sphere's Cl would have to be collected for a long-term effect. The conversion of power to ionization would be below unit efficiency, and the amount of Cl collected would be less than the number of Cl$^-$ ions produced. In fact, Wong *et al.* (1) show that in a laboratory experiment the ionization density must be 20 times the density of Cl molecules in order for O_3 remediation to occur.

Weight is another problem if one is going to remove Cl from the stratosphere. The stratospheric Cl content is equal to 2.4×10^9 kg. Removing the Cl would require transporting at least this mass from the stratosphere to the ground. If the Cl were in any form other than Cl or Cl_2, transporting even more weight would be required. One of the proposed schemes (6) requires releasing positively charged water molecules to balance the release of negative charge. This scheme would require even more weight to be transported because many water molecules are needed per charge in a multiply charged droplet. Additionally, much of the water may evaporate in the atmosphere, thereby not only increasing the weight that must be transported but also humidifying the atmosphere.

Perhaps a simple way of looking at these weight and energy problems is to realize that in the remediation scheme, a large fraction of the world's total accumulated production of chlorofluorocarbons must either be tied up as negative ions or collected by processes performed on either airplanes or balloons. Another potential problem is that ionization in air often produces large quantities of radicals such as nitrogen oxides and OH. The amount of radical production is usually orders of magnitude greater than the amount of ion production. The production of such radicals would also increase the energy required, resulting in reduced efficiency of Cl$^-$ production as well as seriously altering the neutral chemistry of the stratosphere.

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Use of a Sound-Based Vibratome by Leaf-Cutting Ants

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Leaf-cutting ants harvest fresh vegetation that they then use as food for symbiotic fungi. When cutting leaf fragments, the ants produce high-frequency vibrations with a specialized organ located on the gaster. This stridulation behavior is synchronized with movements of the mandible, generating complex vibrations of the mandibles. The high vibrational acceleration of the mandible (up to three times the gravitational force at peak acceleration at about 1000 hertz) appears to stiffen the material to be cut. An identical effect is achieved when soft material is sectioned with a vibratome. This hypothesis is supported by experiments simulating the cutting process with vibrating isolated mandibles: When tender leaves were cut, the vibration of the mandible reduced force fluctuations and thus permitted a smoother cut to be made.

Leaf-cutting ants harvest fragments of leaves on trees and bushes (1). During the cutting process, the ant anchors herself to the leaf edge by her hind legs and pivots around them while cutting with her mandibles arcs out of the leaves. The sizes of the harvested fragments depend on, among other parameters, the size of the forager, the quality of the leaf, and the harvesting situation of the colony (2). Depending on the size of the fragment being cut, an ant performs approximately 20 to 50 single bites for collecting a single piece of leaf.

It has been observed previously that leaf-cutting ants stridulate during the cutting process and that the produced sound, in the form of substrate-borne vibrational signals, attracts nest mates to the cutting site (3). Stridulation is produced when the ant moves her gaster up and down, so that a cuticular file located on the first gastric tergite is rubbed against a scraper situated on the postpetiole (4). These vibrations are conducted into the leaf through the ant's mandibles and legs (3). Because most of the energy is transmitted through the mandibles, we investigated whether these vibrations facilitate the cutting process in the manner of vibratomes (5), which are instruments frequently used for histological preparations. In order to obtain smooth and very thin sections of soft material, the cutting knife in a vibratome vibrates (6). The vibratome then accelerates and thereby stiffens the object to be cut. This has an effect similar to hardening the material by freezing or by chemical fixation.

