

an Article from

**SCIENTIFIC
AMERICAN**

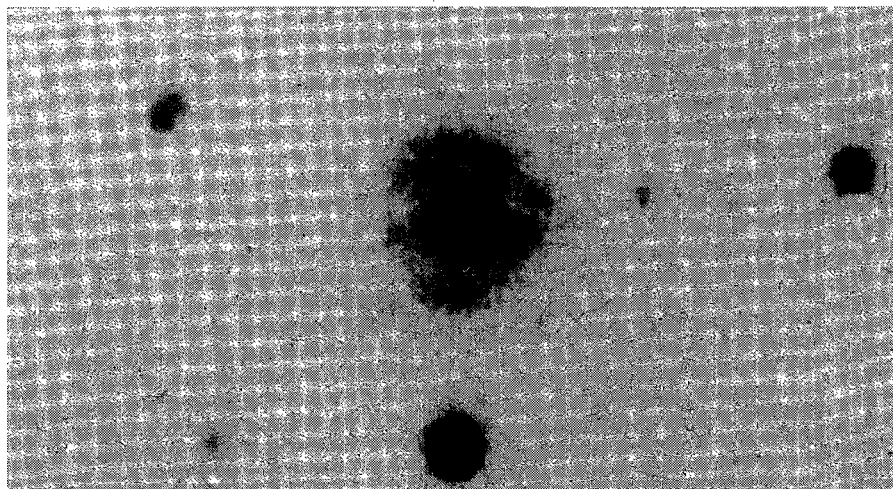
APRIL, 1981 VOL. 244, NO. 4

the shell is expanding in a region where the tenuous gas of interstellar space is relatively dense, the collision between it and the interstellar gas can be a highly energetic one. Such a collision may well explain the unusual appearance of the shell of GK Persei, a brilliant nova of 1901, which left one of the largest and hottest shells known. The shell of DQ Herculis of 1934, on the other hand, is evidently expanding without interference from interstellar gas; it lies off the central plane of our galaxy, where most of the interstellar gas is. Free to expand without any additional input of energy, the shell of DQ Herculis has been cooling steadily. The electrons that were stripped from the atoms are now being recaptured by the ions. The time required for the electrons to be completely recaptured, however, is substantially longer than the time it takes for the gas temperature to drop. The result is that the shell has now cooled to far below its original temperature, and yet most of the electrons have not been recaptured; hence the seeming paradox of a cool gas that is still highly ionized.

When we completed our analysis of the shell spectrum, we found that the combined abundances of carbon, nitrogen and oxygen with respect to hydrogen are a factor of 100 higher than they are in normal stars. According to the conventional nova models, such abundances would be expected to correspond to those of a fast nova. Since DQ Herculis was a slow nova, however, the spectral analysis and the models are in apparent conflict.

Care must be taken in generalizing the results from a single object to other novae, and therefore John S. Gallagher of the University of Illinois at Urbana-Champaign and I are now examining other nova systems with extended shells. We have completed work on two additional objects, the envelopes that surround the slow novae RR Pictoris, which flared up in 1925, and T Aurigae, which did the same in 1891. The spectra show that the shell of RR Pictoris is substantially enriched in helium and nitrogen; the shell of T Aurigae is enriched in helium, nitrogen and oxygen. Gary J. Ferland and Gregory A. Shields of the University of Texas at Austin have conducted a similar study of V1500 Cygni, the fast nova of 1975, and have found that its shell, still too small to be resolved in photographs, is much richer than normal stars in many of the heavier elements, including carbon, nitrogen and oxygen.

Several other nova shells, some in the sky of the Southern Hemisphere, are accessible for analysis, and their composition is being studied. On the basis of the results available so far it seems that most novae, fast and slow, show enrichments in various of the heavier elements. The source of the enrichments is



RECURRENT NOVA T PYXIDIS has undergone five outbursts since 1890, the most recent one in 1966. Recurrent novae brighten by a factor of only about 1,000 during an outburst, an increase considerably smaller than that of a normal nova. It has been discovered only recently that recurrent novae also throw off observable shells (as is demonstrated in this negative print of a picture of T Pyxidis, obtained electronically with an image tube on the four-meter telescope of Kitt Peak National Observatory). The shell was discovered in 1978 by Harvey R. Butcher of Kitt Peak and D. A. Kopriva and the author in a search for shells around novae.

not known, but it is quite possibly the interior of white dwarfs, which are known to be rich in carbon and oxygen.

The presence of the high abundances of heavy elements in fast novae is not at all surprising. The discovery that the shells around the slow novae DQ Herculis, RR Pictoris and T Aurigae are enriched in heavy elements, however, is at variance with the theoretical calculations. In particular the shell of DQ Herculis contains amounts of carbon, nitrogen and oxygen that, if they had been present before the outburst, should have generated enough energy to make DQ Herculis a fast nova.

The difficulty in reconciling the observed enrichments in the shells of slow novae with the predictions of the CNO runaway models has prompted some theorists to speculate that nova eruptions may not always involve the CNO cycle of reactions. The enrichments could be explained if nova outbursts were generated by nuclear reactions capable of synthesizing carbon, nitrogen, oxygen and other elements directly out of hydrogen or helium, which the CNO cycle does not do. There are, for example, thermonuclear reactions in which three helium nuclei (alpha particles) fuse to yield carbon 12, from which other heavier elements can be formed by the subsequent capture of protons. This "triple alpha" process is known to be an important source of energy in red-giant stars. There is probably ample helium on the degenerate surface of white dwarfs for this reaction to occur, and so it seems possible that some nova flare-ups could be due to the triple-alpha process rather than to the CNO cycle based on hydrogen.

Additional evidence for the fusion of

helium in some nova outbursts may be indicated by the abundance of helium in accretion disks before the outburst compared with its abundance in nova shells after the outburst. Recent studies of old novae at the Steward Observatory have demonstrated that the amount of helium in the ejected shells is less than that commonly found in the gas accreting onto the white dwarfs. A logical explanation for this apparent decrease in the helium content of the gas is that triple-alpha reactions have occurred during the outburst and have converted helium into carbon and other elements.

