animals that are positioned between annelids and chordates on the evolutionary tree (Figure 1), particularly groups with a contrasting organization of ventral musculature. These missing data need to be generated before we can be sure if this similarity is based on shared ancestry or convergence.

Only when similar mesodermal precursor cells are revealed at the ventral midline of animal groups that bridge the evolutionary distance between annelids and chordates or show different ventral mesodermal architectures (such as hemichordates, nemerteans, brachiopods, priapulids, flatworms) can we more confidently reconstruct that character in their stem species. Furthermore it remains unclear whether and how the genes expressed in the ventral mesodermal cells interact in annelids to specify and pattern the resulting structure. The data so far are only based on the combined expression of genes and not their functional interactions. Such functional studies would be critical, as only two transcription factors, *brachyury* and *twist*, are separating the combinatorial fingerprint of the mesodermal candidate cells from the neighboring cells of nerve cord in *Platynereis* (Figure 1).

Homology implies a common evolutionary origin and can only be discriminated from homoplasy — similar structures that do not share a common evolutionary ancestry — on the basis of a solid phylogenetic framework [3]. This comparative approach can tell us whether a common structure is evolutionarily conserved or whether it is convergent. It thus can help us to escape from being tricked into asserting common origin by superficial similarities. Although Lauri *et al.* [6] suggest a possible homology of the annelid 'axochord' and the chordate notochord, these two structures are not likely to be homologs. Many similarities the authors describe — such as similar developmental origin, position in the animal between nerve cord and blood vascular system and the function as stiffening tissue to which lateral muscles are attached — are probably homoplasies, as annelids and chordates are separated by multiple lineages that appear to lack such elaborated structures. The combinatorial gene expression in the cells that give rise to both structures may well play an early role in the specification of the ventral mesodermal precursors. However, the resulting structures (notochord, axochord) are a further developmental elaboration of these precursor cells and may be regulated by contrasting downstream effector genes, suggesting that the structures may have evolved convergently.

The significance of this debate should not be underestimated: if early bilaterians were small, simple animals with modest body plans, then subsequent bilaterian evolution was characterized by innovation, novelty and independent convergent evolution of complex body plans in several lineages [10]. However, if they were complex, as implied by homology of axochord and notochord or a complex central nervous system, then bilaterian evolution is defined by pervasive loss of morphological complexity in the majority of bilaterian lineages and conservation and modification in a few.

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[1]Sars International Centre of Marine Molecular Biology, University of Bergen, Norway. [2]Hopkins Marine Station, Department of Biology, Stanford University, USA.
E-mail: andreas.hejnol@sars.uib.no, clowe@stanford.edu

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Climate Change: Bees and Orchids Lose Touch

Spring temperature increases could differentially affect flowering times and pollinator flight periods, leading to asynchrony and reduced pollination. A specialist orchid–bee study combining herbarium, museum and field data shows that bee flight dates are advancing faster than orchid flowering, which could lead to significant future uncoupling.

Pat Willmer

Back in the 1970s and 80s, when we first began to wake up to the causes and predicted consequences of global warming, some biologists were already concerned that a warming world would gradually provoke the uncoupling of important species interactions. An upset to the delicate balances between partner organisms involved in mutualisms such as pollination or seed dispersal could occur in earlier and/or warmer springs through differential thermal effects on mobile animals (able at least in principle to move away from areas where the climate became unsuitable) and on sessile plants (whose ability to 'migrate' may operate on a much longer timescale). In turn this could potentially destabilise ecosystems and have severe knock-on effects for human food security. However, nailing down some real evidence for this particular climate change outcome has proved tricky, not least because it could require expensive and very time-consuming long-term monitoring programmes. As reported by Robbirt *et al.* [1] in this issue of *Current Biology*, though, we see the first tight demonstration of an uncoupling relationship.

