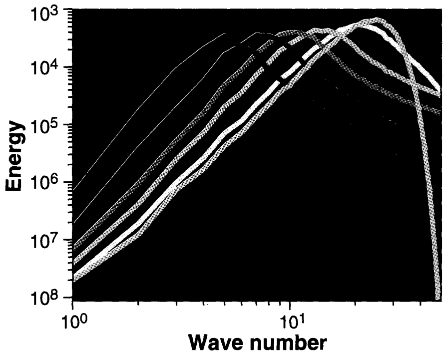
scope, to be launched in 2007, is expected to detect fields as weak as 10^{-9} gauss (*9*). Later missions are likely to detect even weaker fields. In the meantime, theorists are making ever more detailed predictions of the temperature and polarization signatures of a primordial magnetic field.

Particle physicists have come up with rather speculative processes, which may have generated huge magnetic fields during or just after inflation (the period of very rapid expansion before the universe was 10^{-30} s old) (*9*). These fields would have been diluted during the subsequent "normal" cosmological expansion, probably to something close to the detection limit of PLANCK. Initially, it was not clear how they could have any bearing on the question of large-scale magnetic fields. A field generated at such an early time would not exceed the scale of the horizon, which was just ~3 cm at 10^{-10} s. Such a field would now be at a scale of the solar system, ~10 orders of magnitude smaller than the scale of galaxies.

An unusual feature of turbulence physics may provide the answer. A random magnetic field can display an "inverse cascade" (*4*). This means that structures do not just split up into ever smaller scales, as in ordinary turbulence. Rather, the opposite happens. This is because in highly conducting fluids, in addition to total energy, another quantity is conserved: magnetic helicity, which measures the twist and mutual linkage of magnetic flux structures. Think of the field as being made up of helically polarized waves. There is a limit to how much magnetic helicity can be packed into a wave of given wavelength. If two helical waves interact, it is very hard to dispose of the helicity at small scales without violating magnetic helicity and total energy conservation. It is much easier to accommodate the magnetic helicity in a wave of larger wavelength.



Growth of magnetic structures. In this simulation, the spectral energy propagates to successively smaller wave numbers, that is, successively larger scales, as a result of inverse cascade turbulence. Red line, initial time; blue lines, later times (increasing from right to left).

CREDIT: ADAPTED FROM (*10*)

A dramatic example of such behavior is seen in a numerical simulation (see the second figure) (*10*). An initially random and helical magnetic field was left to decay through viscous and Joule dissipation. The dissipation happens mostly at small scales. At all other scales, magnetic energy gets pumped into progressively larger scales. These results suggest that we may well expect primordial fields at the scales of galaxies if the field has helicity (*11*). It remains uncertain whether the net magnetic helicity required to drive the inverse cascade comes mostly from the original field (*12*) or whether small helicity perturbations can grow to substantial levels.

The increase of the length scale of the primordial magnetic field will not be of much interest if its magnitude was small. Upcoming space missions will soon provide hard facts. If the field was weak, then the fields we observe today must have been generated later. On the other hand, if a strong field (expanded to a present-day value of 10^{-9} gauss) was present, then its detailed structure could be determined and interpreted, with important consequences for the theory of galaxy formation.

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PERSPECTIVES: EVOLUTION

Haploids—Hapless or Happening?

Sarah P. Otto and Philippe Jarne

In biology, it seems, there are exceptions to every rule, although sometimes finding these exceptions can be exceedingly difficult. Typically, animal cells are diploid, that is, they carry two copies of each chromosome, except during a brief phase when haploid gametes (sperm and egg) with half the normal chromosome complement are produced. Although haplodiploidy (haploid males and diploid females) has arisen many times during evolution, so far no animal has been found to exist exclusively in the haploid state (*1*). Enter the false spider mite *Brevipalpus phoenicis* on page 2479 of this issue, a daring exception to the rule that diploidy dominates (*2*). The discovery by Weeks *et al.* (*2*) that *B. phoenicis* exists only in the haploid state calls into question the dogma that diploidy has been selected for during animal evolution because of the fitness benefits it confers.

