition. Two new papers, by Davison *et al.*, and Koene and Schulenburg, might further pique researchers' interest, because they show how the full potential of**

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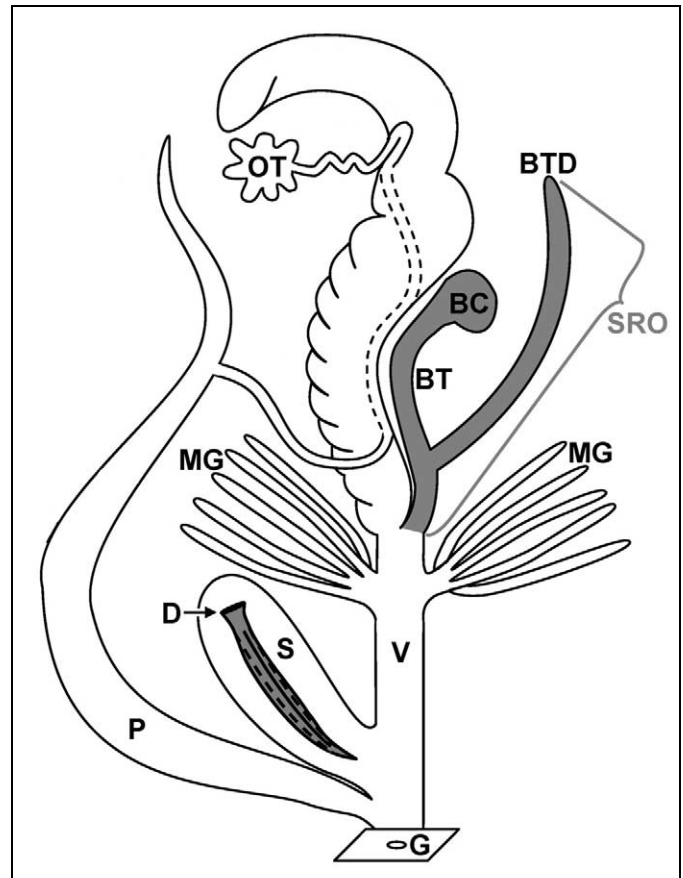
## darts can be tapped for studies of sexual selection in hermaphrodites.

### Hermaphrodite sex

Simultaneous hermaphrodite animals have the unenviable task of being a father and a mother at the same time. Because they unite female and male reproductive morphology and physiology within a single body, the orthodox views of sexual selection (i.e. females choosing males or vice versa) do not apply. For this reason, students of sexual selection have, for a long time, tended to ignore them. Recently, however, the realization has come that sexual selection does play an important role in hermaphrodite evolution [1]. As long as sperm are cheap and eggs are limiting, selection will favour those individuals with male reproductive systems that enhance the success of 'auto-sperm' (i.e. their own, outgoing sperm), and with female genitalia that can select from the foreign, incoming 'allosperm'. Although the need for compromise within a single organism can place limits on the strength of sexual selection [2], the abundance and diversity of extreme reproductive measures found in hermaphroditic animals suggest that sexual and sexually antagonistic selection are important factors in their evolution [3]. Most studies, however, have focused on single species and particularly striking structures and behaviours. A more analytical approach would be to apply phylogenetic reconstruction and comparative research across many species to gain a better understanding of the processes involved and how these are influenced by the ecological and behavioural idiosyncrasies of the species. Two new studies by Davison *et al.* [4] and Koene and Schulenburg [5] now take such an approach to understanding the evolution of 'love darts' in the hermaphroditic pulmonate snails and slugs (Gastropoda: Pulmonata).