In *Atta cephalotes*, the two mandibles play different roles during the cutting pro-

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cess: While one mandible is actively moved, the other remains almost fixed (cutting mandible). The steps in one bite are as follows (Fig. 1A): The motile mandible is opened (abducted) and anchored with its tip to the leaf tissue. The cutting mandible is not abducted, but held steady. As a result, the cutting edge of this mandible describes an angle of 70° to 90° with the leaf surface; it touches the rim of the leaf roughly at its middle point (Fig. 1). During the opening of the motile mandible, the cutting mandible is pushed against the leaf by lateral head movements. Next, the motile mandible is closed (adducted), pulling the cutting mandible further against the leaf, which increases the incision (Fig. 1A, 1 to 3). In this phase also, the adducting mandible moves deeper into the leaf surface, thus preparing the way for the cutting mandible. As soon as both mandibles meet (Fig. 1A, 4), the cycle starts again by abduction of the motile mandible (Fig. 1A, 1). During the cutting process, the foreleg ipsilateral to the cutting mandible is anchored on the leaf margin and pulls up the fragment being cut, which probably results in an increased mechanical tension of the leaf tissue.

Motile and cutting mandibles, the "teeth" of which are hardened by zinc (7), are morphologically indistinguishable. Individual ants use both right and left mandibles as the cutting mandible and switch between them without any identifiable pattern. A different cutting technique is used, however, when an ant encounters a thick vein: She grasps the material with both mandibles and moves her entire body from one side to the other to sever it.

We analyzed the temporal relation between mandible movements and stridulation by videotaping the cutting behavior and simultaneously recording the vibrational signals from the leaf surface with the aid of laser vibrometry (8). The ant did not stridulate continuously (Fig. 1, B and C). Stridulation occurred most often when the mandibles were closing (Fig. 1C). This pattern was the same regardless of the kinds of leaves cut: tender privet leaves (9), tough *Prunus laurocerasus* leaves (9), or tulip floral petals.

In order to obtain detailed measurements of the mandible vibrations caused by stridulation, we mounted ants at the thorax, so that their heads remained fully movable. Ants tethered in this way frequently stridulate (4). Two laser vibrometers (8) that make use of the Doppler effect and were aimed at the mandibles of the ant (we investigated five individuals) showed that each mandible performed a complex, three-dimensional vibration, with the major movement component in the long axis of the mandible (Fig. 1, D, F, and G). To test the effect of such vibrations on the mechanical quality of the cutting procedure, we imitated this process with isolated mandibles ($n = 14$). In each case, one mandible was mounted on top of a calibrated force meter (8) that in turn was attached to a vibrator. It moved the mandible against the edge of a leaf held by crocodile clips (Fig. 2A), so that the movements resembled those of the cutting mandible during a naturally occurring cut as shown by video analysis (that is, 1.5 s for the closing of the mandibles and 0.5 mm for the cutting depth with a sinusoid time course between zero and maximum) (Fig. 2B, 4). With a second vibrator, the mandible could be vibrated with oscillations either parallel or perpendicular to the mandible's edge (Fig. 2A). The mandible vibrated during the entire cut. In separate cuts, we tested frequencies from 800 to 1200 Hz and a peak acceleration of 15 m/s^2 (Fig. 2B, 1; for comparison, see naturally occurring parameters in Fig. 1, D and E).

In this way, we were able to compare the forces developed during the leaf-cutting with a vibrating ("stridulating") and a nonvibrating mandible, using both tender and tough privet leaves, tulip floral petals, and fiber bundles of *P. laurocerasus*. We tested not only the initiation of a cut at the edge of the leaf, but also the continuation of an already existing incision. Pushing the nonvibrating mandible against the edge of a

