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NAVIGATION BY SUN-COMPASS

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BIRD MIGRATION AND CELESTIAL NAVIGATION

BY DONALD R. GRIFFIN

Professor Griffin has worked extensively on the problems of bird migration, and his enthusiasm has led him to unusual accomplishments for a biologist. Of his work in the early 1940's he writes "I was also studying migratory birds, first by homing experiments in which they were carried some distance from their nests and released. Many of the sea birds studied in this way (herring gulls, terns, petrels, and gannets) found their way home. But homing experiments only tell the time required and the percentage returning at all. So I decided to learn to fly myself and trace the actual routes flown. I managed to do this with a number of gulls and gannets, circling in a Piper Cub for as long as ten hours at a stretch while the bird did its cross-country flying." The number of hours aloft for Dr. Griffin has decreased, but his interest continues. The following article is adapted from his recent book in the Science Study Series, Bird Migration.

THE LATE GUSTAV KRAMER, a German ornithologist, studied the orientation of European warblers in a circular orientation cage. The top of the cage was exposed to the night sky, and the birds were observed closely for many hours in the season when they were exhibiting migration restlessness. Since Kramer wished the birds' view of the sky to be as nearly the same as during actual nocturnal migratory flights, he used no artificial illumination, but watched the warblers through a transparent plastic floor of the orientation cage while lying on his back and looking up at the bird silhouetted against the stars. The cage was surrounded with an opaque cylindrical wall to shield the birds from lights and prevent them from seeing

ABOVE: tern uses "directional sun-compass orientation"

any local landmarks. A few individual warblers would show clear indications of preparation for flight, or even the preliminary motions of flight itself, on many nights in the main season of migration. These preliminaries were examples of so-called intention movements, small-scale versions of some vigorous activity that often follows them under natural conditions.

Orientation of Migration Restlessness

Warblers tended to head in directions roughly the same as those in which they would have been migrating, had they been at large under natural conditions. Furthermore, the directions of their headings in the orientation cage changed with the season, roughly south in fall and north in spring. In between seasons of migration there was little restlessness in the cages, and no significant directional tendency. This result was interesting enough, but in the course of experiments under various weather conditions it turned out that overcast skies disrupted the headings altogether. When the stars were not visible, the headings scattered widely, and were either quite random, or tended to concentrate slightly in the direction of any slightly brighter portion of the sky. If the experiments were conducted near cities, the artificial lights reflected from the clouds seemed to influence the birds' headings. Similarly, if the moon was visible the birds often headed in its direction. This sort of heading toward the brightest available light in an otherwise nearly dark cage does not seem to be part of the normal process of orientation during nocturnal migration. Perhaps it is more closely related to a bird's tendency to escape from its darkened cage out into brighter light. Another possibility is that without stars for guidance birds tend to fly toward any bright light. Possibly this explains why under certain conditions they are attracted to lighthouses and "ceirometer" searchlights at airports — often with disastrous results.

Bird Song and Orientation

A few years after Kramer's discovery that migration restlessness was sometimes correctly oriented, similar experiments were started by Franz Sauer, an energetic young zoologist at the University of Freiburg. Sauer and his wife had been engaged in another, equally laborious type of research on bird

behavior, the study of how birds come to sing the particular patterns of song that are characteristic of their species. It had been a matter of active debate whether young songbirds learn from their parents, or other adults of their species, just what sequence and pattern of notes is appropriate for a male to employ in announcing that he has staked out a territory and is ready to set up housekeeping. A direct, but burdensome approach was to raise young birds from the egg in complete isolation, in soundproof rooms, where they could grow to maturity without any chance to hear the songs of other birds. The Sauers chose European warblers for this purpose, because they have characteristic songs that differ from one closely related species to another. In the course of their experiments on the development of singing ability, the Sauers necessarily became expert at this art of mothering nervous and delicate baby warblers until they grew to healthy adult birds ready to breed, sing, or migrate. The outcome of the experiments on song development was fairly clear evidence that in European warblers an almost normal song is produced even in total seclusion with no possibility of learning by hearing other, experienced, birds. This topic is outside the scope of this article, but interested readers will find it fully and lucidly discussed in W. H. Thorpe's book, *Bird Song*, Cambridge University Press, 1961.

The Sauers used a circular cage similar to Kramer's, and they studied the headings of their birds not only under the natural sky but also in a planetarium. This "artificial sky" had many advantages for experiments. Cloudy weather was no problem, and the heavens could be imitated not only as they would appear naturally at Freiburg on the night of the experiment but as they would appear at some other place on the earth's surface, or at some other season. Furthermore, the Sauers had available adult warblers, in full breeding condition, but totally inexperienced with the real world outside their soundproof rooms, birds that had never seen the sky at all.

The results of the Sauers' early experiments were as dramatic and exciting as Rowan's first demonstration that lengthened days in winter would bring birds prematurely into breeding condition. Certain especially co-operative warblers in the Freiburg laboratory did indeed show consistent directional tendencies that corresponded to the normal migratory

headings of their species at the season of the experiments. As illustrated, these headings were equally accurate whether the birds were shown the natural sky or the star pattern reproduced on the dome of a planetarium. As in Kramer's experiments, cloudy skies elicited only disoriented and virtually random choices. Evidently these warblers were indeed able to select the appropriate direction for their migration on the basis of the stars. Furthermore, these directional choices were reversed with the season. The same bird exposed to approximately the same star pattern, in the same experimental situation, would head north in spring but south in fall. By injections of appropriate hormones the Sauers were even able to bring one or two warblers into breeding condition in between the normal seasons of migration, and these birds showed the spring headings.

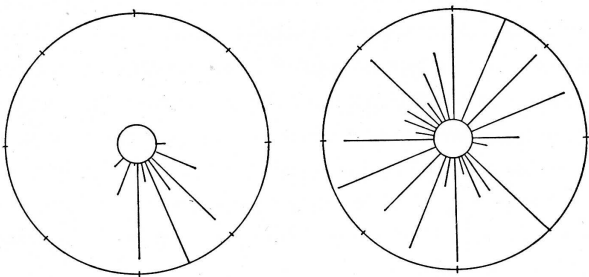
All this was remarkable enough, but the Sauers' experiments also indicated that in at least two individual warblers the appropriate directional response to the star pattern occurred the first time the individual bird was allowed to see the sky. These experiments, summarized below, were carried out with hand-reared warblers that had been kept indoors ever since they were very young nestlings. Yet when placed in the orientation cage as adults, in periods of migration restlessness, they made essentially appropriate choices of direction. This result is so striking that many biologists have found it difficult to believe. The natural next step of repeating the experiment has been very difficult, simply because of the enormous

labor involved in hand-raising birds such as European warblers and keeping them sufficiently healthy to show migration restlessness and give headings in an orientation cage.

