protozoa, such as those that cause sleeping sickness, leishmaniasis, and even malaria, predominantly reproduce clonally, which is, of course, of considerable medical significance. In May 1991, Tibayrenc returned to my lab, now at UC Irvine, for 14 months of additional research. We have continued collaborating to the present.

Are science and religion compatible? Evolution and religious beliefs need not be in contradiction. Indeed, if science and religion are properly understood, they *cannot* be in contradiction, because they concern different matters. Science and religion are like two different windows for looking at the world. The two windows look at the same world, but they show different aspects of that world. Apparent contradictions only emerge when either the science or the beliefs, or often both, trespass their own boundaries and wrongfully encroach upon one another's subject matter.

Could intelligent design be taught in the schools as an alternative to the theory of evolution? Intelligent design is not a scientific theory. It asserts, first, that organisms have been designed for certain functions and ways of life. Then, it adds that only an omnipotent Creator could account for their functional design. Science advances explanations concerning the natural world, explanations that are tested by observation and experiment. Intelligent design does not advance any scientific hypothesis that can be tested by observation and experiment (except for some negative claims that have been shown to be wrong). Intelligent design may be considered natural theology, which is what William Paley called it in his *Natural Theology* of 1802. It could be taught in history or religion classes, but not in science classes, because it is not scientific. The theory of evolution needs to be taught in the schools because nothing in biology makes sense without it.

You have said that intelligent design is incompatible with the religious belief in God: what do you mean? One difficulty with attributing the design of organisms to the Creator is that imperfections, dysfunctions, and cruelty pervade the living world. Consider the human jaw. We have too many teeth for the jaw's size, so that wisdom teeth need to be removed and orthodontists can make a decent living straightening the others. Would we want to blame God for this blunder? A human engineer would have done better. Evolution gives a good account of this imperfection. Brain size increased by natural selection over time in our ancestors. The remodeling of the skull to fit the larger brain entailed a reduction of the jaw, so that the head of the newborn would not be too large to pass through the mother's birth canal. More disturbing yet for intelligent design proponents has to be the following consideration. About 20 percent of all recognized human pregnancies end in spontaneous miscarriage during the first two months of pregnancy. This misfortune amounts at present to more than 20 million spontaneous abortions worldwide every year. Do we want to blame God for the deficiencies in the human reproductive system? Is God, as a matter of consequent fact, an abortionist on a monumental scale?

Who are your scientific heroes? Dobzhansky is one, as are two of his contemporaries, George Gaylord Simpson and Ernst Mayr. I came to know them first through Dobzhansky, when I was still a graduate student at Columbia University. I came to befriend them, although they were a generation older than me. Mayr and I had extensive discussions, and frequent but friendly disagreements, about evolutionary theory. Another hero was the philosopher, Karl Popper. In 1972, he attended a meeting I had organized and became a sort of mentor. Among them, Dobzhansky was the most tolerant of alternative ideas; he was never patronizing, not even when I was a graduate student.

What do you do for fun? Research and writing about science and related issues. I wake up every morning anxious to get to my office to work. I enjoy teaching. I travel a lot throughout the world lecturing at universities, but also enjoying the sights and art museums. I enjoy classical music, ballet and opera, and serve on the boards of various institutions dedicated to music. And I enjoy a good read: literature, history, art, criticism, and all sorts of essays.

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Quick guide

Orchid bees

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What are orchid bees? Orchid bees are a remarkable group of insect pollinators (~200 spp.) that occur exclusively in the lowland forests of the Neotropical Region. Most orchid bees are brightly colored and have an elongated proboscis for obtaining nectar from tubular flowers (Figure 1A). All species of orchid bees belong to a single monophyletic clade, dubbed Euglossini, which translates as the '*true long-tongued bees*'. Orchid (or euglossine) bees have fascinated biologists since the time of Darwin, mainly because of the intricate associations between male bees and the hundreds of plant species they collectively pollinate as they forage for fragrances.