### Stabs in the dark

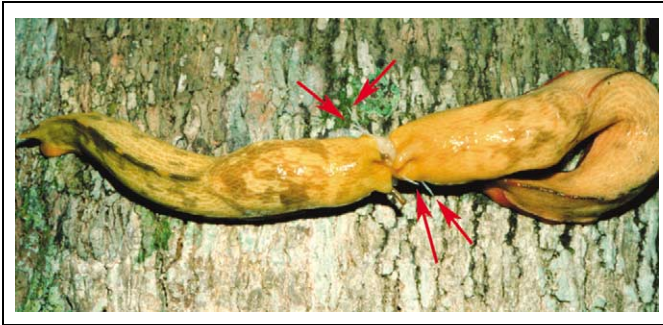
The list of unusual sexual behaviours that hermaphroditic molluscs engage in includes the penis chewing of *Ariolimax* [6], the entwining of the 70 cm-long penes of mating *Limax cinereoniger* [7], and the postcoital spermatophore-carrying of *Aeolidiella glauca* [8]. Best-known, however, is dart shooting. In many groups of terrestrial snails and slugs, the genitalia are equipped with a specialized organ, the dart-sac, in which a calcareous or chitinous love-dart is produced (Figure 1). Upon copulation, this long sharp dart can be forcefully pushed through the skin of the mate. Although darts have been documented in the literature since the mid-17th century, their potential evolutionary benefits have only been revealed during the past ten years. During copulation, partners place large spermatophores in the spermatophore-receiving organ (SRO) of their partner (the bursa copulatrix and/or its associated diverticulum). The spermatophore is then digested in the SRO, and only ~0.1% of the spermatozoa escapes via the spermatophore tail to the higher regions of the female reproductive system, where sperm storage and fertilization occur [9]. Ronald Chase and co-workers have shown that the use of



**Figure 1.** The reproductive system of a pulmonate snail. The common gonad (ovotestis; OT) produces eggs and sperm. Own sperm ('autosperm') are carried to the penis (P), whereas eggs are fertilized by incoming 'allosperm'. Allosperm are delivered into the vagina (V) as a spermatophore, which is stored and digested in the sperm-receiving organ (SRO, indicated in grey), comprising the bursa copulatrix (BC) and sometimes a diverticulum (BTD) to the bursa tract (BT). The love dart (D), produced and stored in the stylophore or dart sac (S), is shot by eversion of S through the genital pore (G). The mucus glands (MG) deposit a hormone on the dart before shooting. Reproduced and adapted with permission from J.K. Koene and [5].

the love dart (laced with hormones [10] from the dart sac-associated mucus glands) increases the number of escaping spermatozoa by inducing peristaltic movements in the SRO and by reconfiguring the copulatory canal [11]. Thus, by darting its partner, a snail can increase its chances of paternity [12].

The elucidation of the evolutionary background of love darts is, however, by no means the end of the story. Instead, it enables deeper investigation of the phenomenon, for dart shooting occurs in many ways, and the darts in many shapes and sizes. Some species have dart sacs, but no darts whereas others have multiple darts (Figure 2); some use them before penis intromission, others afterwards. In some groups, darts remain attached to the body of the shooter and are retracted and reused. In *Arianta arbustorum*, dart shooting is optional [13], but in other species it is obligatory, except for virgins [12]. The Japanese *Euhadra subnimbosa* uses its darts to stab its partner >3000 times during 22 min of 'foreplay' before copulation (Koene and Chiba, personal communication). The new papers by Davison *et al.* [4] and Koene and Schulenburg [5] now begin to address the many questions



**Figure 2.** Copulating *Trichotoxon heynemanni* from Kenya. Just before the photo was taken, each partner pierced the other with two darts, which can be seen protruding from their heads (indicated by arrows). Reproduced and adapted with permission from the Natural History Museum and Bernard Verdcourt.

related to the phylogenetic distribution and diversity of love darts and their deployment.

### Duelling with darts

Davison *et al.* [4] make use of a dichotomy in mating behaviour among pulmonates [14] to gain an insight in dart evolution. Whereas some species mate face-to-face (FF), others mate by shell mounting (SM), with the shells held parallel. FF is usually associated with flat or globular shells (or with slugs) and involves reciprocal penis intromission, whereas SM is found mainly in tall-shelled snails and tends to be associated with unilateral penetration. The authors reasoned that the reciprocal nature of FF means that mating species are potentially locked into an escalating cycle of sperm digestion and investment, which could promote the evolution of alternative responses, such as darts. In SM, the mating partners are more likely to assume their desired role: male if they already have sufficient good-quality allosperm, female if they have not mated for some time. Following this rationale, Davison *et al.* expected to find that darts were predominantly associated with FF mating. They tested this hypothesis by reconstructing a molecular phylogeny (based on nuclear rRNA genes) for 144 genera of pulmonates, and mapping shell shape, mating position (FF or SM), reciprocity, and the presence of darts onto the tree.