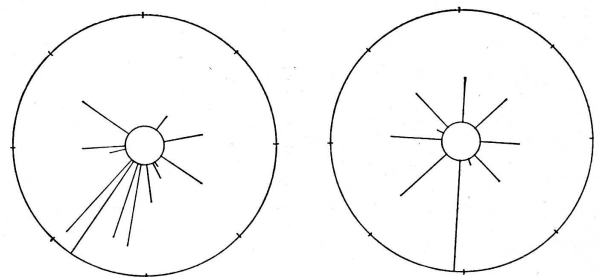
The implications of the Sauers' experiments are far-reaching, because they apparently show that, built into the organization of the brains of migratory birds, is some mechanism that causes them to react in a specific way to the pattern of stars. Such a mechanism must also include provision for a reversal of this directional choice between fall and spring, presumably dependent on the bird's internal physiological and endocrine balance. Presumably the genetic make-up of the particular species must determine whether or not such directional choices are made, and to some degree must dictate the angle relative to the star patterns that the bird will select. If the Sauers' findings apply generally to migratory birds, then various species must have genetically determined recognition patterns appropriate for the latitudes and seasons of their migrations. Penguins swimming through the South Atlantic have very different star patterns to guide their migrations from those that are visible to plovers starting south from the shores of the Arctic Ocean.

Experiments with Bobolinks

Recent experiments by William J. Hamilton, III, in San Francisco, have shown that bobolinks also make directional choices during migration restlessness, when they have only the stars as directional cues.



Directional headings of a warbler during the autumn period of migration restlessness. The orientation cage was in a planetarium. The length of each line represents the proportion of the time that the restless bird spent heading in the direction indicated. At the left, headings under the autumn sky of Germany; at right, random headings with diffuse illumination from the planetarium dome.



Directional headings of two warblers reared in complete isolation and then tested in the Sauers' orientation cage under the outdoor sky in late summer or early fall. Both birds tended to head south to southeast during their migration restlessness, even though they had never before seen the sky or star patterns on which this orientation must have been based.

This species performs a very long migration from well south of the equator into the northern United States and southern Canada. Hamilton found bobolinks somewhat more variable in their directional responses in orientation cages than the Sauers' warblers had been in the most clear-cut of the latter's experiments. To the Sauers' procedures Hamilton added the playing of tape recordings of bobolink call notes, a conspicuous feature of the nocturnal migratory flights of bobolinks and some other night migrants. The recorded call notes served to intensify the directed intention movements of the bobolinks in the orientation cages. One complication that developed in Hamilton's results with bobolinks, to a greater extent than in the Sauers' earlier experiments with European warblers, was a bird's tendency to alternate between southward headings in the fall and choices of the exact opposite direction. Even when these south and north headings were alternating in an unexplained fashion, some sort of celestial orientation was evident, since intermediate, easterly or westerly headings were quite rare. Two bobolinks that had been hand-reared from a very early stage of development showed directional choices of this type. But more than birds captured as adults would do, they displayed a tendency to oscillate back and forth from the appropriate southward heading in autumn to a reversed, northward choice. Even these bobolinks that were seeing the star pattern for the first time were not random in their headings, for north and south predominated heavily over east or west. Hamilton's experiments with bobolinks provide at least partial confirmation of the Sauers' remarkable finding that directional reactions to the stars are genetically built into the nervous systems of migratory birds.

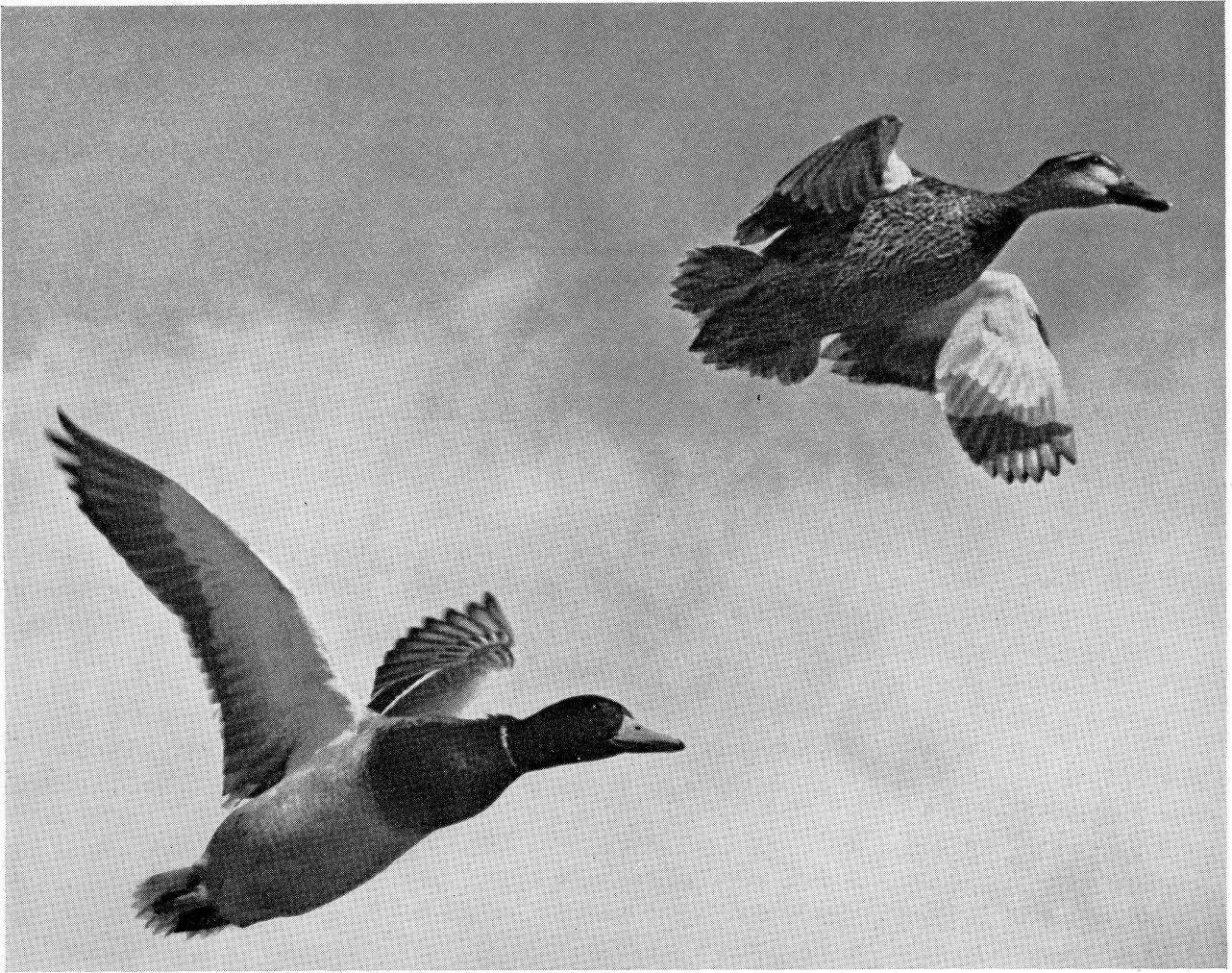
Even in the clearest of the Sauers' or Hamilton's experiments in orientation cages the majority of the headings are spread over forty-five to sixty degrees, with a few headings scattered in many other directions. This dispersion requires that any difference between headings of two groups of birds must be distinctly greater than sixty degrees before it can be accepted as significant. In some of the Sauers' planetarium experiments warblers that had shown directed migration restlessness under an accurate reproduction of the autumn sky over Germany were then presented with the sky as it would appear at

