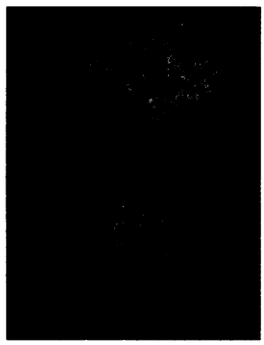
on the side of the seed that contains the embryo and then spreads to cover the whole thing, but in the mutants aleurone formation stops after covering only about half the seed. "This suggested that we were ... interrupting some signaling event involved in propagating the aleurone," says McCarty.



JUNE NASRALLAH/CORNELL UNIVERSITY

Ovule bound. Pollen tubes are growing in a crucifer pistil, but peptide signaling may prevent this if self-pollination occurs.

The current work, in which the team cloned *cr4*, supports that idea. The gene's sequence reveals that its protein has the overall structure characteristic of the receptor kinases seen in animal cells. Such receptors—which are so called because their inner segment is a kinase, an enzyme that can add phosphates to other proteins—often transmit developmental and other types of regulatory signals.

The portion of the CR4 kinase that probably protrudes from the cell and binds to some signaling molecule proved to be particularly interesting, Becraft says: It looks like the corresponding part of the receptor that, on animal cells, binds tumor necrosis factor. And because TNF is a polypeptide, containing some 157 amino acids, that similarity suggests that CR4 also binds a peptide. Becraft cautions, however, that until that peptide is found it's just "a hint at a possible peptide signal."

Other systems are providing similar hints, as several additional receptor kinase candidates have been identified in plants. Two of these so far have also been linked to plant development. One is encoded by the *Erecta* gene of *Arabidopsis thaliana*, which helps determine the shape of the plant's leaves and flower clusters and has been cloned by Keiko Torii of the University of Tokyo, Norihiro Mitsukawa of the Mitsui Plant Biotechnology Research Institute in Tsukuba, Japan, and their colleagues. (The results appear in the April issue of *Plant Cell.*) And in as-yet-unpublished work Steve Clark of the University of Michigan, Ann Arbor, has traced another developmental mutation in *Arabidopsis* (*Clavata 1*)—this one resulting in an abnormally thick stem and extra flower parts—to a gene encoding a protein that appears to be receptor kinase.

Still other plant receptor–like kinases have nondevelopmental functions. For example, the one encoded by a gene called *Xa21*, which was cloned last year by a team led by Pamela Ronald of the University of California, Davis, confers resistance to an important rice pathogen, the bacterium *Xanthomonas oryzae* pv. *oryzae* race 6 (*Science*, 15 December 1995, p. 1804). And a kinase encoded by a gene in the self-incompatibility (S) locus of plants in the crucifer family, which includes broccoli, cauliflower, and *Arabidopsis*, is needed to prevent the plants from self-pollinating. Work by June Nasrallah's team at Cornell University indicates that the S locus receptor kinase (SRK) detects a signal—presumably a peptide made by pollen—that tells the cells on the pistil, the female reproductive organ, to block pollen grains from the same plant from adhering and forming pollen tubes.

While all the other investigators who study possible peptide signaling in plants have identified only signaling peptides or receptors, never a matched pair, Nasrallah says she has a strong candidate for the SRK ligand. This is a protein, also encoded by a gene within the S locus, that is expressed only in the anther, the male organ that produces the pollen. "It has the right smell for a ligand," Nasrallah says, "but we're still in the process of determining whether it is."

Just how such a peptide signal might cross the cell-wall barrier is still a mystery, although molecular "ferries" may aid in the transport. The Nasrallah team has found that still a third gene in the crucifer S locus encodes a protein that accumulates in the cell wall and has a sequence very similar to that of the extracellular portion of SRK. She proposes that this protein may bind whatever ligand a pollen grain uses to signal its presence and shuttle it to SRK itself.

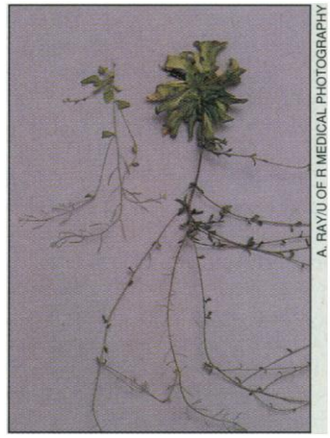
Further work will be needed to confirm that picture, and also to pin down the missing ligands for the other receptor kinases. But already it seems that investigators are on the verge of listening in on a new and unexpected language of plant-cell communication.