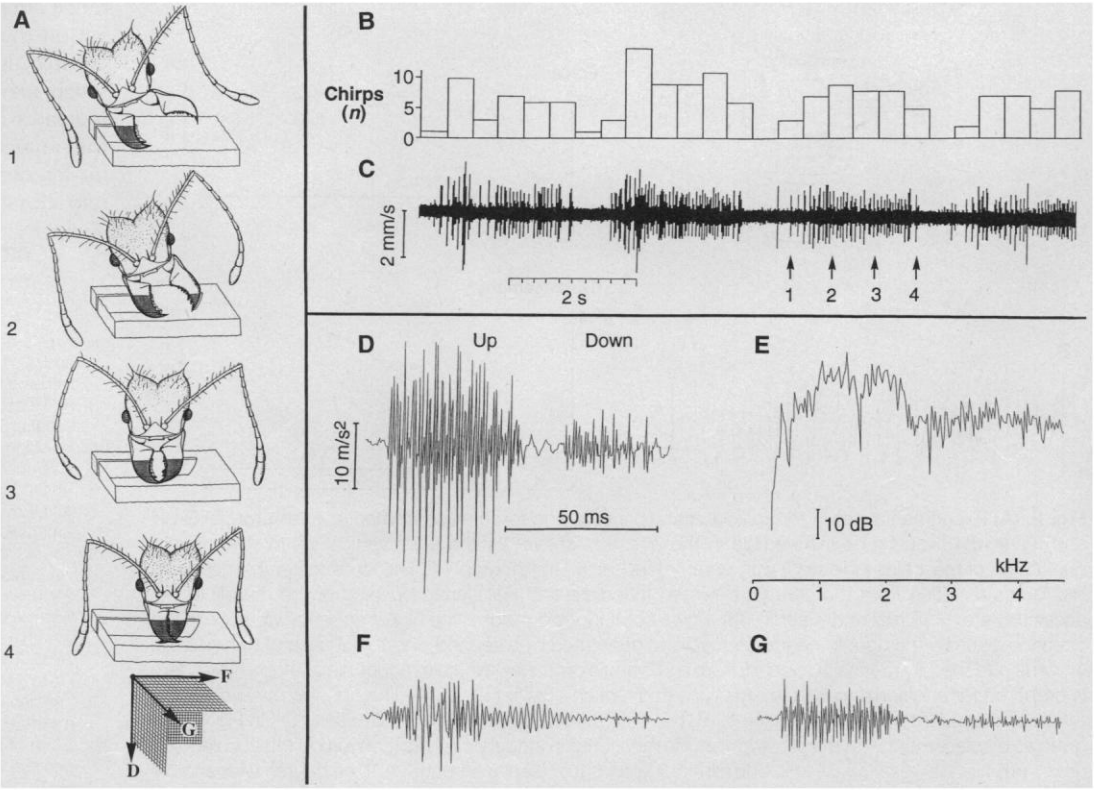

Fig. 1. Mandible and head movements, stridulation, and mandible vibration during one "cut" into a tender leaf. (**A**) Head and mandible positions as well as the incision into a leaf from the beginning (1) to the end (4) of one single bite. For the time intervals between the four stages, see the arrows in (C). Note that the long incision results from the cutting mandible but also that the motile mandible makes a short cut. (**B** and **C**) Stridulation during four bites. In (B) is shown the number of chirps counted at a bin width of 400 ms. The arrows denote the temporal occurrence of the four cutting stages shown in (A). In (C) is shown original laser vibrometry (Doppler) of stridulations on the leaf, measured 2 cm away from the head of the animal. Each spike is a complete chirp as shown in (D), (F), and (G), measured as the velocity of the leaf surface. (**D** through **G**) Vibration of the mandible in the three spatial axes shown in (A) as caused by the stridulation. The original laser data (velocity) were converted into acceleration, which is the relevant quantity for stiffening the leaf to be cut. One single chirp (stridulation) is plotted for each direction [compare with temporal resolution in (C)]. The fast Fourier transform spectrum (for the short nonperiodic signals, we used a "uniform window") for (D) is given in (E) (beyond 2.5 kHz the signal vanishes into the noise). In (D), "up" and "down" denote the stridulatory up and down movement of the gaster, which can also be identified in (F) and (G). Calibration bars in (D) are also valid for (F) and (G).