latitudes farther to the south. It seemed in some cases that the headings turned from southeast to south at just the latitude of the Mediterranean Sea, but the overlap between the two sets of directional choices was not sufficient to make the evidence firmly conclusive. Pending more extensive and detailed experiments of this type, most students of the matter are convinced only of the Sauers' basic finding that northward or southward headings are displayed under the real or planetarium sky at the appropriate seasons. Further embellishment upon the available data does not seem warranted.

Types of Orientation

It is important to distinguish two distinct types of orientation that seem to be employed by birds in natural migration, in homing experiments, or in orientation cages. The simplest is often called *directional orientation*. This term means that the bird has the ability to select a particular compass direction and, presumably, to fly in that direction if free to do so. Kramer's or the Sauers' migrants which headed roughly south in fall would be good examples. The second type of orientation is called *goal-directed orientation* and is exemplified by Matthews' experiments with homing pigeons and Manx shearwaters. These birds flew off approximately toward home regardless of the direction in which they had been carried from their loft. Goal-directed orientation is obviously more difficult to explain than directional orientation, because the bird must somehow determine the appropriate direction to reach its home or other goal area, and then manage to select that direction. Furthermore, goal-directed orientation is more difficult for an experimenter to demonstrate. No single release point can suffice for such a demonstration, no matter how many birds are employed, nor how accurately they head toward home. Only if they head for home from two or more different directions can we conclude that they are exhibiting goal-directed orientation.

Kramer put the key question rather well when he pointed out that for birds sun-compass or star-compass orientation literally takes the place of a man's use of a compass to find his way. But a compass is of little use to man or bird unless he knows the direction in which he wishes to travel. In ordinary human practice we use compasses (or the equivalent) in



Mallard ducks are capable of practicing "star-compass and moon-compass orientation," page 8

conjunction with maps, or some knowledge of geographical relationships that serve the same purpose as a map. Before his untimely death in a mountain-climbing accident, Kramer emphasized on many occasions that biologists could account for the compass used by homing birds, but not the map. In other words, he felt that some other, and still completely unknown, factor must be combined with sun-compass orientation to explain the homing of the best strains of pigeons, as well as the navigation of Manx shearwaters.

The Sun-Arc Hypothesis

When Matthews was faced with these same facts, he attempted to explain them by assuming that the

sun alone suffices to provide birds with the information needed to achieve essentially correct homeward headings and display a high order of goal-directed orientation. Sun-compass orientation implies the use of the birds' biological clocks as a basis for selecting a progressively changing angle relative to the sun's position in the sky. This ability has been amply demonstrated not only in birds but also in lizards, fishes, insects, and in many other invertebrate animals. Expressed in human terms, one might imagine that the birds say to themselves, "It is now noon, and since I want to go north I should fly away from the sun," or later in the day, "Now it is fairly late in the afternoon; therefore, to fly north I must keep the sun over my left shoulder."

Matthews postulated that the birds might compare the sun's altitude above the horizon with the altitude that could be expected at the bird's home at the time in question. Transposed again into human expression, the bird's thought might be, "I know by my biological clock that it is early morning, but the sun is too high for this time of day; either they have carried me south, where the sun is higher in the sky at this hour, or they have carried me east, where it rose earlier than back home." At this point one might well stop imagining bird geometry and assume that our bird, having guessed this much, would decide to make the best of an uncertain situation, in which its location could be anywhere between east and south. This it could do by splitting the difference and heading northwest.

An English ornithologist, Tunmore, postulated a type of behavioral reaction on the bird's part that can be expressed even more simply. His hypothetical rule for a bird finding itself in unknown territory after a homing experiment is this: "If the sun is higher than you expect at your home area, fly away from the sun. If the sun is lower than expected, fly toward it." Much of the time a bird obeying Tunmore's rule would indeed head within thirty or forty-five degrees of the homeward direction. But at other times of day, especially near sunrise and sunset, Tunmore's rule would produce deviations of ninety degrees or more. Some of the best homing performances and initial headings of Matthews' pigeons occurred under these conditions. But the simplicity of Tunmore's rule is very appealing, and even though it may not apply to all birds under all conditions, perhaps it can explain some of the essentially correct initial headings that have been observed by Matthews and Kramer.

Matthews postulated that birds do something rather more complicated—namely, observe the sun's movement through the sky and, on the basis of its rate of ascent or descent relative to the horizon, extrapolate its arc across the sky to the noon, or highest position. He assumed that the bird judges not only how high the sun would be at noon, but how long a time before or after the moment of observation the sun would in fact be in its noon position. If all this has been accomplished with sufficient accuracy, the bird could then judge the direction of its displacement by the experimenter. Success would depend, of

course, not only on the precision of the bird's measurement of the sun's altitude and rate of change of altitude, but also upon the accuracy of its internal clock. Since birds have not been shown to possess any of these measuring abilities to the necessary precision, and because of the complexity of the postulated extrapolation of the sun's arc, Matthews' theory has not won wide acceptance. But a considerable amount of homeward orientation could be explained by some modified form of sun-arc theory, such as Tunmore's simple rule, "Fly away from the sun if it is unexpectedly high, and toward it if it seems too low." Once again a full explanation awaits the initiative of future investigators.