In spite of uncertainties in some of the details, there is now general agreement that nova eruptions are probably caused by thermonuclear reactions on the surface of white-dwarf stars in close binary systems. The process is initiated by the transfer of material from an expanding companion star. The infalling material strikes the degenerate surface of the white dwarf at such high velocity that the surface is heated to the 20-million-degree temperature needed to trigger runaway nuclear reactions. Nova models based on the reactions of the CNO cycle have successfully accounted for many of the observed characteristics of novae. Recently, however, new data on the composition of old nova shells are requiring modification of some of the former ideas about the nature of the outbursts. Further study of old nova shells should prove stimulating not only because of the information it must inevitably yield about novae but also because the shells have already introduced astronomers to unusual environments quite unlike any heretofore encountered in our galaxy.

Filter-feeding Insects

Insects of three orders hatch underwater and gather food with nets, brushes and other fine-mesh filters. They play a role in opposing the tendency of ecological systems to lose organic matter downhill

by Richard W. Merritt and J. Bruce Wallace

Many insects, notably the moth larva we call a silkworm, spin threads to build a cocoon. Less familiar are the insects that spin threads to trap food. They not only weave fine-mesh nets in order to collect the organic matter they ingest but also conduct the enterprise entirely underwater. The net spinners belong to the group of filter-feeding insects that hatch in streams, lakes and other aquatic environments and pass their immature lives entirely submerged. Ten of the 27 orders of insects have aquatic representatives, but only three—the true flies (the Order Diptera), the caddisflies (the Order Trichoptera) and the mayflies (the Order Ephemeroptera)—include species that are known to be filter feeders.

The true flies and the caddisflies are endopterygotes: they are wingless until the pupal stage, when the wing structures develop as the larva assumes its adult form. The mayflies are exopterygotes: wing structures are present from the time the organism hatches until it reaches adulthood, the immature insect's appearance in general presages its adult morphology and it does not pupate at all. Endopterygote larvae molt several times during their approach to the pupal stage. Exopterygote young, generally called nymphs, also increase in size through a series of molts; the adult insect emerges after the final immature stage.

Whatever their life cycle, various species of true flies, caddisflies and mayflies occupy aquatic habitats as diverse as swift alpine streams, meandering rivers, quiet lake bottoms and tidal estuaries, and their habitats frequently overlap. Whatever their order, they are generally divided into two groups: species that live where active water currents allow a passive mode of food collection and species that live where currents are minimal and the insect itself must make the water move.

What nourishes a filter-feeding insect? Numerous analyses of their gut contents show that they frequently do not distin-

guish between inorganic and organic material in the water and therefore ingest particles of silt and small grains of sand along with such plant foods as bacteria and algae and such animal foods as protozoans and small invertebrates. By far the largest part of their ration, however, consists of organic particles, often of unidentifiable origin, known collectively as fine detritus. Among the sources of the organic particles are, first, the feces of scavenging aquatic insects, the "shredders" that feed on decaying vegetation; second, the feces of other aquatic animals that prey on smaller animals or eat living plant tissue; third, organic matter transported from land to water by runoff and, fourth, aggregations of organic matter that has come out of solution. Each detritus particle may also support a frosting, so to speak, that consists of the flora of decay: bacteria, fungi and other microorganisms.

The fine detritus, usually the most abundant food available to filter feeders, is the least rewarding in terms of assimilation efficiency, that is, the percentage of ingested food the feeder absorbs. The assimilation-efficiency rating for the detritus ranges between 2 and 20 percent, compared with 30 percent for algae and better than 70 percent for animal tissue.

This account of the feeding strategies of filter-feeding insects will begin with representatives of those filter feeders whose habitats are in fast currents. One of the least elaborate filtering mechanisms is that of the nymph of the mayfly genus *Isonychia*. The insect's forelegs have a dense fringe of setae, long bristlelike structures. Each bristle bears two rows of fine hairs. The hairs of one row are moderately long and the hairs of the other short and hooked. When the hooked hairs of one bristle are engaged with the long hairs of the next, the filter formed by the interlocked hairs can trap particles with a diameter smaller than one micrometer (one thousandth of a millimeter). To gather its food the

mayfly nymph attaches itself to some convenient surface, faces into the current and raises its forelegs with their arrays of setae interlocked. After a time the insect brings its forelegs within reach of its mouth parts, sweeps off the captured particles and ingests them.

The larvae of two caddisfly genera, *Brachycentrus* and *Oligoplectrum*, have a system almost as simple. They build portable oblong shelters, working with inorganic materials and plant debris held together and anchored with their silklike secretions. The open end of the shelter faces upstream. The larva takes refuge inside the shelter, and when it is filtering, it extends all six of its legs outside the opening to form a fanlike array. Its hind legs and middle legs bear rows of bristles. As food particles are captured by these four filters, the insect works with its forelegs to comb the bristles clean and form the collected particles into a pellet suitable for ingestion. *Brachycentrus* larvae do not rely exclusively on filter feeding; they also graze on microscopic plants.

The larvae of the black-fly family Simuliidae have evolved a feeding system that is both structurally and behaviorally well adapted to a fast-current habitat. They are legless but have a circle of hooks at the end of their abdomen. With the aid of silklike secretions from their salivary glands they attach the hooks to rocks or submerged plants and then twist their body so that the lower surface of their head, with its mouth parts, faces into the current. This preferential positioning constitutes the behavioral aspect of the insects' adaptation to their habitat.

One structural aspect of the black-fly larva's adaptation consists of a pair of unusual mouth parts called head fans: retractable organs between the antennae and the mandibles. When the larva has assumed its position with respect to the current, the head fans are extended to form a filtering apparatus considerably larger in area than the head itself. The head fans are then re-

tracted one after the other, and the larva cleans off and ingests the captured particles with its mandibles.

That is not the black-fly larva's only structural adaptation. Analysis of the contents of the larvae's gut shows that they capture algae, detritus particles, their associated bacteria and bits of sand and silt in a range of sizes from as large as 350 micrometers to as small as .01 micrometer, which is considerably smaller than the mesh of the head-fan filter. A possible mechanism by which such a filter could capture the smaller particles has recently been pointed out by Douglas H. Ross of the University of Georgia and Douglas A. M. Craig of the University of Alberta. It appears that the black-fly larvae secrete mucus from glands at the front of their head and that the movement of their mandibles spreads this sticky material over the surface of the head fans. When the small particles strike the mucus in passing through the fan, they adhere to it. A number of filter-feeding marine inverte-

brates are known to secrete mucus, but until now such secretions were unknown among aquatic insects.