Their results show that darts occur in eight families (belonging to three monophyletic groups, the Philomycidae, Helicoidea, and Limacoidea, of which the latter two appear to be unrelated). Although this suggests that darts have evolved repeatedly, the deeper nodes of the tree are not well supported, which makes it hard to estimate how often this evolution has occurred. The evidence for the frequent loss of darts is clearer, however: several dart-less taxa fall within larger dart-bearing clades. More interestingly, all genera with darts are found in clades with FF mating. Snails that mate by SM never carry darts. The authors' prediction is thus borne out. However, some tall-shelled species in the SM group, such as the Achatinoidea, do mate simultaneously and reciprocally. Thus, it is possible that the causes for the origin and loss of darts are mechanical rather than (or in addition to) enforcement of reciprocity: in SM positions, darts might be shot too inaccurately. Mating position itself is strongly influenced by shell shape, which, in turn, is influenced by the habitat

of the snail. Thus, a complex chain of contingencies could underlie the evolution of darts.

### Cupid's workshop

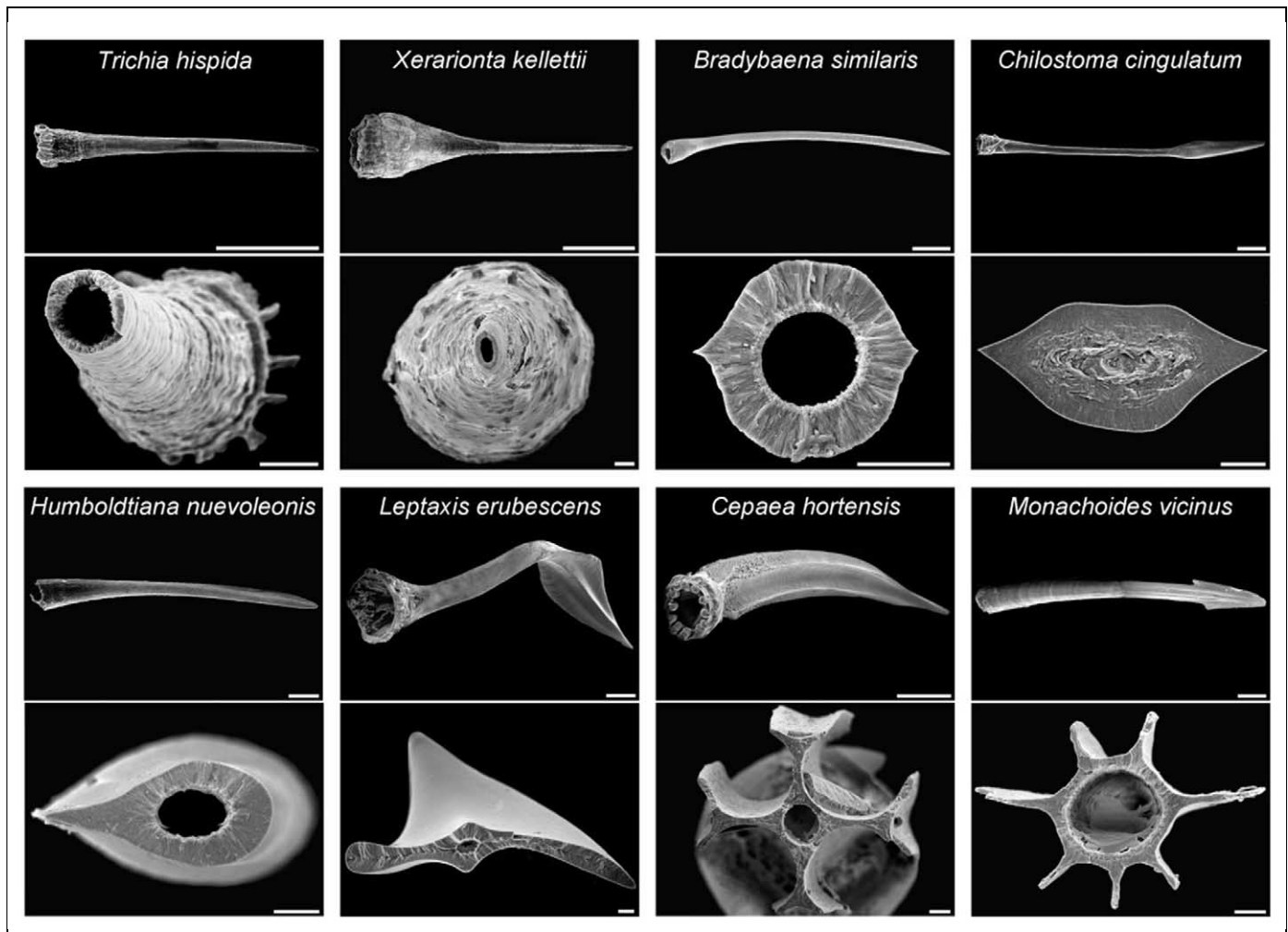
Koene and Schulenburg [5] focus on the Helicoidea, one of the three monophyletic dart-bearing groups identified by Davison *et al.* [4]. Koene and Schulenburg assumed that dart evolution is part of cycles of sexually antagonistic selection: darting benefits male function by increasing paternity, but it might hamper female function by preventing cryptic female choice. Several rounds of measures and countermeasures can thus be expected. In an attempt to reveal traces of such an arms race, the authors reconstructed a phylogeny based on the 28S rRNA region for 51 helicoid species. For each species, they studied several reproductive character complexes, including dart shape and number [which can vary wildly, as Koene's prize-winning scanning electron micrographs (Figure 3) show], but also, among other things, the complexity of the SRO.