Natural Conditions

Directional orientation can be based on the sun or stars, but there are also other ways it can be accomplished, at least in theory. Sea birds might maintain their headings by flying at some definite angle relative to the patterns of waves on the sea below them, although this has never been demonstrated conclusively. If this kind of navigation does occur, it would be an instance of directional orientation based on a consistent visual signal from the environment. Or birds might fly consistently downwind, which, as far as we know, they could only do by visual reference to the ground to determine which way the wind is influencing their flight paths. When evidence becomes available to show that a migrating bird is employing a certain type of directional orientation, we shall obviously have progressed a very long way toward accounting for its ability to maintain a correct course on a long migratory flight. A further problem is to account for changes in direction that may occur at certain points along the way, such as the shift from southeast to south when shore birds from northwestern Canada reach the Gulf of St. Lawrence. There also remains the truly formidable problem of explaining how the nervous system of a bird is organized to recognize a celestial signal for one directional orientation in the spring and another in the autumn.

Puzzling Directional Orientation

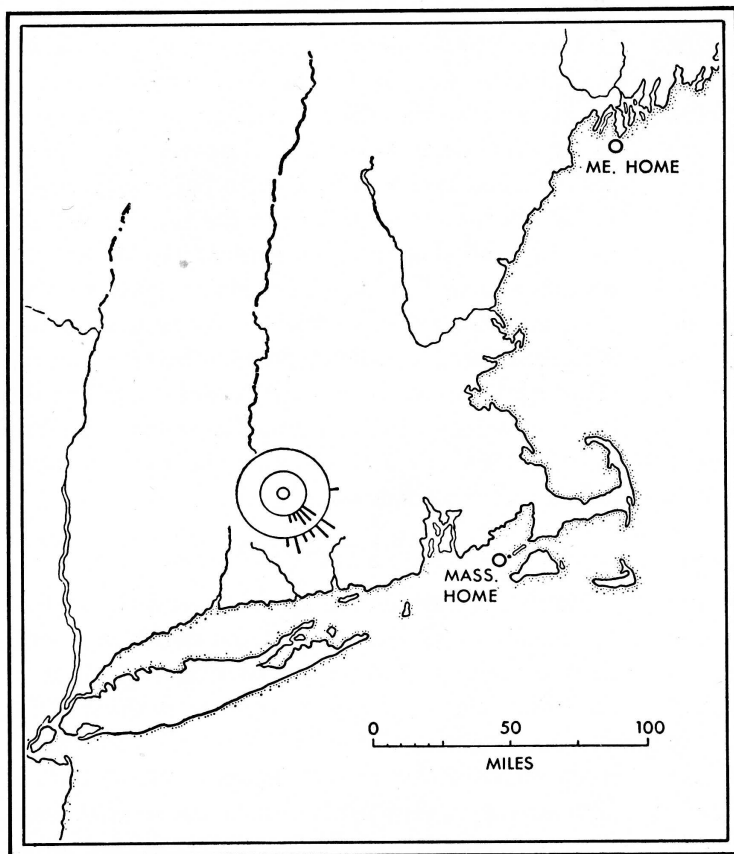
Shortly after Matthews' and Kramer's experiments had been reported, T. H. Goldsmith and I decided to study the initial headings of common terns, which

nest in considerable numbers on Penikese Island near Cape Cod. We selected suitable inland release points with a clear view in all directions, and as free of lakes that might prove distracting as any place we could find in southern New England. Wishing to keep terns in captivity as briefly as possible, we first released them at Storrs, Connecticut, the closest suitable release point that seemed far enough inland so that terns would be unlikely to see the ocean. To our pleased surprise, the terns did take off quite consistently southeast, and the average of their initial headings was almost directly toward their home island. Furthermore, when we repeated these experiments at other inland release points the same southeast headings were evident.

But all our release points were roughly northwest of Penikese Island, and, as pointed out previously, accurate homeward headings from a single direction cannot be accepted as goal-directed orientation. We therefore brought additional terns from a nesting colony on the coast of Maine to the same release

point at Storrs. For these birds the home direction was northeast. To our further surprise, and disappointment, the Maine terns headed southeast just as consistently flying toward Penikese Island as had the terns that nested there—*see map*. Neither group showed any consistent headings at all under overcast skies. Hence, we were dealing with a type of directional sun-compass orientation. It is not at all clear why common terns released inland should fly southeast, although one theory is that such a habit helps them to regain the Atlantic coast if they are accidentally carried inland by storms. But we later found that common terns nesting near Lake Michigan also headed southeast, as did control terns from Massachusetts, when both were released in upstate New York.

An equally puzzling case of directional orientation has been discovered in mallard ducks. Matthews has studied a nonmigratory population of these very abundant ducks at the Slimbridge Waterfowl Research Station on the Severn Estuary near the west



Initial headings of terns transported from their nests on two islands off the coast of Maine and Massachusetts to the same inland release point in Connecticut (small circle at center of directional heading diagram). The inner bars represent birds from the Massachusetts colony, the outer bars terns from the island in Maine. Each short bar represents a single bird; the longer bars show directions taken by two birds.

coast of England. Initially he wished to determine whether they would home to Slimbridge when released in flat, open country away from water courses. To his surprise, they always tended to fly northwest, regardless of the direction in which they had been carried away from Slimbridge. Bellrose carried out similar experiments with mallards in central Illinois, and his ducks tended to head north, even though they had been trapped on their fall migration. Both in England and in Illinois the mallards scattered at random under overcast skies. Like our New England terns that headed southeast, mallard ducks showed their northward headings only if the sky was clear.

"Nonsense Orientation"

In all three cases sun-compass orientation was underway, but the particular choice of direction has so far defied explanation. Matthews has shown recently that another population of mallards, from the parks of London, tends to fly off in other directions than the northwest headings of their Slimbridge relatives. Matthews calls this type of directional orientation "nonsense orientation," implying not that it serves no biological purpose whatsoever, but that its function is unknown to us. Many of the mallards that Matthews observed heading northwest were later recovered in all directions around the release point. Evidently the consistent northwest headings are maintained for only a short time. Possibly this behavior makes it more likely that a flock dispersed by danger can reassemble shortly afterwards.

