

tulates that sets of two “true” segments are incompletely fused to form “diplosegments.” In pill millipedes—short-body arthropods that roll up like armadillos—there is another complication due to the putative fusion of anterior dorsal plates (see the figure).

Developmental genetics had been completely silent about the mechanisms of millipede segmentation, until Janssen *et al.* analyzed segmentation in the pill millipede



Glomeris marginata (5). They report that segmentation genes in the dorsal and ventral sides of the embryo are expressed independently. They argue that the dorsal and ventral segments are independent units and not dorsal and ventral aspects of trunk segments or diplosegments. They discovered that the *wingless* gene is expressed in ventral segments only, whereas *engrailed*, *hedgehog*, and *cubitus interruptus* are expressed both dorsally and ventrally but in different expression patterns.

The major divergence from the developmental gene expression patterns of the fruit fly *Drosophila* and other arthropods is the dorsal expression of these genes, which is shifted by half a segmental unit that is delimited by intersegmental grooves in the growing embryo. In the pill millipede, gene expression seems to mark the posterior borders of the millipede’s dorsal plates. As these plates are mineralized (6), they may be analogous to the shell of mollusks, the margin of which is demarcated by expression of the *engrailed* gene (7). Dorsal expression of *engrailed* in the pill millipede could be related to biomineralization rather than to segmentation. This does not imply conservation of biomineralization from mollusks to arthropods, but rather provides evidence of repeated independent cooption of the *engrailed* gene among different phyla. Later in development, the dorsal and ventral segments of the pill millipede become aligned, giving rise to the serial organization of the animal’s trunk. In terms of function, the result is no different than if the trunk had been built out of a series of “true” segments. It is clear that the millipede body is not formed by serially adding complete segmental units one after the other. “True” segments simply do not exist, at least in this arthropod.

The Janssen *et al.* findings raise two interesting phylogenetic questions. First, are the independent expression patterns of segmentation genes found in the pill millipede

shared by other members of this group, including those with a more typical cylindrical shape (5)? The basal position of pill millipedes among the Diplopoda (8) supports this prediction.

Second, within arthropods, is segmentation in the pill millipede a primitive or derived event? I suspect that the mismatch in gene expression between dorsal and ventral segments is an ancient feature, particularly given the morphology of several long-extinct groups. It is possible that those Paleozoic arthropods with different serially repeated structures may eventually be grouped with millipedes in a clade that excludes other modern arthropods. Recent advances in arthropod molecular phylogeny make this a hypothesis worth testing (9, 10). A better understanding of segmentation mechanisms will enable the validity of the recently defined subphylum Myriochelata (the Chelicerata plus the Myriapoda) (9) to be tested. In members of this putative group, both extinct and extant, there is nothing comparable to the “textbook” segments regarded as the true building blocks of arthropod bodies. All of these animals share a series of in-

dividual features that are serially repeated along the main body axis. These features are not integrated into anatomically and functionally individual segments, as is usually the case in the insect thorax and abdomen. Far from being a primitive feature of arthropods, these units may be the product of historical changes in the genetic mechanisms of segmentation that have been fostered by the adaptive value gained from the different resulting morphologies (11, 12).

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EVOLUTION

Sex...Only If Really Necessary in a Feminine Monarchy

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The honey bee society was famously described as “The Feminine Monarchy” by the cleric Charles Butler in 1634. Honey bees and their relatives—including all hymenopteran societies—qualify for this label because their colonies are headed by one or a small number of fertile queens. These queens produce a large number of sterile or nearly sterile daughter workers and, later, with their assistance, produce a smaller number of fertile sons and daughter queens (1). The complex and diverse life cycles and social organization of the feminine monarchies are matched by their equally complex and diverse strategies for sexual and asexual reproduction (2). On page 1780 of this issue, Percy *et al.* (3) uncover a new dimension in the complexity of hymenopteran reproduction.