–Jean Marx

PLANT EVOLUTION

Probing Flowers' Genetic Past

Mother Nature did some major redecorating early in the Cretaceous period, about 120 million years ago. That's when the first angiosperms—plants whose reproductive structures are showcased inside flowers—appear in the fossil record. But while botanists have long believed that angiosperms evolved from simpler nonflowering plants, their understanding of the gene changes that gave modern angiosperms the ability to make petals and other floral organs has remained rudimentary. Now studies of a unique mutation in the weed *Arabidopsis thaliana* have uncovered what may be a living record of plants' leap from drabness to floral glory.



A. RAYUU OF R MEDICAL PHOTOGRAPHY

Late bloomer. Plants without *SIN1 (right)* grow extra leaves and stems before flowering. Plant at left is normal.

Plant evolutionists believe this transition came about when some of the genes controlling the development of female ovules, or eggs, began moonlighting as flower-building genes, helping transform the seed-bearing leaves of earlier plants into leaflike floral organs such as sepals and petals. In that case, some of the genes that give form to ovules in modern angiosperms should retain this double duty, helping to switch on flower growth at the appropriate time spurring the growth of specific flower parts. But botanists hadn't found any examples of the hypothetical timekeeping genes—until the current work.

In the September issue of *Development*, a research team lead by Animesh Ray of the University of Rochester in New York reports that an *Arabidopsis* gene called *Short Integument* (*SIN1*) plays a key role in regulating both the development of ovules and the time of flowering. "We know so little about angiosperm evolution," says Detlef Weigel, a developmental geneticist at the Salk Institute in La Jolla, California. "If *SIN1* does turn out to be the first gene to act on both [ovules and flowering time], that would be very nice."

One part of *SIN1*'s activity—its role in ovule development—has been known since 1992, when breeding studies by Harvard University plant geneticist Robert Pruitt showed that plants in which both copies of the gene are mutated have poorly formed ovules, rendering them sterile. But Ray, a molecular biologist, suspected that the gene might be doing much more. He observed that these mutant specimens also have many more leaves, are taller, and take much longer to flower than normal plants. That indicated that the plants' meristems, regions of rapidly dividing cells at the tips of growing shoots that give rise to all of the plant's specialized

organs, were spending too much time in their first two developmental stages: the vegetative phase, when they build leaves, and the inflorescence phase, when they build the stems that will later bear flowers.

At first, Ray didn't suspect that the mutation was having a direct effect on flower-building. He thought it might simply be altering the plants' response to changes in day length, which normally trigger flowering. But he found that short-day conditions led to a similar slowing of growth in normal and mutant plants, an indication that the mutants' responses to day length were intact. Next, Ray and colleagues Jean Lang, Teresa Golden, and Sumita Ray crossed the mutant plants with other mutant strains to test whether the protein encoded by *SIN1* is a required component of some other regulatory pathway known to affect the timing of flowering. The results suggested that it isn't.

For example, investigators had already identified a gene called *Terminal Flower 1* (*TFL1*)—because mutations in the gene produce plants in which the central meristem is capped by a flower rather than remaining indeterminate—that apparently suppresses the expression of floral organ-building genes such as *LFY* and *AP1*. The transition from stem-building to flowering occurs when still other genes down-regulate *TFL1*, increasing expression of the flower-building genes. But plants bred to have mutations in both *SIN1* and *TFL1* produced 19 leaves on average, as opposed to six for plants with a mutation in just *TFL1* and 25 for those with a mutation in just *SIN1*. This intermediate result indicates that there is no direct interaction between the two genes. And that leads Ray to speculate that *SIN1* is a master timekeeper gene—hurrying the meristem on its journey toward flowerhood by regulating its ability to respond to other genes, such as *LFY*.

Ray is hoping to test this timekeeper hypothesis by cloning the gene. With both the gene and its protein product in hand, the researchers will be able to chart exactly when and where the gene is expressed during development—and whether its activity shows a telltale overlap with that of other genes involved in flower development. "If one found similar expression patterns," says Weigel, "that would certainly make a very strong point" that ovules set the pace for flower development—in the Cretaceous and every time an angiosperm blooms today.