The nonsense orientation of Matthews' mallards seems rather uninteresting in comparison with the star navigation of the Sauers' warblers, or the transatlantic homing of a Manx shearwater. But mallard ducks have proved to be excellent experimental animals, because they are abundant, live well in captivity, and because their northwest headings are so consistent, even though as yet they make no sense to us. Matthews has used his aspect of mallard behavior to discover some significant new facts about the celestial navigation of birds. He released many groups of mallards at various suitable points in all directions from Slimbridge, at all hours of the day, under clear skies, and when the sun was completely hidden by clouds. Neither the location of the release point relative to Slimbridge nor the time of day made any appreciable difference in the consistent north-

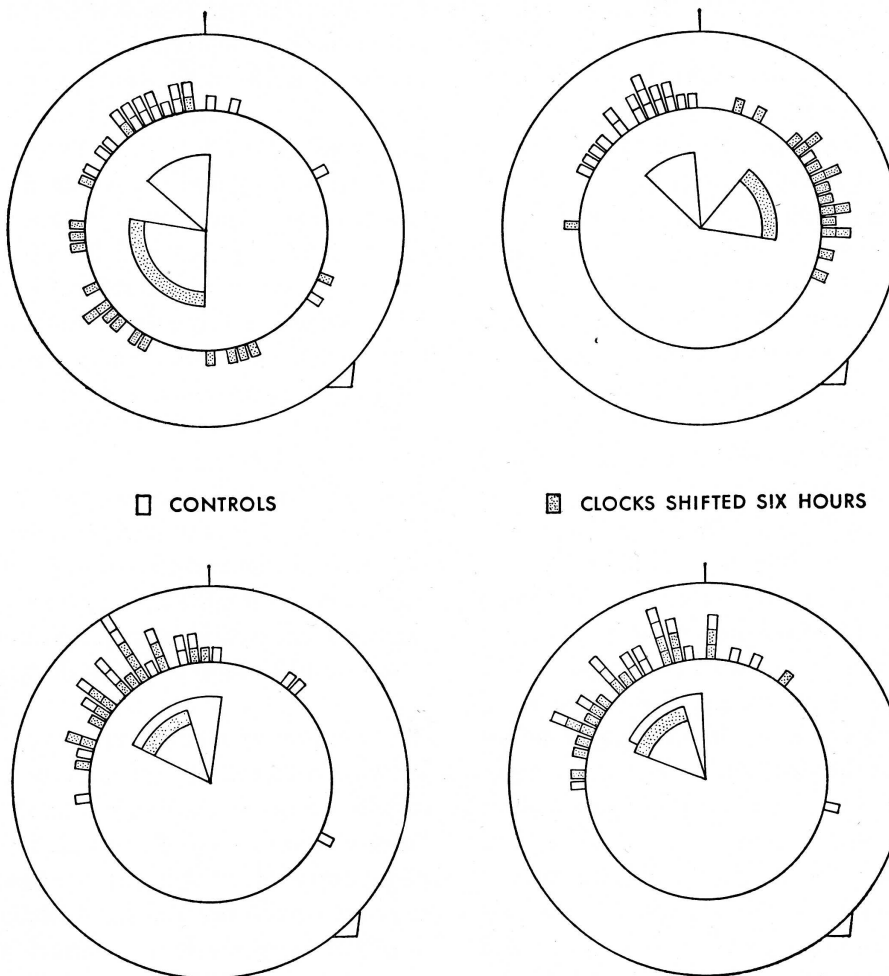
west headings. Aside from very strong winds, which deflected the birds to some extent, the weather was without effect so long as the sun was visible, either directly or as a recognizable bright spot in a thin layer of clouds.

Both Matthews and Bellrose have released mallard ducks at night. In order to follow them in the dark they attached small flashlights to the ducks' legs. These lights consist of the battery from a "Penlite" and a bulb, fastened to the battery terminals just before attachment to the bird. The lights can be followed at night for about as far as a flying duck can be seen through binoculars in daylight. The battery is secured to the duck's leg by paper tape that softens quickly in water; the bird does not remain encumbered even with this minor burden for more than an hour or two after it reaches some pond or stream. On one occasion when I had the opportunity to accompany Matthews on a release during the night, one of the ducks chose to land in a deep roadside ditch instead of flying off immediately. The flashlight traced its underwater course as the mallard dove and swam for a few minutes until the tape soaked through and the light fell off.

The results of many observations of initial headings at night were similar to those made by day. If the skies were clear, the Slimbridge mallards tended to fly northwest. Bellrose also found that Illinois mallards headed north both in daylight and at night. Evidently these ducks can use the stars as well as the sun, and their nonsense orientation is equally consistent whether based on sun-compass or star-compass orientation. Matthews observed on a few occasions that his mallards flew northwest when the stars were obscured by a thin cloud layer but the moon remained visible. Hence "moon-compass orientation" is also practiced by mallards and presumably by other birds as well.

North Star Mallards

Matthews next shifted the biological clocks that must have been operating in the ducks to permit them to head northwest consistently, regardless of the time of day or the sun's apparent position in the sky. Kramer and others had discovered that when birds were displaying sun-compass orientation in circular cages, they made the expected directional errors after their internal "clocks" had been reset.



The effects on initial headings when the biological clocks of mallard ducks are shifted. In all diagrams the open rectangles represent the headings of control birds that had not been subjected by Matthews to any clock-shifting treatment; these ducks tended to fly northwest. Stippled rectangles show headings of birds kept for several days on a shifted light cycle that reset their biological clocks six hours ahead (left-hand graphs) or behind (right-hand graphs). The sectors at the center of each graph show the angular range within which half the headings were contained. The two upper graphs show results obtained in daytime when birds had a clear view of the sun; the resetting of biological clocks produced the expected changes in headings. Evidently these birds were using sun-compass orientation.

The two lower diagrams show the result of the same experiment performed on clear but moonless nights. With the full star pattern available, the directional headings were not significantly affected by resetting the biological clocks. Were these ducks using the North Star?

Matthews used exactly similar methods to reset his mallards' clocks. He kept them in closed rooms under an artificial schedule of light and darkness for several days, until their cycles of activity, feeding, and sleeping were altered to conform to the new conditions. One group of ducks was shifted six hours ahead, another six hours behind the actual time of daybreak and dusk, and a third group was shifted 12 hours out of phase with the true day and night. Finally a control group was kept in outdoor cages under completely natural daylight and darkness.

When these four groups of mallards were set free on clear days, Matthews found the expected changes in their headings as a result of the resetting of their clocks. The controls headed northwest as usual. Those whose clocks were set ahead six hours behaved as though it was six hours later in the day, and headed roughly southwest. Similarly the ducks whose artificial schedule was six hours slow deviated in the opposite direction. The mallards twelve hours out of phase with real time headed southeast, just opposite to their usual northwest headings. As one can see from the diagrams, all these directional choices show a variation of about plus or minus thirty degrees, but the effects of resetting the birds' clocks are so clear that there can be no doubt as to their reality or significance.