In the Hymenoptera, males are typically haploid and females are diploid (see the figure). It has been shown that sex is determined

by a highly variable sex determination locus such that homozygosity (a very rare possibility, given the low probability of a female mating with a male having the same allele as herself) or hemizyosity (expected in all haploid individuals) results in male development, whereas heterozygosity results in female development (4). In social Hymenoptera, virgin queens make nuptial flights during which they acquire sperm from one or more males and store and nurture the sperm in their spermatheca—a tiny gland that opens into the oviduct. Queens have perfect control over the sex of their offspring. To produce daughters, a queen lets sperm flow from the spermatheca into her oviduct and then lays fertilized diploid eggs. Whether the diploid eggs develop into sterile workers or fertile queens depends on the nutritional environment of the young larvae. To produce sons, however, a queen prevents the flow of sperm into the oviduct and lays unfertilized haploid eggs. Such parthenogenetic development of males—known as arrhenotoky—is a universal and well-known feature of the Hymenoptera. Less widely known (and apparently rather infrequent) is another form of

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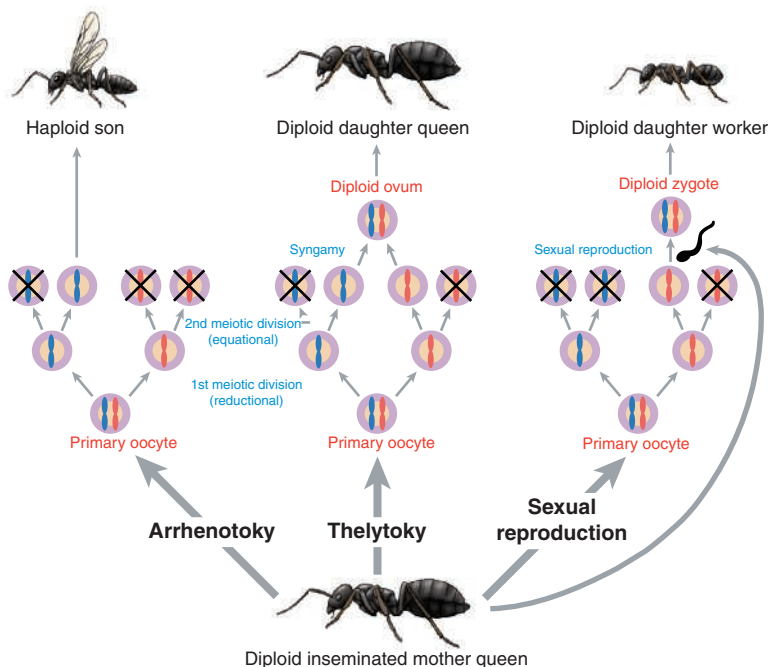
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parthenogenesis known as thelytoky, which permits the production of diploid daughters without the need for a paternal genome (1).

Thelytoky (of the kind referred to as automictic) involves the secondary fusion of two nonsister haploid nuclei after the meiotic second division. Automictic thelytoky restores diploidy and yet has the potential for maintaining heterozygosity at the sex determination locus, so that the sex of the resulting adult is female. Although thelytoky has been suspected as a minor form of reproduction in many species, it has been unequivocally demonstrated in one honey bee species (*Apis mellifera capensis*) and five phylogenetically distant species of ants. In all of these six cases, workers use thelytoky to produce diploid female offspring, even though they cannot mate. Thelytoky thus gives workers a degree of freedom from their queens, inasmuch as they themselves can produce both male and female offspring. For this reason, thelytoky may also be interpreted as an attempt by the workers to revolt against the hegemony of the queen, and as a potential early step in the eventual loss of sociality (5).