In the last two decades there have been several papers speculating on why and how uncoupling might occur [2,3] and where it might be most serious, leading to species extinctions. The worst effects might occur in entomophilous plants with specialist pollinators, and those that flower in early spring. Field data from at least five decades do show that bees emerge earlier in warmer springs [4], with roughly linear temperature/phenology relationships. There are also suggestive data from experimental shifts in flowering time [5] or from modelling of floral availability [2] or range shifts [6,7] that might result from warming. However, ten bee species in North America showed no evidence for differential phenology change compared to the best available data for their preferred flowers [8]. Before we become too complacent on this point, though, we need to consider more specialist relationships [9]. Robbirt *et al.* now demonstrate that there are indeed worrying effects if the phenological data are improved, at least in one well-known specialist partnership; the famous orchid *Ophrys sphegodes* is advancing its flowering less rapidly than the solitary bee species (*Andrena nigroaenea)* it exclusively depends on for pollination, and the relationship can convincingly be projected to uncouple at present warming rates.

The authors chose their example wisely, as this well-studied species pairing represents one of the most specialist flower/pollinator interactions, with extremely precise signals by which the orchid flowers lure in their pollinating bees [10–12]. As in many orchids, the flowers resemble the females of the bee they want to attract in shape, size, and colouration, luring male bees to approach and attempt to mate with them in so-called ‘pseudocopulation’. During this the male bees, though getting no food from the flower, do inadvertently pick up the orchid’s pollen packages (pollinia) on their backs. So they are completely deceived but can potentially deposit pollinia in the next conspecific flower they hopelessly attempt to mate with. *Ophrys sphegodes* flowers go further than many such deceptive orchids, as they also faithfully mimic the complex scent of the female bees, emitting all but one of the 15 known compounds that females use as their own mate-attracting pheromones. And even more bizarrely the flowers also have an ‘off switch’; once pollinated, some of their scent emissions decline and a new specific volatile component (farnesyl hexanoate) is added, which female bees use to line their nests for egg-laying once they are mated [13]; so the signal to nearby male bees is then ‘don’t copulate with me, I’m already mated — go find a virgin bee’. Hence an orchid initially attracts a male but then sends later ones away once the job is done.

Such a system of deceptive rewardless pollination only works where the flowers are not too common and where the bees (or sometimes wasps or flies) are protandrous (males routinely emerging as adults before the females). Those first naïve males have no true partners to mate with or to compare with the temptingly offered flowers acting as ‘pseudo-bees’. So this offers unique opportunities to test potential effects of rising ambient temperatures; not only must the adult bee emergence match the timing of orchid flowering, but the male bees must also continue to emerge those crucial few days before females or the deception will break down.

Robbirt *et al.* show that the orchid already does show signs of earlier flowering and that the crucial bee pollinator will become progressively out of phase with the flower at both the species and gender level. Their evidence for advancing flowering time came from herbarium specimens [14], a resource now shown to limit the need for direct long-term monitoring [15,16]. Peak dates of specimen acquisition significantly correlate with midpoint flowering times, and prove to be valid proxies for field observations of peak flowering date [14]. Museum specimens of the bee (dating from the 1890s) also reliably map the bee’s activity period and show a significant change of peak flight date (supported by field records since 1975), with flight time advancing by around 11 days $^{o}C^{-1}$ mean spring temperature. Average warming of just 2°C thus leads to males flying earlier, but it also increases the proportions of early-flying females, since these prove more responsive to temperature change. Therefore, in a warmer spring there are more male bees flying before the flowers open (the orchids only achieve about 6 days earlier opening $^{o}C^{-1}$), and more female bees are also already emerged for them to mate with. The chances of a male then being fooled into pseudocopulation with an orchid clearly diminish progressively as warming continues.