These results obtained under sunny skies were in complete accord with expectations based on the previous discoveries of Kramer and his colleagues. But there was an unexpected difference when Matthews released his mallards at night, under clear skies, after resetting their biological clocks in exactly the same fashion, six hours fast, six hours slow, and twelve hours out of phase. *Under the stars all three groups showed the same northwest headings*, whether or not their clocks had been reset. This experiment tells us at once that the birds can learn more from the stars than from the sun. The sun provides only a single point of reference, and with the aid of their internal clocks birds and other animals can use it for a directional, sun-compass orientation. But Matthews' mallard ducks were using the stars for a new and more impressive type of directional orientation, which was not thrown into error, as is sun-compass orientation, by resetting their internal timing mechanisms.

There has not yet been time for Matthews' latest

discovery to be followed up by other investigations that may help to explain just how the mallards use the pattern of stars to select their favored northwest direction. One obvious possibility is that they rely on the North Star, or some group of its immediate neighbors. If so, they must have learned that these particular stars are reliable guides for orientation. Even when they find the rest of the heavens ninety degrees from their expected positions, the ducks ignore this discrepancy and fly off somewhat to the left of the North Star. Matthews may be able to obtain evidence on this point if, in the future, he is able to release mallards with their clocks shifted when a large cloud covers the sky around the North Star but leaves other stars visible. Reliance on the North Star seems to us the simplest way to achieve star-compass orientation in the face of uncertainty or error in one's judgment of time. But it is not the only aspect of the star pattern that would permit correct star-compass orientation, at least in theory. Since additional investigations will clearly be required to settle this question, it would be premature to discuss it further here.

AFTER THE PAST TWENTY YEARS of research on bird navigation it is clear that migrating birds are quite capable of setting courses by the sun, moon, or stars. Before 1940 it seemed absurd to think that they might correct for the apparent movement of sun or stars across the sky and use celestial guides to the direction appropriate for annual migrations. Still more ridiculous was the notion that the North Star might be picked out from all its fellows as a beacon for migratory flight. This last hypothesis has not been established, but it is now at least a reasonable one, well worth testing. If it is not correct, the birds in Matthews' latest experiments must be accomplishing some equivalent feat of star mapping.

Occam's razor and the "molecular" approach proved in this case to be unduly limiting. The actual facts turned out to support what had seemed romantic speculation. This does not mean that wishful thinking will prove correct in more than a handful of other cases. But the celestial navigation of migratory birds has demonstrated that all facets of biology are not yet reduced to dull and routine affairs. So many biological phenomena still defy adequate explanation that we may realistically hope, in due course, for other future developments as pleasantly surprising.

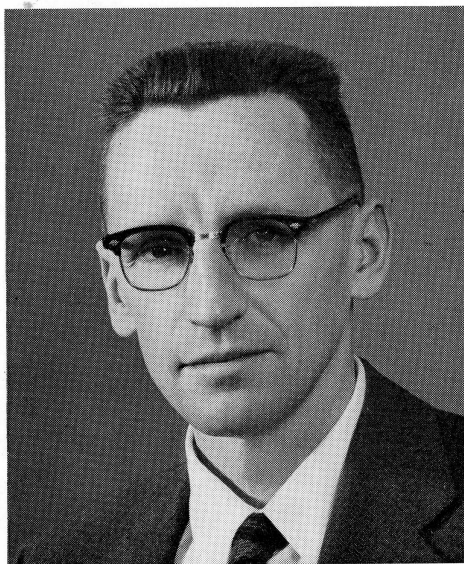
NEW FACULTY

ELEVEN NEW appointments to the faculty were announced by President Bronk in August. These appointments include a biologist, two mathematicians, a comparative pathologist, a physicist, and a philosopher.

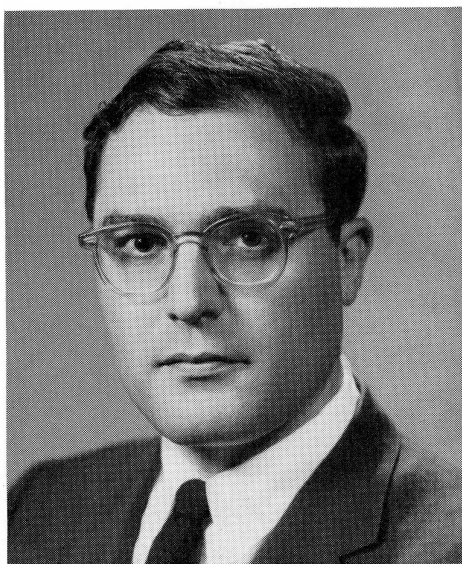
Donald R. Griffin and Gian-Carlo Rota have been appointed Professors in the University. Dr. Griffin, a biologist, was graduated from Harvard College in 1938 and received the M.A. and Ph.D. degrees from Harvard University, the latter in 1942. He then progressed from Assistant Professor to Professor in the zoology department at Cornell, and since 1953 has been Professor of Zoology at Harvard, where he also served as Chairman of the Department of Biology from 1962 to 1965. Dr. Griffin, an authority on animal physiology and behavior, is best known for his work on the way bats and other animals orient themselves and find food by echolocation. His investigations have touched upon a wide range of zoological phenomena, from the ability of fish to hear underwater sounds, to the devices that enable small birds and mammals to survive the arctic winter. In 1962 he received the Daniel Giraud Elliot Medal of the National Academy of Sciences for his first book, *Listening in the Dark* (1958). He is also the author of the

books *Echoes of Bats and Men* (1959), *Animal Structure and Function* (1962), and *Bird Migration* (1964). A chapter from the last book, adapted for the *Review*, is republished in this issue. Dr. Griffin is organizing his new laboratory at the University and will also begin research in animal behavior under the joint sponsorship of The Rockefeller University and the New York Zoological Society. One of Dr. Griffin's first projects will involve the development of a wind tunnel for studying birds in flight.

Gian-Carlo Rota, Professor of Mathematics, was born in Vigevano (Milan), Italy, and became an American citizen in 1961. He received the B.A. degree from Princeton University in 1953 and the M.A. and Ph.D. from Yale University in 1954 and 1956. The following year he was a postdoctoral fellow at the Institute of Mathematical Sciences of New York University and Benjamin Peirce Instructor in Mathematics at Harvard, continuing in the latter post until 1959 when he was appointed Assistant Professor in the mathematics department at the Massachusetts Institute of Technology. He remained at MIT, becoming Associate Professor and then Professor of Mathematics, until joining the faculty at Rockefeller. Dr. Rota is a specialist in combinatorial theory and



DONALD R. GRIFFIN



GIAN-CARLO ROTA

in problems of analysis arising from probability theory. He is also interested in applications of combinatorial techniques to problems in physics and other sciences, and in the foundations of mathematics. Dr. Rota is author of the book *Ordinary Differential Equations* (1962) and is on the editorial board of several mathematical periodicals, including the forthcoming *Journal of Combinatorial Theory*, which he helped organize. At Rockefeller Dr. Rota will continue his research in combinatorial theory which, simply stated, is the science of counting, and one of the earliest branches of mathematics. It deals with the classification and properties of finite and discrete structures, in contrast with classical mathematical analysis, whose object is the continuum. Some typical elementary problems are the discovery of all types of symmetry, the construction of comma-free languages, and the probability of a nonself-intersecting random walk. Dr. Rota's long-range plans include taking a closer look at combinatorial problems arising in the life sciences.