The false spider mite and its relatives *B. obovatus* and *B. californicus* reproduce by parthenogenesis, that is, females produce only female offspring from unfertilized eggs. The eggs and adult cells of these female mites contain two chromosomes, but it has been difficult to decipher whether the two chromosomes are unrelated, indicating a haploid state, or duplicates of each other (homologs), indicating diploidy. Weeks *et al.* prove that these two chromosomes are genetically distinct and conclude that the female mites are haploid. They found that only one of the two chromosomes contains a nucleolar organizing region, and only one carries an 18*S* ribosomal DNA gene (if the two chromosomes are homologs, they would carry copies of the same genes in the same locations). Furthermore, even though the investigators surveyed 45 clonal lines of *B. phoenicis* at seven highly polymorphic microsatellite loci, they were unable to find any individuals that carried more than one copy (allele) of a particular gene, indicating that these mites are indeed haploid.

How did these haploid oddities arise? Weeks *et al.* noticed that the eggs of *B. phoenicis* were laden with intracellular bacteria. Treatment with antibiotics led to loss of bacteria in roughly half the eggs. The infected offspring continued to develop as females, as expected, but the cured offspring developed into males! This ob-

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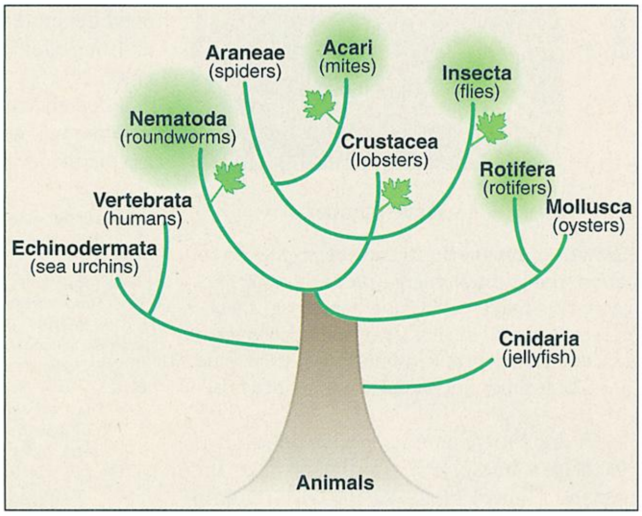
S. P. Otto is in the Department of Zoology, University of British Columbia, Vancouver V6T 1Z4, Canada. P. Jarne is at CEFE-CNRS, 34293 Montpellier Cedex 05, France. E-mail: otto@zoology.ubc.ca

servation is not as bizarre as it seems. Closely related mites (*B. russulus*) are haplodiploid yet reproduce sexually, indicating that haploid males must have been present among the ancestors of this group. Weeks *et al.* suggest that infection of a sexual haplodiploid ancestor with "feminizing" intracellular bacteria caused haploid eggs that normally developed as males to develop into females. The obvious culprit to suspect is the infamous intracellular bacterium *Wolbachia* (phylum Proteobacteria), which infects a variety of insect species, feminizing the males or killing them off (see the figure) (*3*). In the case of the false spider mite, however, *Wolbachia* is innocent. In fact, as Weeks *et al.* report, the bacterium infecting *B. phoenicis* is not even closely related to *Wolbachia*, but belongs to a different phylum (Cytophaga-Flavobacterium-Bacteroides) altogether.



The mighty mite. The false spider mite, *B. phoenicis*, is the first animal known to exist solely in the haploid state. In contrast, haplodiploidy (male haploids, female diploids) has arisen at least 17 times during animal evolution (groups highlighted in green). Intracellular bacteria that affect sexual development (especially *Wolbachia*) have been found in many of these haplodiploid groups (indicated by a leaf). The tree shape (but not branch lengths) is based on a molecular phylogeny of the animal kingdom (*14*). Examples of the different animal groups are given in parentheses. [The distribution of haplodiploidy and *Wolbachia* in the animal kingdom is presented in (*15*).]