This brings us to the filter feeders mentioned at the beginning of this article: those that spin nets. A good place to start is with the caddisfly family Hydropsychidae. The larvae of certain members of this group first build a shelter of organic and inorganic debris that they bind together with their own silk. The open end of the shelter faces upstream. Next the larva builds a hooplike oval frame that will support a food-catching net at the open end of the shelter. Then the net itself is spun, starting near the base of the frame, with the larva swinging its head in a series of motions following the path of a figure eight.

The first strand of sticky silk is drawn from one side of the frame diagonally to the base. The second strand is drawn in the same manner but from the other side. The alternation continues, with the strands on each side running parallel to

one another. The end result is a net with a rectangular mesh and a central seam that divides one half from the other. The German entomologist Werner Sattler, who had studied the caddisfly genus *Hydropsyche*, observed that the larva needs from seven to eight minutes to weave its net. If the net is torn, the larva will patch it in a random manner; if the net is badly damaged, the larva will weave a new one.

The caddisfly larva molts several times before it reaches the adult stage. The catch nets constructed after each molt are successively larger and coarser in mesh and their threads are heavier. Although the nets with coarser meshes are less efficient in capturing small particles, they not only are larger but also are often set up in places where the current is faster. Then they filter a greater volume of water than a fine-mesh net in a slower current does.

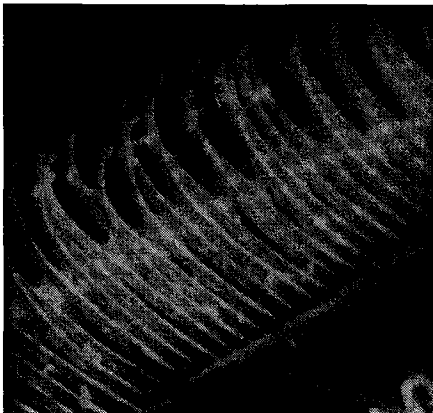
Theodore J. Georgian, Jr., of the University of Georgia and one of us (Wallace) have developed a model of particle



TWIN FANS on the head of a larval black fly can be seen in these scanning electron micrographs. At the left they are in their retracted position between the antennae and the mandibles. At the right the fans are extended with their rays spread so that they filter food parti-



cles out of the water. The particles adhere to a covering of mucus on the rays, and the larva feeds by bringing the rays to its mouth and removing the particles with its mandibles. Both of the micrographs were made by Douglas A. M. Craig of the University of Alberta.



FANLIKE ARRAY of bristling setae on the foreleg of a nymph of the mayfly genus *Isonychia* appears in the scanning electron micrograph at the right. Visible at a greater enlargement at the left are the



tiny hairs on each seta; half of them are short and hooked and the other half are longer and curved. The hooked hairs on one seta engage the long hairs on the next to form a filter that can trap fine food particles.

capture by net-building caddisflies in a stream in southern Appalachia. The model suggests that the larvae of all caddisfly species, regardless of their stage of maturity and the mesh size of their nets, manage to filter out more food than they need. Most of their catch, however, is detritus, a low-quality foodstuff. Analysis of the gut contents of various caddisfly species indicates that those with large-mesh nets feed primarily on relatively scarce and relatively large particles of animal tissue, whereas those with fine-mesh nets feed primarily on detritus of smaller particle size, which is far more plentiful. Hence the advantage of a large volume of water passing through a coarse net, compared with a small volume passing through a fine net, is that the coarse net may be more selective for

animal foods. The differences observed in mesh size in the nets of caddisfly larvae of different species and at different stages of growth appear to be related more to the selection of different kinds of food than to the selection of particles of any given size.

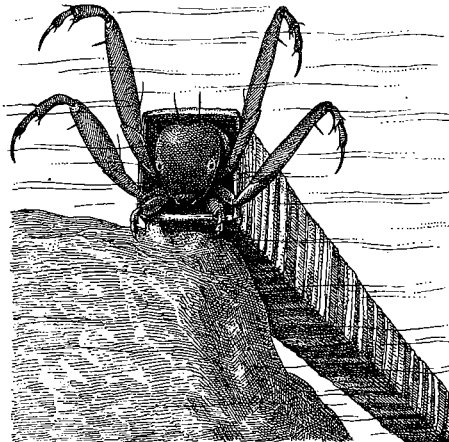
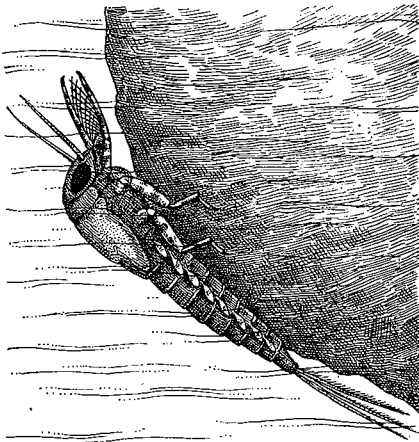
Having captured food particles, large or small, in nets of coarse or fine mesh, how do caddisfly larvae ingest them? Like the filter feeders that do not spin nets, the net spinners have developed diverse behavioral and structural adaptations. For example, one of the coarsest meshes woven by any member of the hydropsychid family is that of the genus *Arctopsyche*, which preferentially inhabits waters with fast currents. The larvae of this genus often capture living prey in their nets, and their spiny forelegs are

useful for that purpose. The larvae of the genus *Macronema* inhabit quieter waters and spin nets with a very fine mesh through all their successive stages of growth. Their forelegs and their mouth parts are equipped with dense arrays of bristles; with these "brushes" the larvae collect and ingest the food particles that accumulate in the net. The larvae of two other caddisfly genera, *Phylocentropus* and *Protodipseudopsis*, also collect food particles from their nets with brush-bearing forelegs.