tender leaf revealed the following: The leaf tissue was first compressed and slightly vaulted as the mandible moved forward, which caused an increase of the exerted force, until suddenly the tissue broke with a subsequent release of the force. These "force jumps" covered a range of 10 to 30 mN. This sequence can occur up to three times during a single "bite" (Fig. 2B, 2, dotted line). However, when the cutting mandible vibrated, either in direction "D" or "G" (Fig. 1A), the force fluctuation was significantly attenuated down to maximally 5 mN (Fig. 2B, 2, solid line)—that is, the force exerted by the mandible remained relatively even during the cut through the leaf tissue. This effect was especially obvious when tender leaves were cut. With tough leaves, fiber bundles, or the thick basis of floral petals, such force fluctuations were much weaker or totally absent, even without additional mandible vibrations. In such cases, high-frequency oscillations did not have a noticeable effect on the force dynamics during the cutting process (Fig. 2B, 3). In general, however, considerable variability in the time course of forces was found, mainly depending on the texture of the leaf being cut. Yet, the basic pattern remained for each kind of tissue, whether at the beginning of the cut at the leaf edge or at the continuation of an already advanced incision inside the leaf.

The same mechanical principles found in the leaf cutting of *Atta* appear to apply to vibratomes used for histological preparations. Smooth sections with a vibratome are best obtained with knives moving elliptically in the plane of the knife blade (*6*). In our experiments, therefore, the force output during cutting might have been even steadier if we could have vibrated the mandible simultaneously in three directions as it occurs in stridulating ants. The vibratome effect does not necessarily increase the energetic effectiveness of leaf cutting. Cutting speed in ants that were stridulating (averaging 0.22 ± 0.09 mm/s) and nonstridulating (averaging 0.23 ± 0.08 mm/s) proved to be similar. Even if we would have found a significant difference, it would be impossible to distinguish between enhanced cutting efficiency that was a result of stridulation and that which was a result of more intense mandibular activity during cutting; both factors would positively influence cutting speed and are expected to be strongly correlated. The vibratome, however, resolves a biomechanical problem by making possible the smooth cutting of tender leaf fragments, the most desirable harvest for the ants.