Robert W. Leader has been appointed Associate Professor in the University, where he will establish a new laboratory of comparative pathology. He will also assume the task of extensive renovation and enlargement of experimental animal facilities. Dr. Leader was educated at Washington State Univer-



ROBERT W. LEADER

sity, receiving the B.S. and D.V.M. degrees in 1952 and the M.S. in 1955. He continued at Washington State, progressing from Instructor to Professor of Veterinary Pathology, until joining Rockefeller. He has done considerable work on canine hepatitis and hypergammaglobulinemia and other systemic changes in Aleutian disease in mink. Dr. Leader will also carry on his research on hereditary abnormalities of the lysosomes in leukocytes of children, cattle, and mink — a cooperative project in which he has collaborated with Professor James G. Hirsch's group for about two years. As Visiting Professor of Pathology at New York Medical College, Dr. Leader will continue another joint project, on the study of connective tissue diseases, with Dr. Bernard Wagner.

William Feller is a Visiting Professor in residence at Rockefeller. Professor Feller, a mathematician, was born in Zagreb, Yugoslavia. He received the M.S. degree from the University of Zagreb in 1925 and a year later the Ph.D. from the University of Göttingen. He has been a faculty member at the universities in Kiel and Stockholm (where he was mathematical advisor to the Institute of Experimental Biology); and at Brown University and Cornell. Since 1950 he has been Eugene Higgins Professor of Mathematics at Princeton University. Dr. Feller was the first Executive Editor of *Mathematical Reviews*, doing much of the original work involved in founding that periodical, and has served as President of the Institute of Mathematical Statistics. He is author of the highly influential book *An Introduction to Probability Theory and Its Applications, Volume One* (1950), which has been widely used as a textbook and as a compendium for mathematicians and scientists, both academic and industrial. Volume One has been translated into numerous languages, and Volume Two is to be published early next year.

Visiting Associate Professors will be Oscar W. Greenberg, from the Department of Physics and Astronomy at the University of Maryland, who will be working with Professor Pais, and Dudley Shapere, a philosopher of science from the University of Chicago. New appointments to Assistant Professor include Emil C. Gotschlich, Jerome L. Knittle, Egon Macher, Mart Mannik, and Morton P. Printz. The appointment of Carl Pfaffman as Vice President and Professor has already been announced in the *Review* for January-February 1965.

FACULTY PROMOTIONS



MERRILL W. CHASE

FIFTEEN MEMBERS of the faculty have received promotions, President Bronk announced on August 6.

Merrill W. Chase has been appointed a Professor in the University. Dr. Chase received the A.B. and Sc.M. from Brown University in 1927 and 1929. During this period he was a Demonstrator in Biology, teaching bacteriology and immunology. He then spent what he considers an especially significant year studying at the University of Chicago, and received

the Ph.D. from Brown in 1931. After conducting an advanced course in pathogenic bacteria at Brown for a year, Dr. Chase came to Rockefeller to work with Dr. Karl Landsteiner. From 1944 to 1955 he worked under Professor René J. Dubos, and since 1956 he has conducted his own laboratory of immunology. His present work is on the mode of induction and cellular transfer of delayed-type hypersensitivity (for which studies he raises "isogenic" lines of guinea pigs), immunologic unresponsiveness, and the manner of conjugation of chemical haptens *in vivo*. Dr. Chase is on the editorial board of the *Journal of Immunology* and has served as President of both the American Association of Immunologists and the New York Branch of the American Society for Microbiology.

Promotions to Associate Professor include Doctors M. A. B. Bég, Enoch Gordis, Stephen I. Morse, Edward Reich, Martin Rizack, Maria Rudzinska, and Curtis A. Williams. Newly promoted Assistant Professors are Marvin Barsky, Barbara Bowman, Eric H. Davidson, Teh-Yung Liu, Priscilla J. Ortiz, Michel Rabinovitch, and Gaynor Wild.

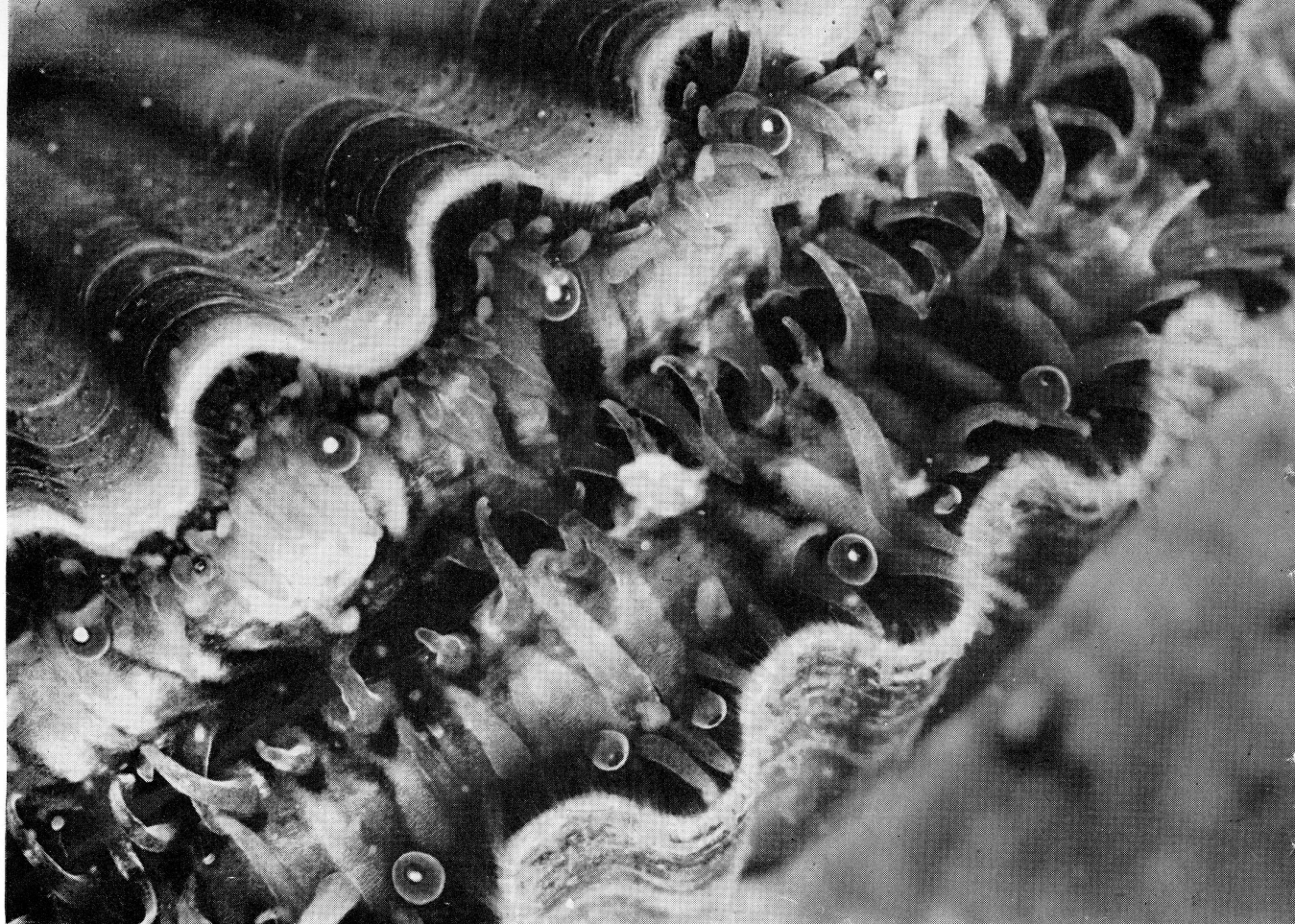
Francis O. Holmes, Rebecca C. Lancefield, and John B. Nelson have been appointed to emeritus status and will continue their research — Dr. Holmes at his farm in New Hampshire and Doctors Lancefield and Nelson at Rockefeller.