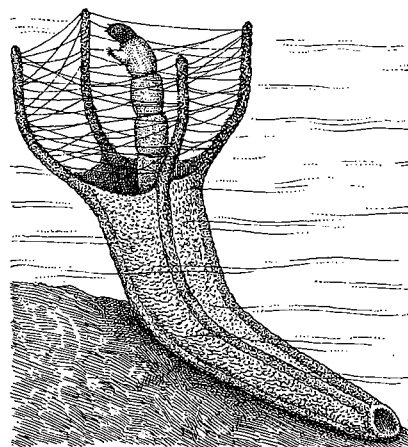
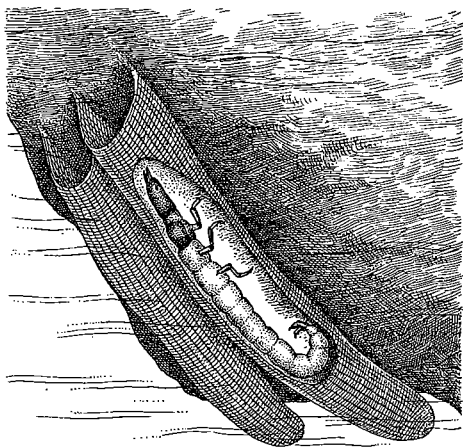
Some net-weaving caddisfly larvae collect food by other methods. Those of the philopotamid family build a sac-like tube that serves simultaneously as a shelter and a catch net. These sacs are remarkable in two respects. First, they are large: as much as five centimeters long and three centimeters in diameter. Second, their mesh is extremely fine. For example, the millions of individual rectangular mesh openings in the sac that larvae of the genus *Dolophilodes* construct in their final larval stage measure .5 micrometer by 5.5 micrometers. The mesh openings of the genus *Wormaldia*, formed by superposed layers of rectangular mesh, measure only .4 by .4 micrometer. The fine-mesh shelters have a large opening at the upstream end and a small opening at the downstream one. Inside the shelter the philopotamid larva periodically sweeps the particles of fine detritus from the mesh into its mouth, working with an array of bristles on its upper lip.

The larva of the small midge *Rheotanytarsus*, a filter feeder in the order of true flies, builds a tubelike shelter on the surface of submerged stones or plant debris. The structure is made out of silt particles bound together by the larva's silklime saliva; the upstream opening is large and the downstream one small. To this structure the larva adds two to five slender arms projecting upward from the large end, and between the arms it strings several threads to snare passing detritus. From time to time the larva emerges halfway from its shelter, eats the threads along with whatever food particles have adhered to them and attaches a new set of threads.

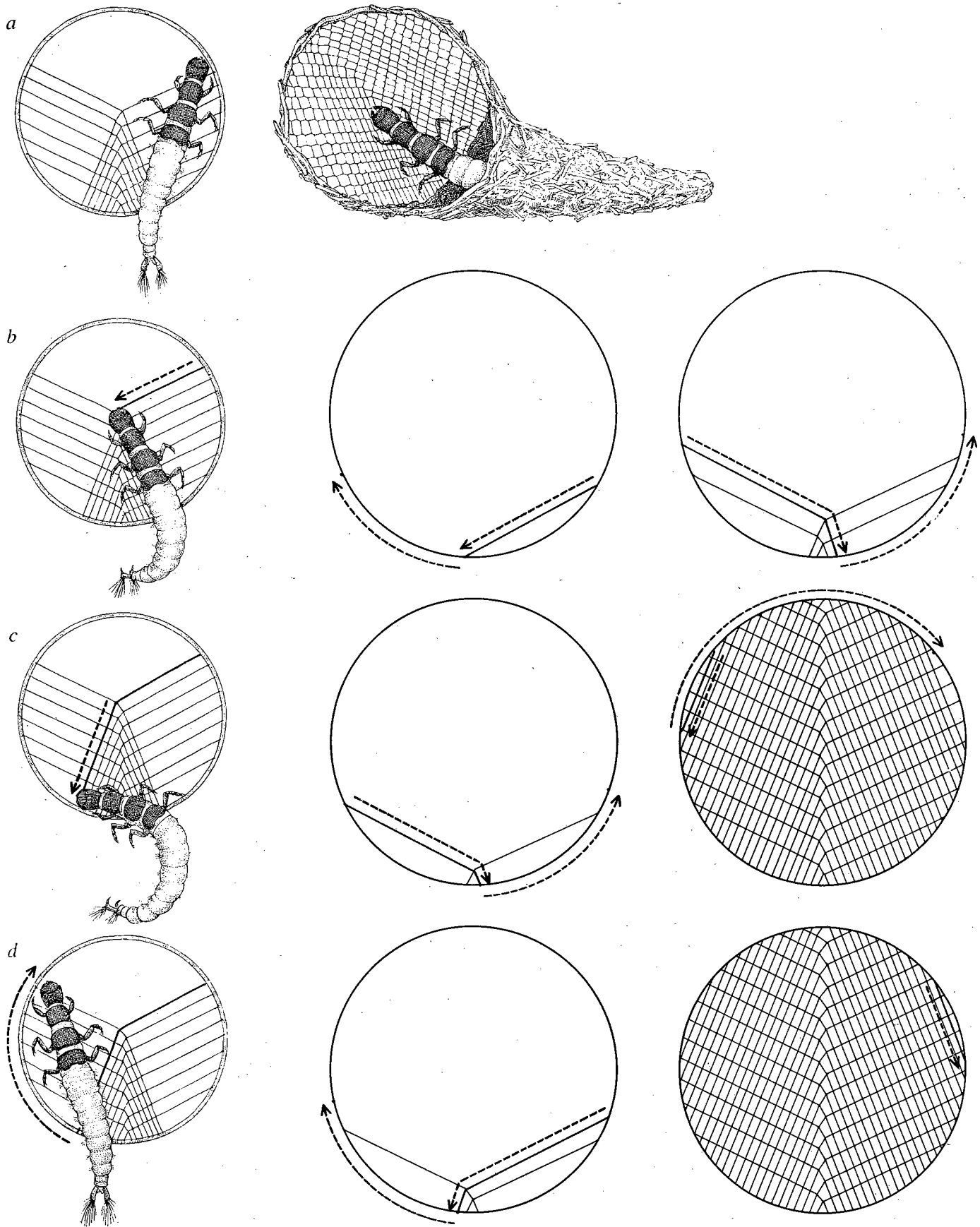
Various filter-feeding caddisflies, mayflies and true flies spend their immature stages in slow-moving or still waters. The best-known of these are the true flies of the family Culicidae: the mosquitoes. Mosquito larvae, called wrigglers because of their active body movements, feed on suspended organic matter in the water with a pair of modified mouth brushes. The brushes are similar to the head fans of the black-fly larva in structure, musculature and function. The water the mosquito larvae occupy need not be clean or of any great extent. Wrigglers are found in tree hol-



MODIFIED LEGS are used by the nymph of the mayfly genus *Isonychia*, at the left, and the larva of the caddisfly genus *Brachycentrus*, at the right, to capture food particles. The mayfly nymph faces the current and uses the brushes of its mouth parts to comb its foreleg setae clean of trapped food particles. The caddisfly larva builds a portable shelter that it occupies after anchoring it to face upstream. It then pushes all six of its legs out into the current. Its filtering arrays of short setae are on the hind legs and middle legs; these it sweeps clean with its forelegs.