Feminizing bacteria could have spread rapidly through the ancestral population of *B. phoenicis*. Because the bacteria cause all offspring of infected mites to develop into females, infected mites do not have to divide energy resources between sons and daughters. Thus, feminizing bacteria have enabled *B. phoenicis* to avoid the costs of sexual reproduction (*4*). Whether meiosis (cell division in which the chromosome complement is halved) is suppressed immediately in newly infected haploid females is still not known. If meiosis continues after infection, the lack of homologous chromosomes would result in aberrant chromosome segregation during cell division. Also unclear is whether infected female mites can reproduce sexually with haploid males that may arise intermittently. Haploid males must have existed during the initial spread of the bacterial infection and have been found in some field populations (*5*). Furthermore, in the laboratory, males can be readily produced by cultivating the mites at high temperatures or by treating them with antibiotics (*2*). Rare matings between infected females and cured males would dramatically increase genetic variability within an otherwise clonal population, especially if the resulting diploids are infected and produce haploid daughters without fertilization. In short, these haploid mites avoid the costs of sexual reproduction although they may occasionally indulge in sex, thus gleaning many of its benefits.

Why has it taken so long to uncover a case of haploidy among female animals? Given that haplodiploidy (haploid males, diploid females) has arisen repeatedly, one might expect to see animals with reverse haplodiploidy (haploid females, diploid males). Yet reverse haplodiploidy has never been observed, perhaps because it poses several evolutionary dilemmas (*6*). If haploid daughters were to inherit their father's genome, there would be strong selection on mothers to avoid producing such daughters, which lack the maternal genome. On the other hand, if haploid daughters were to inherit their mother's haploid genome, the female lineage would be entirely devoid of genetic recombination, giving rise to problems concomitant with asexuality (such as the loss of genetic variability). Furthermore, although the standard form of haplodiploidy enables an unfertilized diploid female to colonize new habitats and to produce sons with whom she can mate, reverse haplodiploidy provides no such benefit. It is intriguing that this first example of a haploid female animal involves feminization of haploid males rather than a reversal of the usual form of haplodiploidy.

Counterexamples to supposedly general rules can be extremely useful, especially when they reveal a false premise upon which the rule is based. The fact that nearly all animals are diploid has been taken as evidence for the inherent superiority of the diploid state, arguably because the extra copy of each gene masks the deleterious effects of mutations. This argument is specious, however, because haploid development is common in almost every other group of organisms (*7*) and because masking mutations allows mutant alleles to accumulate over time so that diploid populations generally have a lower long-term fitness. An alternative possibility is that diploidy became a "frozen accident" early in the evolution of multicellular animals, after which reverting to the haploid state became problematic (*8*). One can imagine that mechanisms evolved that restricted mitosis (cell division in which the chromosome complement remains the same) to diploid cells. An example of such a mechanism in mammals is the requirement for a balance between maternally and paternally imprinted genes. The discovery of female haploid animals, along with the fact that haploid males have evolved repeatedly (see the figure), demonstrates that there is no process that absolutely prevents animals from developing as haploids.

Another reason why the diploid state may have become "frozen" within animal groups is that haploids, when they arise, may perish immediately from the full impact of deleterious recessive alleles, which are masked but reach appreciable frequencies in diploid populations (*9*). In humans, for example, the frequency of these nefarious alleles is so high that any haploid offspring would carry twice the lethal load of these alleles and would die before reaching maturity (*10*); fortunately, unaffected copies of mutated genes allow us to survive. Plants express 60 to 70% of their genes during the haploid gamete-producing stage (*11*)—the expression of so many genes acts as a sieve, limiting the accumulation of recessive deleterious alleles. In animals, however, this sieve is thought to be virtually absent. Gene expression during the haploid gametic phase decreased dramatically in our protist ancestors when they evolved a compact sperm nucleus (*12*). Later, there was a further drop in haploid gene expression with the evolution of a metabolically quiescent egg, which subsists on gene transcripts produced primarily during an early diploid stage (prophase I) of meiosis. But some gene expression in the haploid state of animals does remain, even among vertebrates (*13*), albeit with considerable variability.

We need to compare gene expression patterns in the haploid and diploid states as well as mutation rates among mites and other animal lineages that have given rise

SOURCE: A. WEEKS

to haploid individuals. In this way, we may discover why haploidy has arisen in some, but not other, groups of predominantly diploid organisms.

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PERSPECTIVES: PALEOCLIMATE

Extending the Calibrated Radiocarbon Record

Edouard Bard

Since the 1950s, radiocarbon measurements have been used to obtain accurate dates for archaeological artifacts, climatic records, and other records of past events. While alive, organisms equilibrate with the atmospheric ^{14}C/^{12}C ratio, but when they die, the ratio starts to decrease as ^{14}C decays. The ^{14}C/^{12}C ratio of biological remains therefore correlates with their age.