Why do male orchid bees collect fragrances? Males of all species of orchid bees have unique, specialized structures for gathering and storing chemical fragrances (perfumes) that naturally occur in the bees' habitat, such as those from orchid flowers (Figure 1B). When a male orchid bee finds a fragrance source, it lands on its surface and spreads lipid secretions from its labial glands to dissolve the compounds that he will collect. This method is comparable to the so-called *enfleurage*, a technique that perfume manufacturers use to extract aromas from plant materials. Then, through stereotyped leg movements, the male bees transfer and store the oily fragrant mixture into specialized leg 'pockets' located in their enlarged hind tibia (Figure 1A).

Male orchid bees spend much of their lives accumulating perfumes, which include a wide variety of highly volatile terpenoids and aromatics. Later, during courtship display, the male bees expose their perfumes at perching sites. The bouquets are thus thought to act as exogenous pheromone analogues. It is believed that female orchid bees use the chemical information contained in the male perfumes as fitness indicators and/or conspecific signals to avoid

Figure 1. Orchid bees.

(A) Male orchid bee of the genus *Euglossa* gathering fragrances. The arrow indicates slit opening of enlarged hind tibiae where males store perfumes. Picture by Bernhard Jacobi. (B) Male *Euglossa* collecting fragrances from flowers of the orchid *Notylia.* Picture by Rodrigo B. Singer.

hybridization. Recent genetic analyses have shown that female orchid bees are singly mated, which is consistent with the idea of there being strong selective pressure on mate choice.

Male orchid bees accumulate species-specific perfume blends, and although their chemical composition varies geographically, conspecific males seem to share chemical motifs across wide geographical distances. A recent comparative analysis of fragrance evolution found that the qualitative and quantitative chemical composition of perfumes evolves rapidly during the early stages of lineage diversification. This finding suggests that perfumes may play a role in maintaining reproductive isolation among closely related lineages.

Did orchid bees coevolve with their orchid hosts? Among the lineages of flowering plants that have specialized in producing male-attractive fragrances in exchange for pollination services, approximately 85% of the species (~700 spp.) belong to the family Orchidaceae. However, whereas most orchid-bee-pollinated orchids depend exclusively on male bees for cross-fertilization, populations of orchid bees may actually persist in the absence of their customary orchid hosts. Male orchid bees can obtain fragrances from multiple sources besides orchid flowers, including flowers from at least ten different plant families as well as decaying wood, resin exudates, and fungi. It has thus been hypothesized that the evolutionary trajectories of orchid bees may have strongly influenced the diversification of their orchid hosts, but the contrary may not necessarily hold true.

Are orchid bees social? Approximately 20% of all bees (superfamily Apoidea) are truly social (i.e. eusocial), which means they exhibit overlap of generations, reproductive division of labor, and cooperative brood care. Although orchid bees form part of a monophyletic clade that includes honeybees, stingless bees and bumble bees, all of which are eusocial, they are primarily solitary nesters.

Female orchid bees can occasionally nest communally with other, usually related, females. In such cases, a foundress bee can overlap with her first offspring batch and impose reproductive skews by eating the eggs laid by her own daughters and replacing them with those of her own. On the other hand, male orchid bees typically leave the nest soon after they emerge and never return. Division of labor, as observed in truly eusocial insects, has not been documented among orchid bees. Two out of five orchid bee genera are obligate cleptoparasites (or cuckoo parasites) of other nest-building euglossine genera.

Do orchid bees sting? Female orchid bees, like the rest of the aculate Hymenoptera, have a sting apparatus, which evolved from modified ovipositor structures. Although quite painful, people rarely get stung by orchid bees, mainly because orchid bees are solitary and do not aggressively defend their nests. Also, most researchers work with stingless males, which can be easily lured to synthetic chemical baits.

Why should I care about orchid bees? The ecological impact of orchid bees in the Neotropical rainforests is immense. For instance, females of an individual species in the genus *Euglossa* from a single locality can pollinate up to 74 flowering plant species belonging to 41 different families. Moreover, female orchid bees can fly long distances (up to 23 km) when foraging for nesting materials and thus may promote cross-fertilization of flowering plant species with low population densities. Considering that orchid bees are abundant and present throughout virtually the entire Neotropical Region, euglossine bees are likely to figure among the most important clades of pollinators of the Neotropical flora, by far the most species-rich on Earth.