SIMPLE NETS are built by a larva of the caddisfly philopotamid family, at the left, and a larva of the fly genus *Rheotanytarsus*, at the right. The caddisfly larva constructs a long, saclike net with a very fine mesh, anchored so that the larger opening faces upstream. The larva occupies the net and periodically uses the brush on its upper lip to remove the food particles trapped on the net's inner surface. The fly larva builds a tubular shelter out of particles of silt bound together with silklime saliva and adds projecting arms to its upstream end. It then strings sticky threads between the arms and usually eats the threads and the food particles adhering to them.



COMPLEX NET is built by larvae of the caddisfly genus *Hydropsyche*. It is shown at the top with its hooplike frame in place at the entrance to the larva's underwater shelter. The sequence at the left shows the method of construction, described by Werner Sattler. The larva grasps the frame and netting and attaches a strand of silk to the right-hand edge of the frame. It draws out the strand (*color*) first to

the center of the net and then down to the edge of the frame on the other side. A swing up to the left and a mirror-image repetition of the first motion completes the larva's figure-eight movement and adds another strand to the net. The idealized diagrams in the middle and at the right outline the attachment of the first four strands and last two. The larva is able to construct its net in seven to eight minutes.

lows, in snow pools and even in the water droplets that collect at the base of a leaf; they are also found in brackish water and latrine pits. They can thrive in such stationary habitats because the motion of their mouth brushes generates small currents that bring food particles within reach.

Some groups in the mosquito family are not filter feeders but have evolved mouth parts modified for browsing. Where the filter-feeding wrigglers tend to sweep up particles just below the surface of the water, the browsers generally feed on the bottom. Their modified mouth parts make it possible for them to scrape food particles off organic bottom debris. Most larvae near the surface capture and ingest particles less than 50 micrometers in diameter.

Studies show that the survival of mosquito larvae is regulated not only by such major environmental factors as day length and the temperature, salinity and oxygen content of the water they inhabit but also by subtle chemical factors. Rex H. Dadd of the University of California at Berkeley has demonstrated that some of these chemical regulatory factors hasten the growth of the larvae by raising the rate of food intake and increasing the time the larvae spend feeding. The ultimate effect of this chemical stimulation would be to

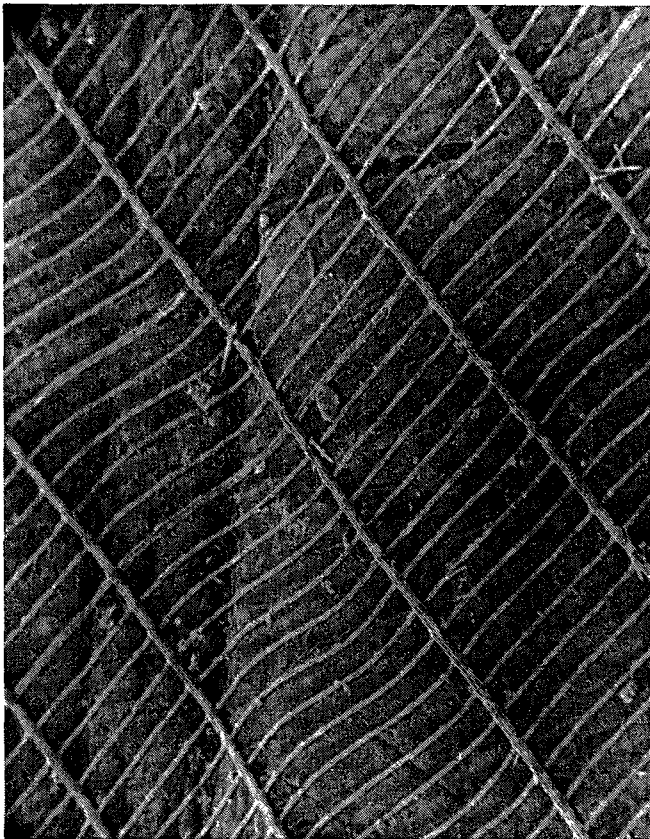
accelerate the buildup of dense larval populations if it were not for the fact that when the maturer larvae grow under crowded conditions, they produce substances that are highly toxic to the less mature ones.

Like mosquito larvae, the silk-spinning midge larvae of the chironomid family favor lakes and other still or slow-moving waters. They may dig a burrow in the bottom sediment or attach their shelter to the surface of a submerged log or the stem or a leaf of an aquatic plant. The midge larvae's spinning abilities have enabled them to adapt to a wide range of habitats. They are one of the most important primary consumers in aquatic food chains and have been known to reach population densities of more than 50,000 per square meter of bottom.

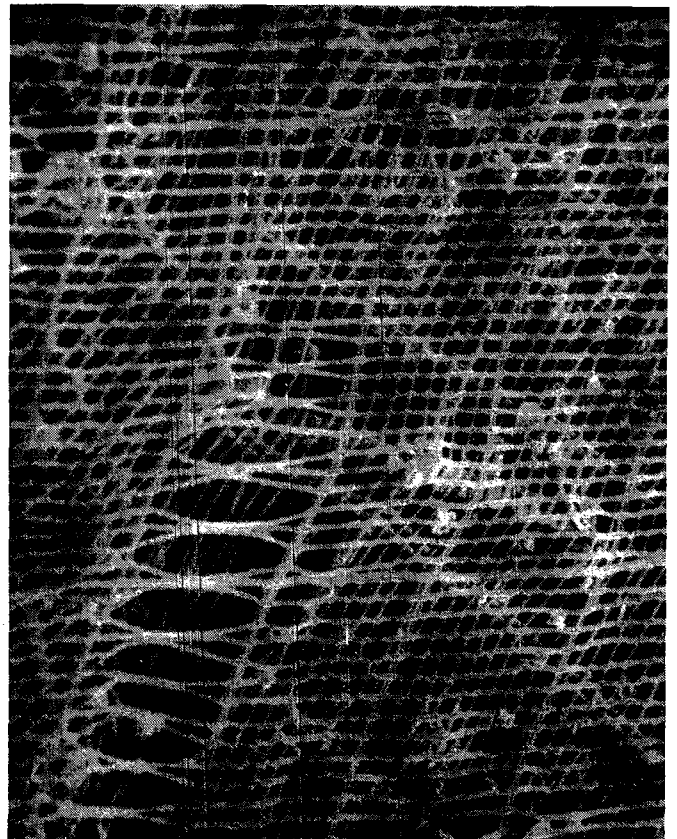
The midge larva may simply dig a burrow in the soft lake sediment or may work with its silk to build a shelter out of available particulate matter. The larva spins a thin conical net across the mouth of the shelter, a task that takes 30 seconds or so, and then, by undulating its body, pumps water through both the net and the shelter. If an accumulation of detritus plugs up the net, the larva reverses its undulations, generating a strong countercurrent that usually clears the obstruction.