Using Bayesian Inference and Shimodaira-Hasegawa tests (which test specific hypotheses of character evolution), the authors first show that most of these character complexes, including the darts themselves, have evolved repeatedly. Then, using phylogenetically independent contrasts, they demonstrate that correlations exist between character complexes, which can be interpreted as counteradaptation. For example, SRO complexity (in particular the presence of a diverticulum) correlates positively with dart shape (e.g. the presence of flanges) and mucus gland complexity. Flanges might make the transfer of hormones (produced and applied by the mucus glands) more efficient. A longer and more complex SRO might be an effective countermeasure to retain control over the sperm digestion and storage process.

### Conclusions

These two new papers give a further boost to the young field of sexual selection and sexual conflict studies in hermaphrodites. Future extensions of the work started by Davison *et al.* and Koene and Schulenburg could attempt a broader and deeper taxon sampling, to bolster the evidence (now only suggestive) of repeated origins and losses of darts. Attempts could also be made to prove, rather than infer, the ancestral states for morphological characters from the reproductive system. Furthermore, the wonderful evolutionary escalation in dart use in some groups of snails (such as the staccato darting in *Euhadra* or the evolution of 'disposable' darts from 'recycled' darts or vice versa) could be understood with the use of fine-scale phylogenetic reconstructions in selected taxonomic groups.

The usage of pulmonate snails and slugs for hermaphrodite sexual selection research need not stop with darts. As mentioned above, the malacological literature is filled with examples of bizarre and enigmatic sexual structures and behaviours. Interestingly, and contrary to expectation [2], these examples are concentrated in the hermaphroditic groups, whereas groups with separate sexes, such as the caenogastropod snails, have more orthodox reproductive behaviours. Rigorous comparative studies, such as the ones discussed here, can help in tapping the potential of



**Figure 3.** Cupid's armament. Scanning electron micrographs of love darts of eight different helicoids, shown in side-view and in cross section. Scale bars=500  $\mu$ m for side views and 50  $\mu$ m for cross sections. Reproduced with permission from J.K. Koene and [5].

pulmonate snails and slugs for studies of evolutionary biology, and could show that the presumed limits to the strength of sexual selection in hermaphroditic animals often do not come into effect. Having two sexes makes hermaphrodites twice as interesting.

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