It was originally assumed that the atmospheric ^{14}C/^{12}C ratio stays constant, but we now recognize that it varies with time. To calculate accurate ages, atmospheric ^{14}C fluctuations must be corrected for with a calibration curve obtained by comparing raw ^{14}C data with true calendar ages derived from independent dating methods. In principle, the radiocarbon record can be extended to ~50,000 years before present (yr B.P.), in the middle of the last Ice Age, but current calibrations only reach 24,000 yr B.P.

On page 2453 of this issue, Beck *et al.* (*1*) report a much needed radiocarbon record for 25,000 to 45,000 yr B.P. (*2*). During this period, large climatic swings occurred abruptly over periods of decades to centuries and sometimes lasted just a few millennia (*3*, *4*). Serious problems arise when we try to compare the timing of climatic changes observed in different types of paleoclimatic records from different parts of the world. For example, there is still no real constraint on the relative timing of major glacial surges (Heinrich events) into the North Atlantic and global sea-level variations between 25,000 and 45,000 yr B.P. Accurate ^{14}C dating is also crucial for evaluating the correlation between climatic events and variations in Earth's orbit around the Sun.

An accurate clock for 25,000 to 45,000 yr B.P. is also important in prehistoric archaeology (*5*). For example, some workers are convinced that Neanderthals overlapped chronologically with modern humans (*6*), raising the possibility of cultural and even genetic transfers. Other specialists claim (*7*) that the last technological and artistic development of the Neanderthals, the Chatelperronian culture, predated by several millennia the Aurignacian culture of the Cro-Magnon people, the first modern humans in Western Europe. Accurate chronological studies will help resolve this controversy and advance our knowledge about this major technological and social revolution.

A rhinoceros herd from the Chauvet Cave. Prehistoric paintings in this cave have been dated at ~31,000 ^{14}C yr B. P. This corresponds to ~38,000 calendar yr B.P. according to Beck *et al.*'s record (*1*), but only ~33,000 calendar yr B.P. using the Suigetsu record (*21*).

CREDIT: FRENCH CULTURE MINISTRY/DRAC RHONE-ALPES

Several approaches have been used to construct the ^{14}C calibration curve. For the Holocene (the past ~11,000 years), fossil trees are abundant, allowing a high-resolution atmospheric ^{14}C/^{12}C curve to be produced by comparing ^{14}C concentrations and tree-ring counts from the same tree sections (*8*). Unfortunately, this "dendrocalibration" cannot be extended much beyond the Holocene because trees are scarce during the preceding Late Pleistocene, a period characterized by an extreme glacial climate. Therefore, other types of records are used to extend the calibration, such as annually laminated (varved) sediments (*9*, *10*) and shallow-water tropical corals that can be cross dated by ^{14}C and uranium-thorium (U-Th) dating (*11*–*14*).

This international scientific effort has led to the periodic release of an "official" calibration curve, which represents a state-of-the-art consensus on this issue. The last of these updates, INTCAL98 (*15*, *16*), extends back to 24,000 yr B.P. with a relatively dense sample coverage (*16*). However, extending the record to older periods is difficult because residual ^{14}C concentrations in samples become extremely low, just a few percent of those in modern samples. Furthermore, old samples have often been altered by geochemical and diagenetic processes.

To extend the record, Beck *et al.* (*1*) measured and compared ^{14}C and U-Th ages obtained from a well-preserved stalagmite of the Bahamas. The backbone of their high-resolution record is a series of U-Th ages measured by thermal ionization mass spectrometry (TIMS) (*17*). The data reveal extremely large increases in ^{14}C concentrations beyond 30,000 yr B.P. (more than double the modern atmospheric ^{14}C/^{12}C ratio). These variations imply extreme, concomitant changes in the overall production of ^{14}C by cosmic rays and in its distribution among different reservoirs of the global carbon cycle.

High values of the atmospheric ^{14}C/^{12}C ratio between 30,000 and 40,000 yr B.P.

The author is at Centre Européen de Recherche et d'Enseignement en Géosciences de l'Environnement, CNRS-Université d'Aix-Marseille III, UMR-6635, Europole de l'Arbois, 13545 Aix-en-Provence cedex 4, France. E-mail: bard@cerege.fr