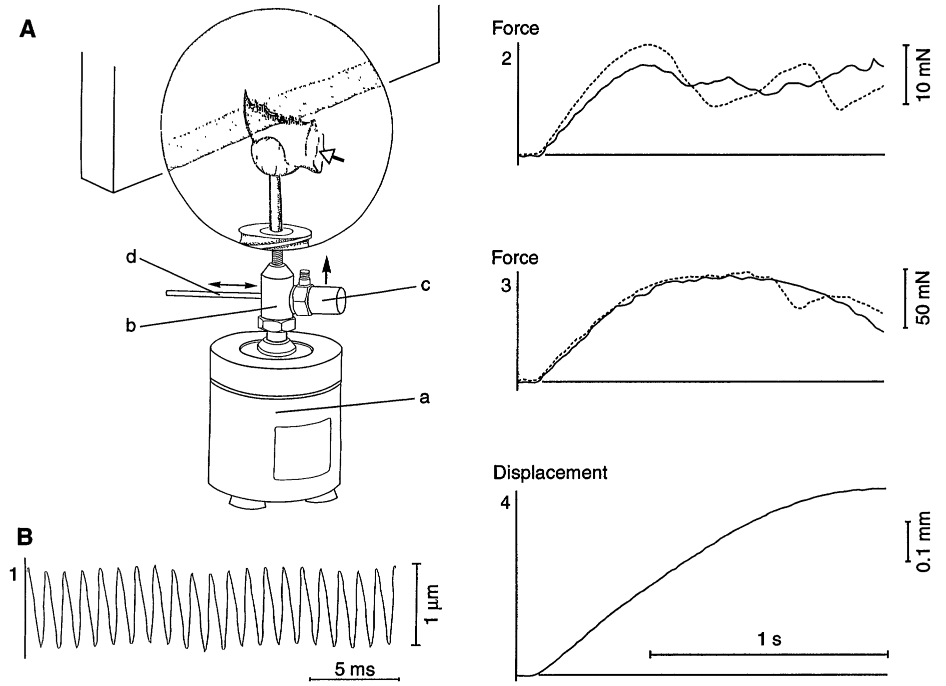

Fig. 2. (**A**) Experimental setup for artificial mandible cuts and force measurements. A vibrator [(a) Bruel and Kjaer 4810] pushes the mandible in the direction shown by the solid vertical arrow (the upright orientation of the leaf is indicated) with parameters shown in (B), graph 4. The force meter (b) measures the forces resulting from the contact between mandible and leaf during pushing of the mandible. An accelerometer [(c) Bruel and Kjaer 4383] allows continuous control of the high-frequency vibration in the direction given by the double-headed arrow, and generated by a second vibrator (Bruel and Kjaer 4810), which is attached by means of a rod (d) from a 90° angle onto the mandible mount. The setup shown here is prepared for additional mandible vibrations in direction "D" in Fig. 1A, 4. The open arrow symbolizes the laser beam for the recording in (B) 1. (**B**) (1), 1-kHz mandible vibration (in direction "D" in Fig. 1A, 4) given as displacement with the same amplitude measured in stridulating ants (converting the acceleration data from Fig. 1D results in 1 kHz corresponding to 1-μm displacement); (4), time course of mandible displacement cutting vertically into the leaf and the forces during the cutting of a tender leaf (2) or a tough leaf (3). Dotted lines indicate the force meter output for a nonvibrating mandible; solid lines indicate the "vibratome effect" onto the force meter output when the 1-kHz vibration is added onto the cutting movement. The 1-s calibration in (4) refers also to (2) and (3).

The use of high-frequency vibration as a mechanical aid might not be so unusual in the insect world. In fact, it has been suggested (*10*) that vibration may aid soil manipulation in Hymenoptera. This may be the basis for the rescue stridulation signal transmitted by *Atta* buried in sand (*4*). Similarly, solitary bees have been found vibrating with their wing muscles, which might also help to loosen soil particles (*11*). Digger wasps (*Philanthus triangulum*) also vibrate their wing muscles during digging (*12*), as bees (*13*) and bumblebees (*14*, *15*) do when shaking pollen from flower thecae.

It is interesting to note that a significantly higher percentage of *Atta* workers stridulate when cutting tender leaves (70%) than when cutting tough leaves (40%) (*3*). Because the vibratome-like effect was observed to be especially useful on tender leaves, it seems reasonable to suggest that stridulatory vibrations in leaf-cutting ants were once used as a mechanical aid during cutting and subsequently have been ritualized during evolution to serve also as close-range orientation cues. However, the observation that almost all ants stridulate when cutting highly attractive leaves [tender and tough leaves coated with sugar water (*3*)] indicates a complex interaction between the physical and chemical features of leaves in determining the production of stridulatory vibrations.

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Experimental Tests of the Roles of Adaptation, Chance, and History in Evolution

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The contributions of adaptation, chance, and history to the evolution of fitness and cell size were measured in two separate experiments using bacteria. In both experiments, populations propagated in identical environments achieved similar fitnesses, regardless of prior history or subsequent chance events. In contrast, the evolution of cell size, a trait weakly correlated with fitness, was more strongly influenced by history and chance.

The diversity of organisms is the product of three fundamental evolutionary influences: adaptation, chance, and history. Their relative contributions to evolutionary change have been the subject of intense debate (*1*). Adaptation has sometimes been regarded as the sole influence on evolution, and some biologists have invoked natural selection to explain almost any phenotypic difference. Unsubstantiated claims that adaptation is the cause of all biological diversity have prompted critics to offer two alternative causes, chance and history, that might account for any particular phenotypic difference. Chance effects include mutation and genetic drift, which govern the stochastic appearance and subsequent loss or fixation of new traits. Chance is usually invoked in the context of molecular genetic traits that are selectively neutral; however, chance is also important for phenotypic evolution, because beneficial mutations arise at random and may be lost soon after they appear, even in large populations. Other evolutionists have emphasized the effects of history, which may constrain or promote particular evolutionary outcomes according to the genetic and developmental integration of the ancestral phenotype. In this view, the set of potential adaptations is severely limited by inherited constitution, so that at every moment the course of evolution is contingent on prior (historical) events.