Where can I find more?

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Primer

The FEAR network

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Mitosis is governed by the oscillation of cyclin-dependent kinase (CDK) activity and ubiquitin-dependent proteolysis. Entry into mitosis is initiated by mitotic cyclin–CDK activation. Anaphase onset occurs upon activation of the Anaphase Promoting Complex/Cyclosome (APC/C), a ubiquitin ligase that promotes the destruction of the anaphase inhibitor securin. Destruction of securin initiates chromosome segregation by activation of the protease separase, allowing it to cleave a subunit of the cohesin complex, which holds the duplicated sister chromatids together. Upon completion of nuclear division, cells exit from mitosis, a process defined by the inactivation of CDKs, disassembly of the mitotic spindle, and cytokinesis. In the budding yeast *Saccharomyces cerevisiae*, a signaling network known as the FEAR network is critical to ensure accurate anaphase chromosome segregation and the integration of this process with other anaphase events. Here, we summarize what is known about the regulation and function of the FEAR network in budding yeast and discuss the potential for conserved FEAR network functions in other eukaryotes.

Control of late mitotic events in budding yeast

In budding yeast, cyclin B–CDK (Clb–CDK) activity drives the entry and progression through mitosis. Inactivation of Clb–CDKs is essential for exit from mitosis. In budding yeast, Clb–CDK inactivation is controlled by Cdc14, an essential phosphatase. Cdc14 promotes Clb–CDK downregulation by two primary mechanisms. Firstly, Cdc14 dephosphorylates the APC/C specificity factor Cdh1, thereby stimulating the APC/C-dependent destruction of Clb cyclins. And secondly, Cdc14 dephosphorylates the Clb–CDK inhibitor Sic1 and the transcription factor Swi5, resulting in the stabilization of Sic1 and Swi5-dependent activation of *SIC1* transcription. Furthermore, Cdc14 counteracts CDK activity by dephosphorylating a host of CDK substrates, allowing for the rapid resetting of cells to the G1 state. Cdc14 activation in late anaphase is controlled by the Mitotic Exit Network (MEN), a GTPase signaling cascade, and results in exit from mitosis (Box 1).

In addition to the essential role Cdc14 plays in Clb-CDK inactivation at the end of anaphase, there is growing appreciation for the ability of Cdc14 to modulate CDK activity in early anaphase. This important function of Cdc14 is mediated by the FEAR network (Cdc **F**ourteen **E**arly **A**naphase **R**elease network).

Cdc14 regulation

Cdc14 activity is tightly regulated. In cell cycle stages prior to anaphase, Cdc14 is sequestered within the nucleolus as a result of its association with its nucleolar-localized inhibitor Cfi1/Net1 (Figure 1). Upon separase activation and entry into anaphase, Cdc14 is released from the nucleolus and spreads throughout the nucleus and, to a significantly lesser extent, the cytoplasm. This early anaphase release of Cdc14 is mediated by the FEAR network and results in a pulse of Cdc14 activity that coordinates many of the anaphase events to be discussed below. FEAR network promoted Cdc14 release from the nucleolus is transient: in the absence of a functional MEN, Cdc14 becomes re-sequestered in the nucleolus during late anaphase and cells fail to exit from mitosis. While not essential, the FEAR network is crucial for the faithful execution of anaphase, as illustrated by the significant loss of viability of cells undergoing anaphase in the absence of FEAR network function. Cdc14 release from the nucleolus during late anaphase is promoted by the MEN (Box 1), which drives the sustained release of Cdc14 in both the nucleus and the cytoplasm and results in exit from mitosis.

The FEAR network

Work over the last eight years has identified a number of proteins that together function to regulate the release of Cdc14 from the nucleolus during early anaphase (Figure 1). These proteins, collectively known as the FEAR network, include