But what Percy *et al.* (3) have found in the European formicine ant, *Cataglyphis cursor*, is radically different. In this species, workers in orphaned colonies were already known to produce diploid female offspring (both workers and queens). Now it appears that queens themselves use thelytoky to produce daughter queens. The authors genotyped workers and queens collected from field colonies as well as laboratory-raised workers and gynes (queens) at four highly polymorphic microsatellite loci. Their results provide unambiguous evidence that perhaps a small fraction of the workers but certainly the large majority of laboratory-raised gynes (54 of 56 gynes studied) were produced by the queens through thelytoky. Confidence in thelytoky as the mode of production of the gynes arises from the fact that all of them only carried alleles that could be attributed to the mother queen. The probability that this could be the result of a chance mating of the queens with males carrying alleles identical to their own is estimated at less than 10^{-28} !

Apparently, then, *C. cursor* queens use arrhenotoky to produce male offspring, normal sexual reproduction to produce worker proge-



Diversity of reproductive strategies. The European ant *C. cursor* uses arrhenotoky to produce haploid sons, thelytoky to produce diploid daughter queens, and normal sexual reproduction to produce diploid daughter workers (3). The process of oogenesis results in one egg pronucleus and four polar bodies at the end of the meiotic second division. The polar bodies degenerate (indicated by an X). During arrhenotoky, the cell bearing the egg pronucleus develops parthenogenetically into a haploid adult male. During sexual reproduction, the cell bearing the egg pronucleus is fertilized by a sperm from the queen's spermatheca to produce a diploid zygote that develops into a female offspring, a daughter worker. In thelytoky, two nonsister haploid nuclei produced during the second meiotic division fuse secondarily to restore diploidy without the need for a paternal genome. The resulting diploid ovum develops into a viable female offspring, a daughter queen.

ny, and thelytoky to produce daughter queens (see the figure). The most striking consequence of this complex strategy, which the authors emphasize, is in the context of the cost of sex. Sexual reproduction involves a twofold cost because, relative to a parthenogenetic mother, a sexually reproducing mother transmits only half the number of her genes to each offspring (6). This genetic cost is thought (more precisely, hoped!) to be offset by the advantages of sexual reproduction in terms of enhanced genetic variability of the offspring. Such genetic variability is expected to be useful in dealing with variable environments—the physical environment to some extent, but biological environments such as rapidly adapting parasites in particular (7). *C. cursor* queens appear to forgo this benefit and save on the cost of sex while producing daughter queens, but reap the benefits of sex while producing daughter workers. Because workers are generally sterile and do not constitute a way for the queens to transmit their genes to future generations, the twofold cost of sex is irrelevant during their production. On the other hand, the benefits of sexual reproduction are expected to be profound. Workers are much more exposed than queens to different physical and biological environments. More important, genetic diversity among workers is known to facilitate efficient division of labor,

driven by a genetic predisposition for task specialization (8). Daughter queens, by contrast, are the mode for transmitting genes to future generations, making the twofold cost of sex entirely relevant during their production. Percy *et al.* (3) make the reasonable argument that queens are relatively protected from the environment, so that the lack of genetic variability may not be as serious a problem for them. In short, *C. cursor* queens seem to have the best of both worlds—they reap the benefit of sex where it is most needed and the benefit of thelytoky where it is most affordable.

If *C. cursor* uses such a wonderful strategy, why don't other social Hymenoptera do so? One possibility is that too few species have been studied in sufficient detail to conclude that this strategy is not more widespread (1). Alternatively, this may be an artifact of gyne production in the laboratory—an unlikely possibility but one that has not yet been ruled out. Perhaps the most

interesting possibility is that the luxury of mixing sex and nonsex in this way is not available to all. What then is special about *C. cursor*? Do their queens not need genetic variability, or do they mix sex and nonsex even while producing queens in nature? Genetic variability may, of course, be more important in some environments than others and more important for some species than others. There is also the intriguing possibility that the advantage of thelytoky for queens may be offset by the danger of such a powerful tool falling into the clutches of the workers, who could then use it for subversive purposes. Clearly, the time is ripe for theoretical and empirical investigations of a new paradigm: sex versus nonsex in the service of queens and workers.

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