In order to feed, the midge larva attaches itself firmly to the silk lining of its burrow with hooked claws and then devours both the net and the food particles adhering to it. In the interval between eating the old net and spinning a new one the larva defecates. The total elapsed time in the cycle, including the 30-second net-spinning interval, is between three and four minutes. Except for the fact that the midge larva creates its own water flow and eats its net rather than cleaning away the adhering food particles, it plays a role in the food chain of slow-moving depositional waters equivalent to that of the net-spinning caddisfly larva in fast-moving erosional waters.

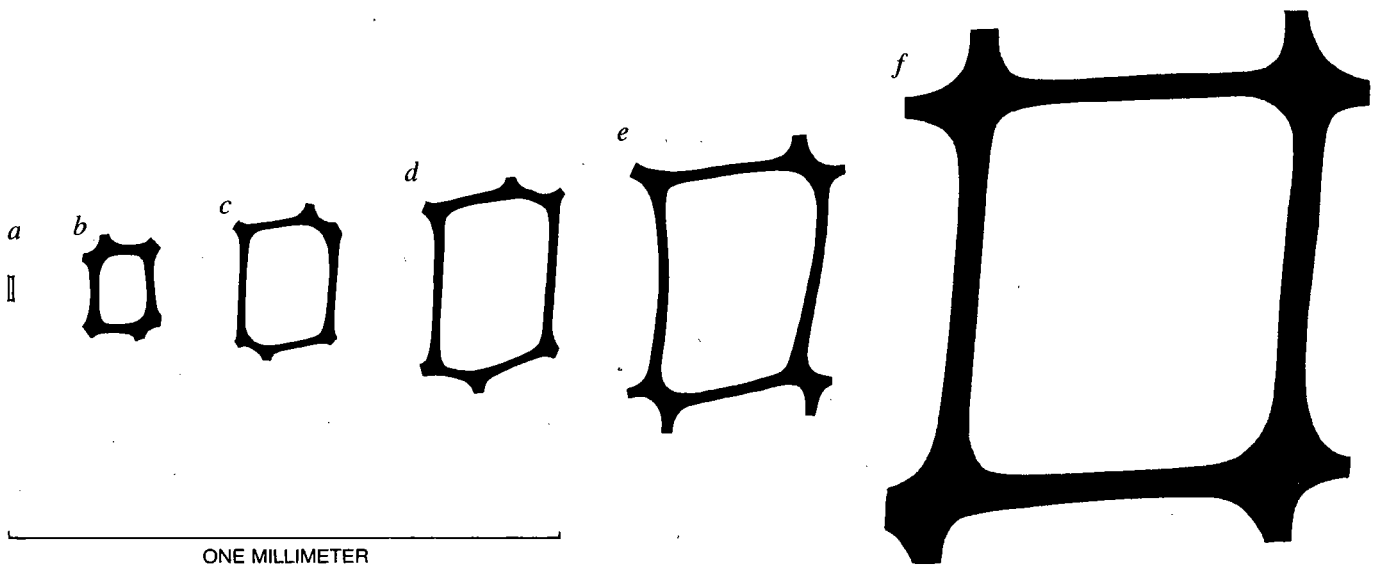
The nymphs of some mayfly genera inhabit the silt and mud of near-shore lake bottoms and slow-moving streams; they may also live in submerged wood, such as tree trunks and dock pilings. Two of the common bottom dwellers are the nymphs of the genera *Hexagenia* and *Ephemera*; both use legs that have been modified for digging to construct a U-shaped burrow in the bottom sediment. Once the nymph is in the burrow it begins to undulate its respiratory gills. The current generated by the movement carries a supply of both oxygenated water and food particles through the burrow. A number of studies suggest that



MESHERS OF TWO SIZES, both woven by caddisfly larvae, appear in these micrographs. At the left is the oblong mesh of the hydropsychid genus *Macronema*; each pore is about five micrometers wide



and 40 micrometers long. At the right is the two-layer mesh of the philopotamid genus *Wormaldia*. Overlap of two rectangular meshes produces the smallest-known caddisfly net pore: .4 by .4 micrometer.



MESH SIZES among different genera of hydropsychid caddisflies vary greatly. The individual pores shown in outline here range from the oblong of *Macronema* (a) to the rectangle of *Arctopsyche* (f). All

six meshes are representative of the nets that the caddisfly larvae of the Savannah River basin construct during their final larval stage. The *Arctopsyche* larvae preferentially inhabit fast-flowing streams.

the nymphs can feed in their burrows by filtering particles out of the passing water. They are also known, however, to emerge and browse on the bottom. In many areas of the U.S. Middle West hordes of these mayflies once blanketed the ground during their brief summer emergence. Their numbers have now been greatly reduced by the pollution of the kind of waters they inhabit.

The nymphs of two tropical mayfly genera, *Povilla* and *Astenopus*, are among those that attack submerged wood. They excavate a U-shaped burrow in the wood with their sturdy mouth parts and take shelter in it after lining it with a silky material. Then they wave their long abdominal gills to generate a flow of water that carries oxygen and food particles through the burrow. They filter the food out of the passing water with dense arrays of bristles on their forelegs, head and mouth parts.

The caddisfly larvae that similarly inhabit lakes and sluggish streams include the larva of one genus, *Neureclipsis*, that weaves a characteristically cornucopia-shaped net. The German entomologist Caroline Brickenstein, studying these larvae, found they took three days to construct their net. The biggest nets may be more than 20 centimeters long and have an opening 13 centimeters in diameter. The silk loses much of its elasticity and strength after a few days, and the larva spends additional time between feeding periods replacing worn-out strands on the interior wall.