Hard evidence that climate change is bringing explicit and measurable problems naturally disturbs pollination biologists but should also worry the wider conservation community, now so much more aware of pollination as an ecosystem service of global economic importance to biodiversity and to food security. The new data should help those urging stronger action to limit greenhouse gas emissions and resultant warming. How far less specialist interactions will become uncoupled does remain uncertain. But we cannot be complacent there: many pollinator–plant interactions are certainly less ‘generalist’ than often predicted from community-based network analyses, since flower visitors too readily assumed to be pollinating agents often turn out to be ineffective, with only a proportion of visitors being true pollinators ([17], and ongoing studies in my research group). Hence we must not assume that if many plants in a warming world lose their current pollinators other visitors will still do the job [3,18].

But there are further exciting angles that could be explored here if we consider effects of climate change beyond just phenology. It is likely that many aspects of an interaction will be susceptible to warming. For the plant, floral duration may change in warmer conditions. Floral appearance may also be affected, since transient thermal changes do alter petal colours, and longer term changes could reduce *Ophrys* flower mimicry with its female bees. Additionally, pollen production or germination may also suffer. For the bee, nesting sites may become restricted, and daily bee activity patterns are strongly thermally dependent [19]. And, most obviously, other flowers from which females acquire essential pollen and nectar will also be changing their flowering patterns. Perhaps most intriguingly, the *Ophrys* system is highly dependent on volatile signals to attract and control the pollinating *Andrena* bees. While flower shape and perhaps size may be relatively insensitive to climate change (especially raised temperature, and increased UV radiation), volatile emissions are sure to be affected, and the associations of scent and reward are learned particularly quickly by bees. Several aspects of the orchid flower scents could change with temperature [20]: rates of emission, the balance of components in the overall bouquet, and persistence in the air (thus over what range they can be detected).

Beyond the simple timing effects, then, even where the *Ophrys* flower and the male *Andrena* bees do still coincide in time and space seasonally we could expect to see daily pattern disruptions and increasingly confused visual and olfactory signals reaching the bees, potentially decreasing the location of and correct interaction with the flowers. In this and in most other plant–pollinator interactions we need to take a broader approach to understanding overall effects of climate change on probable outcomes.

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School of Biology, Sir Harold Mitchell
Building, University of St Andrews,
St Andrews, Fife, KY16 9TH, Scotland, UK.
E-mail: pgw@st-and.ac.uk

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Evolution: Conflict by the Sexes, for the Sexes

A study in spider mites confirms predictions that males and females come into conflict over optimal sex allocation when local mate competition affects sex allocation in haploidiploid species.

David M. Shuker* and Nicola Cook

Sexual reproduction is a contradiction. For species with two sexes, sex requires cooperation, not just for copulation, but for the many behaviours both before and after the passing of sperm from males to females. Not least, the mating partners have to resist any urges to eat each other. But not all species manage even this, and therein lies the contradiction. For all the cooperation that is required to allow males and females to come together to reproduce, sexual reproduction is also a hot-spot for male–female conflict, with males and females having different evolutionary interests in many aspects of reproduction, including where, when and how often to mate, through to who looks after the offspring and to what extent [1]. The tremendous scope for sexual conflict over reproduction decisions is both exemplified and extended by a groundbreaking new study by Emilie Macke, Isabelle Olivieri and Sara Magalhães [2] in this issue of *Current Biology*. They have shown how sexual conflict can arise over sex allocation in the spider mite *Tetranychus urticae*, revealing hitherto hidden influences of males over sex allocation.

The power to uncover sexual conflict over sex allocation — how sex and resources are assigned to offspring — in the work of Macke and colleagues comes from the clear theoretical predictions evolutionary biologists can make about how sex should be allocated amongst offspring. This is particularly true for sex allocation under local mate competition, first explained by Bill Hamilton in 1967 [3]. Hamilton realised that if females produce multiple offspring that develop and reach adulthood together — for instance wasps growing inside a fig or the body of a caterpillar, or juvenile spider mites feeding together on a plant — and if those offspring mate with each other before the daughters disperse to found