S. J. Gould (*2*) has argued for the great importance of historical contingency. He has presented a gedanken experiment of "replaying life's tape" to test the repeatability of evolution and thereby evaluate the roles of adaptation, chance, and history. Of course, one cannot perform an actual experiment on the grand scale envisioned by Gould, but one can perform rigorous experiments, of shorter duration and in simpler environments, to quantify the roles of adaptation, chance, and history in evolution. Instead of replaying life's tape sequentially, one can achieve the same objective by doing an experiment in which replicate populations are propagated simultaneously.

Imagine, first, that a single ancestral genotype is used to create a set of initially identical populations that will be propagated in identical environments. If one measures the initial mean value of some trait for each population, one should find that they are identical within statistical limits of measurement error. If one subsequently measures the mean value of this trait for each of the derived populations, one may still find that none of the derived populations has changed significantly relative either to their common ancestor or to one another (Fig. 1A). In that case, one would conclude that the trait had not evolved. Alternatively, one might find that, although there was no significant change in the grand mean (over all populations) from the ancestral value, there was significant variation among the derived populations (Fig. 1B). One would attribute this among-population variation to chance, because the derived populations had identical ancestors and were subject to identical environments. This chance divergence might reflect mutation or drift or their interactions with other evolutionary processes; attributing this variation to chance makes no specific claims in that regard. A third possible outcome is that the grand mean of the derived populations changed significantly from the value for the ancestor but without significant variation among the replicate populations (Fig. 1C). One would attribute this systematic change in mean value of a trait to adaptation. By invoking adaptation, we do not necessarily mean that the trait was the actual target of selection; it might instead be correlated with some other trait that was selected. Nor do we mean that stochastic processes were not involved; for example, adaptation may depend on random mutations, but similar mutations may be common enough to permit parallel evolution in the replicate populations. A fourth possibility is that both chance and adaptation contribute significantly to the trait's evolution (Fig. 1D).

To visualize the effects of history, imagine that a similar experiment is done using several different ancestral genotypes. One might observe that any initial variation in the value of some trait among ancestral genotypes was eliminated from the derived populations because of the effects of adaptation or chance or both (Fig. 1E). That is, the statistical contribution of initial genetic composition to the value of the derived trait was lost, so that one cannot reconstruct a derived genotype's ancestry using that trait. Alternatively, one might observe

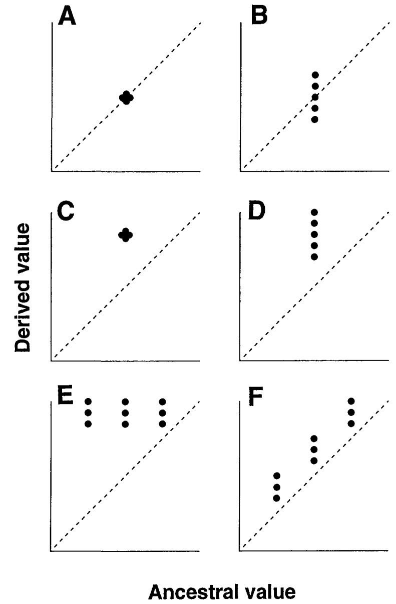

Fig. 1. Schematic representation of effects due to adaptation, chance, and history on evolutionary change and diversification. (**A**) No initial variation and no evolutionary change and hence no effects. (**B**) An effect due to chance only. (**C**) An effect due to adaptation only. (**D**) Effects due to both chance and adaptation. (**E**) An initial effect due to history is eliminated by subsequent effects due to chance and adaptation. (**F**) An initial effect due to history is maintained, with subsequent effects due to chance and adaptation superimposed. See text for further explanation.

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