The *Neureclipsis* larva feeds primarily on small aquatic invertebrates, and so its nets are often found in great abundance in the outflow streams of lakes where these tiny prey exist in large numbers. Although the preferred habitat of the larvae is slow-moving water, they sometimes build their nets in water flowing at

velocities of up to 30 centimeters per second and even higher. The occasional nets seen in such fast-moving streams are noticeably smaller than those found in slower-moving water, suggesting that the higher velocities impose limitations on net size.

The larva of the caddisfly genus, *Phyllocentropus*, is one of the few caddisfly net spinners that live in stream areas where deposition predominates over erosion. It builds a long, Y-shaped tube that is buried several centimeters deep in the stream bottom. One arm of the Y is elongated and extends several centimeters upward into the water; the other arm, which has a bulge in it, is shorter and barely protrudes above the bottom. The larva normally occupies the longer of the two arms. By undulating its body it causes water to flow into the longer arm and out through the shorter one, where the bulge holds a catch net. Between intervals of undulation the larva enters the shorter arm of the burrow and feeds on the very fine detritus adhering to the net and the inner walls of the tube. Gut analyses indicate that most of the particles the *Phyllocentropus* larvae ingest have a diameter of less than 10 micrometers.

The habitats available in a particular aquatic ecosystem are limited in number. How do filter-feeding insects manage to share them? The answer is clear: the various genera have evolved many different adaptive mechanisms, both behavioral and structural. A further mechanism, involving habitat selection, is common among certain filter feeders, particularly black-fly larvae and the net-spinning larvae of caddisflies of the hydropsychid family.

The water of a lake or a reservoir holds products of decomposition (derived from the bottom sediments) and large populations of microscopic plants

and animals. Accordingly these larvae aggregate in great numbers near lake outlets and dam spillways. The time of year when the nutrient-rich water spills downstream in abundance is often spring, and so immature filter feeders near an outlet at that season probably enjoy a selective advantage over insects maturing at other seasons of the year or at habitats downstream. It has been found, as might be expected, that some insect species occupying such nutrient-rich spill habitats grow faster and reach the adult stage sooner than representatives of the same species living elsewhere. The result is an abbreviated life cycle best suited to the exploitation of a seasonal abundance of food.

The tendency of black-fly larvae to aggregate in these spill habitats is presenting a serious health problem in Africa. The bite of the adult female black fly transmits the filarial worm that in man causes onchocerciasis, or "river blindness." The construction of dams and other impoundments in the developing nations of Africa has led to an increase in the number of black-fly breeding sites and a spread of the disease.

The length of a filter feeder's life cycle is affected by factors other than the abundance of food. The water temperature, or more precisely the accumulation of heat over a period of time, is one such influence. Working in Michigan with Ross, one of us (Merritt) found that black-fly larvae took longer to develop when they hatched at near-freezing winter water temperatures than they did when they hatched and developed in the rising water temperatures of spring. The larvae that developed in winter also went through more molts and were larger when they entered the pupal stage than the larvae that developed more rapidly in the spring. In Georgia one of us (Wallace) has observed a somewhat

similar response to water temperature among maturing caddisfly larvae, although the lower temperatures did not result in additional molts. Other investigations have shown that filter-feeding insects living at higher altitudes or in cooler latitudes normally produce one generation per year whereas those at lower altitudes or in warmer latitudes may produce two or even three generations in the same length of time.

Another adaptive factor in the coexistence of filter feeders is a staggering of the life cycle, as when the insects occupy

the same habitat but do not go through the same phases of development at the same time. Such temporal variations in life cycle can serve a number of adaptive purposes. For example, at any one time one population may be consuming foods that are different from those of the other. Or the period of maximum growth of the individuals in one population may be different from that of the other, and so the times of maximum food demand are staggered.

There are also changes in diet with larval development. A number of inves-

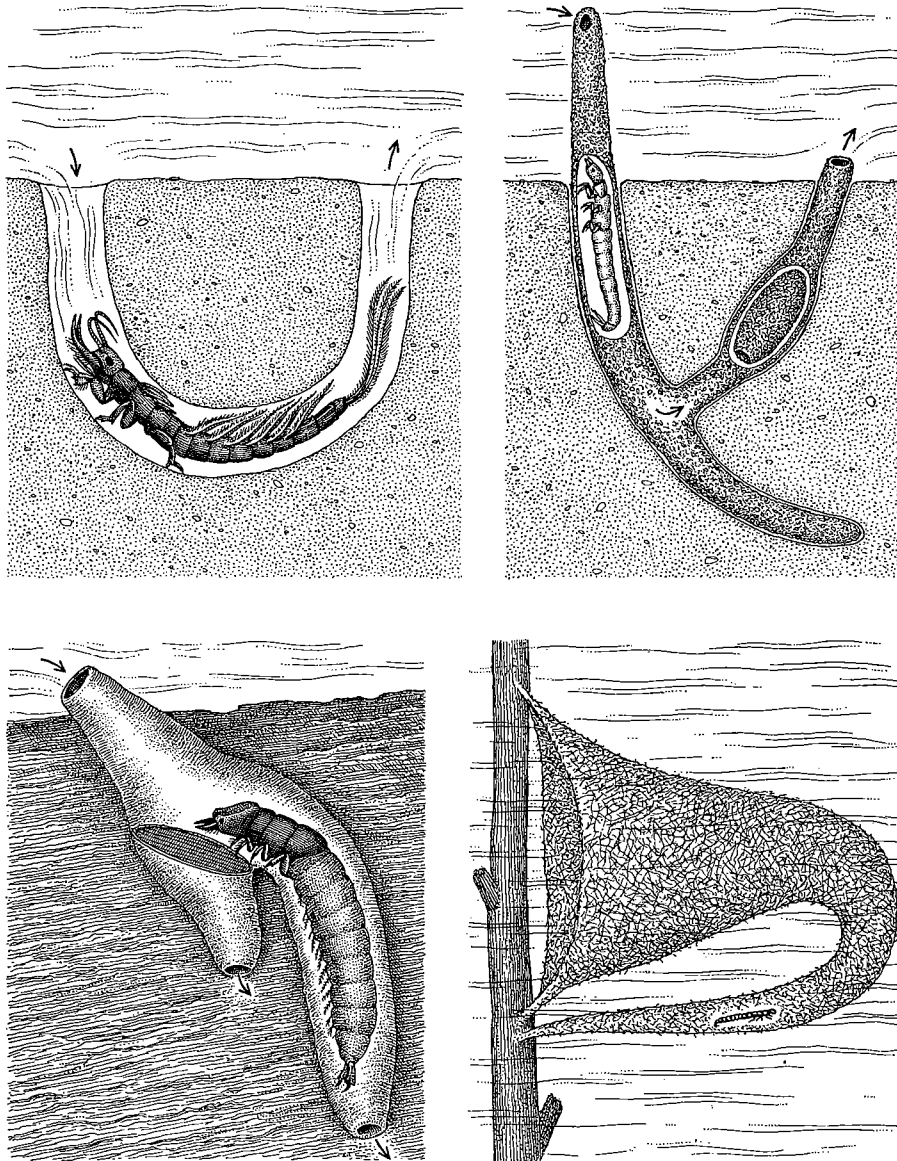
tigations have shown that the early larvae of some hydropsychid caddisflies feed mainly on fine detritus and on diatoms and other algae. As the larvae go through successive molts, however, they begin to consume increasing amounts of animal tissue. The food the filter feeder preferentially ingests during its period of maximum growth is the one it can assimilate most efficiently.