–Wade Roush

PALEONTOLOGY

Viewing Velvet Worms in Amber

Paleontologists are accustomed to piecing together an animal's evolutionary history from fragmented clues. But there are times when the dots are too far apart for even a paleontologist to join. That is the case for velvet worms, odd little invertebrates that look like rolled Persian carpets with legs and may represent an evolutionary link between annelids, the familiar segmented worms, and the wildly diverse arthropods, the phylum that includes insects. Today velvet worms, or onychophorans, are land dwellers up to 15 centimeters long that roam the forests of the Southern Hemisphere. In contrast, the fewer than 30 known velvet worm fossils are mostly marine, all from the Northern Hemisphere—and all are at least 300 million years old. That leaves a wide gulf in space, time, and lifestyle for paleontologists to bridge.

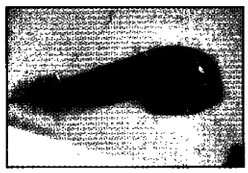
A report on page 1370 "fills in part of that gap," says Doug Erwin, a paleontologist at the National Museum of Natural History. In it, entomologist George Poinar of Oregon State University describes two velvet worm specimens entombed in chunks of amber, 20 million to 40 million years old, from the Baltic region of Europe and the Dominican Republic. The finds don't settle the problem of the velvet worm's family relationships. But the locations of the discoveries, and the fine details of the onychophoran head and appendages on view in the amber, offer what Erwin calls a "wonderful view" of worms that are intermediate in time between the ancient fossils and living animals.

Previously known onychophoran fossils come from sites with spectacular preservation of soft-bodied animals, such as the 530 million year old Burgess Shale of British Columbia and the 300 million year old Mazon Creek formation of Illinois. All of the fossils are found in marine rocks, although the Mazon Creek sediments were deposited close enough to shore that the animals may have washed in from land. All recent velvet worms, however, are unambiguously terrestrial and have a critical adaptation for life on land: a slime pore that squirts a sticky substance used both to entrap prey and fend off predators. And they live on the opposite side of the world from their ancestors, inhabiting forest floors throughout the Southern Hemisphere.

The 40 million year old Baltic fossil, likely the older of the two, provides the first solid example of onychophorans on land and, because it is from northern Europe, proves that terrestrial velvet worms did indeed once roam the Northern Hemisphere. This suggests that unless the animals managed to adapt to land twice, terrestrial forms evolved while all the continents were connected, before the breakup of the supercontinent Pangaea about 180 million years ago, says David Briscoe, a velvet worm expert at Macquarie University in Sydney, Australia. And the dates on the new fossils show that onychophorans survived in the Northern Hemisphere for more than 140 million years before mysteriously becoming extinct.

The fossil from the Dominican Republic, meanwhile, displays an intriguing combination of primitive and modern features, says Poinar, with the head of modern velvet worms but legs that resemble ancient forms. Modern velvet worms walk on fluid-filled legs ending in "feet" with roughened pads and claws. In contrast, the legs on the ancient fossil onychophorans—and the Dominican fossil—sprout claws but show no evidence of distinct feet, Poinar says. But the Dominican fossil apparently possessed slime pore glands on its head, as modern worms do. In fact, Poinar found thick deposits extending from openings on the head, which he theorizes contain the slime expelled when the worm found itself caught in the amber-forming tree sap.


D. ERWIN


G. POINAR


J.W.O. BALLARD

Bridging the gap. The gulf between ancient velvet worm fossils *(top)* and the living animals *(bottom)* may be bridged by new specimens trapped in amber.

The obvious next step in exploring velvet worm evolution is to sample the fossils' DNA, which the amber may have preserved. Poinar says he prefers to wait until more specimens are found, however, for such sampling can be destructive. But without such genetic data, other paleontologists note that even with the new fossils, the record of velvet worms is just too sparse to draw an evolutionary chain from 300 million years ago to the present. Briscoe and Macquarie colleague Noel Tait say that the amber specimens may be a side branch that broke off shortly after the move onto land. "With this kind of group all you get is little snapshots occasionally," Erwin says. But at least now researchers have a couple of exceptionally clear snapshots to study.

–Gretchen Vogel