Aldo S. Leopold, a pioneer in wild-life studies, once pointed out that the processes of nature cause all materials, including organic ones, to move predominantly in a downhill direction. A corollary, Leopold suggested, was that the continuity and stability of upland communities depends on life forms storing nutrients and organic matter and participating in other processes that retard the downhill trend. It is evident that the filter-feeding aquatic insects are among these life forms, but it is difficult to measure their contribution with much precision.

The difficulty arises from the unidirectional flow of water, which is foremost among the downhill carriers of material Leopold had in mind. With an open-ended system such as a flowing stream the relative value of inputs and outputs is not easily calculated. Some commonsense evaluations are nonetheless possible. For example, in comparison with the total downstream transport there is little upstream movement of materials. One can cite instances of net upstream travel by fishes and by bottom-dwelling animals and even by aquatic insects after they have reached maturity and taken wing, but all these movements are trivial compared with the downstream one.

Exactly what do the filter feeders accomplish by way of retarding the downhill process? One of their major contributions may be to retain part of the food they ingest and to alter the rest and pass it along. For example, studies of six species of net-spinning caddisfly larvae in a stream in southern Appalachia indicate that these filter feeders actually add more detritus to the stream than they withdraw from it. Only between 2 and 20 percent of the filter feeder's intake of detritus is actually assimilated. At the same time the larva is also ingesting, but far from completely assimilating, high-quality animal tissue and somewhat lower-quality plant matter. The filter feeder's feces, although they may contain between 80 and 98 percent of the larva's own intake of low-grade detritus, will also contain some unassimilated animal and plant matter. By assimilation the larvae lower the net food value of what they ingest, but their feces, together with whatever colonizing microorganisms the feces may acquire in their travels, are available for reingestion by other filter feeders farther downstream.

This process can be considered the



SLOW-WATER FEEDERS include two, a nymph of the mayfly genus *Hexagenia* at the top left and a larva of the caddisfly genus *Phyllocentropus* at the top right, that occupy tubes or burrows and pump water currents through their retreats by undulating their bodies. The mayfly nymph sets up the flow of water by waving its dorsal abdominal gills and collects food particles with the setal brushes on its forelegs and mouth parts. The caddisfly larva builds its branched tube with silk and sand grains and weaves an irregular net in the shorter branch; body movements pull water into the long branch and push it out of the short one, and the larva periodically sweeps the net and the inner wall of the tube clean with the brushes of its forelegs and mouth parts. Two other caddisflies depend on weak currents to bring food particles to their nets. The larva of the genus *Macronema*, at the bottom left, builds a shelter with its entrance directed upstream and cleans its net with the brushes of its forelegs and mouth parts. The larva of the genus *Neureclipsis*, at the bottom right, constructs a large cornucopia-shaped net that can be 20 centimeters long. The larva usually feeds on live prey that accumulate at the narrow end of the net.



MOUTH BRUSHES of a mosquito larva are seen from below in this scanning electron micrograph made by Craig. A filter feeder of still-water habitats, the mosquito (*Culiseta inornata*) moves the brushes rhythmically to draw a current of nutrient-bearing water toward its mouth.



CADDISFLY MOUTH BRUSHES are used to sweep fine particles from its catch net into its mouth. Seen in this scanning electron micrograph is the larva of a hydropsychid caddisfly of the genus *Macronema*. Objects at the bottom of the micrograph are the larva's mandibles.

starting point of a recycling process that increases the efficiency of a stream ecosystem in terms of the utilization of its organic inputs. If it were not for the filter feeders, much of the organic matter being transported downstream would be utilized only by the microbial components of the ecosystem. In a stream where successive populations of filter feeders are active, however, the organic matter may yield fractions of its stored energy repeatedly on its long journey to the sea.

Jackson R. Webster of the Virginia Polytechnic Institute and State University has applied to this recycling process the term "spiraling." He has done so to emphasize the longitudinal and unidirectional aspects of cycling within a stream environment. For example, particulate matter of high quality such as animal tissue and algae may be utilized quickly and thus can be characterized as having a short spiraling distance. Low-quality detritus can be characterized as having a longer spiraling distance. The shorter the spiraling distance is, the greater will be the proportion of organic matter that is converted by the metabolism of filter feeders into carbon dioxide and is thereby removed from the total amount of organic matter downstream. And the more diverse the trapping mechanisms of the various filter feeders are, the greater will be the efficiency with which organic matter is removed.

This, however, is only one of the factors relating to the efficiency of food utilization. For example, the particulate matter that is most abundant in streams has a particle diameter of 25 micrometers or less. The filter-feeding insects that capture particles in this size range are black flies, midges and certain caddisflies. These are the same filter feeders that select food almost entirely by particle size. Therefore in the overall efficiency of the ecosystem these insects may accomplish more in retaining organic matter than the filter feeders that selectively trap larger particles.

The few studies made so far indicate that over short downstream distances the filter-feeding insects utilize only a small proportion of the passing organic matter. They convert that proportion, however, into organic matter of a more complex form and with a higher food value. That organic matter consists of their own bodies, which are potential food for predators, such as carnivorous insects and fishes higher up the food chain. Hence it is clear that the filter feeders, evolving to occupy a variety of habitats and to employ many kinds of capture mechanisms, act to retard the dominant downhill movement of organic matter by both retaining it and altering it.