NEW STUDENTS

TWENTY-FIVE NEW students have been admitted as candidates for the Ph.D. degree:

WILLIAM H. BEERS, A.B. Harvard College
KATE L. BERNSTEIN, A.B. Radcliffe College
THIERRY BOON, Catholic University of Louvain
ANN E. CAMPBELL, A.B. Bryn Mawr College
WILLIAM R. COLQUHOUN, B.A. The Johns Hopkins University
NORA C. DEBRUNNER, A.B. Hunter College of The City University of New York
DAVID FORMAN, A.B. Harvard College
RONALD FOX, B.A. Reed College
ANNE S. GIFT, B.S. Jackson College in Tufts University
PAUL D. GOTTLIEB, A.B. Princeton University
ROBERT E. JOHNSTON, B.A. Dartmouth College
ISTVÁN KRISKÓ, B.A. Reformed College of Pápa, Hungary, M.S., M.D. Baylor University

WILLIAM W. LOWRANCE, JR., B.A. University of North Carolina
CARL LUNDEEN, B.A. University of North Carolina
LINDA BRODY LYONS, B.A. Pembroke College in Brown University
CARLTON H. PAUL, B.S. California Institute of Technology
SETH L. SCHOR, B.A. The University of Chicago
ROBERT SHAPLEY, A.B. Harvard College
SANDRA WALDMAN SIMON, A.B. Barnard College
ELIZABETH M. STEARNS, B.A. Bryn Mawr College
ARNOLD STERN, M.D. Boston University School of Medicine
CHRISTOPHER T. WALSH, JR., A.B. Harvard College
DAVID C. WARD, B.Sc. Memorial University of Newfoundland, M.Sc. University of British Columbia
TIMOTHY C. WILLIAMS, B.A. Swarthmore College
DAVID D. WOOD, A.B. Harvard College



THE BRIGHT-EYED SCALLOP

THE GODDESS APHRODITE was fashioned of sea foam and, according to some legends, landed on the island of Cythera borne on a scallop shell. It still remains both her special symbol and that of Venus, her Roman counterpart. In the Middle Ages the scallop became the badge worn by pilgrims journeying to Santiago de Compostela in western Spain, the shrine of the apostle St. James, who in life had been a fisherman. Eventually it came to be the identifying emblem of James himself, as immortalized gastronom-

ically in *coquilles St. Jacques*. And almost from the beginning of heraldry, the "escallop" was used as a heraldic device, second only perhaps to the fleur-de-lis and the lion rampant; in a sixteenth-century text on "armorie" it is described as "a shelfishe, engendered of the Ayre and dew . . . the shel thereof is the fairest instrument that can be, being of nature's making."

The artists of the Renaissance also found the scallop a "fair instrument," and just as they liberated other sacred images from religious bondage — using the Madonna figure, for example, to portray their beloveds — so, too, they secularized the scallop shell. From that time on it served as a recurring motif in paintings, architecture, and tapestries; on furniture and fountains; for snuff boxes and bonbon dishes; and it now lives on as the familiar roadside symbol of gasoline service stations.

Pliny called the scallop "Pecten" from the Latin

ABOVE: eyes of *Pecten* irradiates in mantle fringe VISHNIAC

word for comb, the characteristic radiating ridges of its shell resembling the combs worn in the hair of the ladies of Rome. All of the almost three hundred species of *Pectinidae*, found scattered throughout the warmer waters of the world, have this same familiar pattern, although they vary greatly in size, color, and form. The deep-sea scallop, the species harvested commercially, has a shell some six inches in diameter. Colors vary widely, ranging from white through tans, browns, steel blues, reds, and purples, to black. Most shells have the delicate fluting seen in artists' renditions, but some are characterized by heavy, knobby ridges; one species, for example, of which Dr. Floyd Ratliff has a specimen, is known as the lion's paw because of its massive appearance and knucklelike protuberances.

For those accustomed to the more decorous behavior of most bivalves, the most surprising feature about the scallop upon first encounter is its liveliness. *Pecten* can leap through the water a foot or more by clapping its shells together. The valves open to about 30 degrees upon relaxation of the strong internal ligament just inside the hinge and then can close with a snap of the powerful central adductor muscle. This rapid motion expels a forceful jet of water which provides the propulsion. Lining the scallop shell is a smooth coating, or mantle, from which the shell is secreted. A curtainlike fold in the mantle, the velum, controls the direction of water expulsion. With the velum lowered, the water shoots out through the two lugs or "ears" at the hinge point, and so the scallop moves forward. Or by raising the velum on one side *Pecten* can spin itself around — to avoid the molestations of a small crab, for instance — often propelling the intruder away at the same time. When the velum is raised in the front, the jet of water is pushed forward and the scallop leaps backward, hinge-first. This is its escape motion. A freshly caught scallop will beat its shells together frantically on the palm of one's hand until it is exhausted.

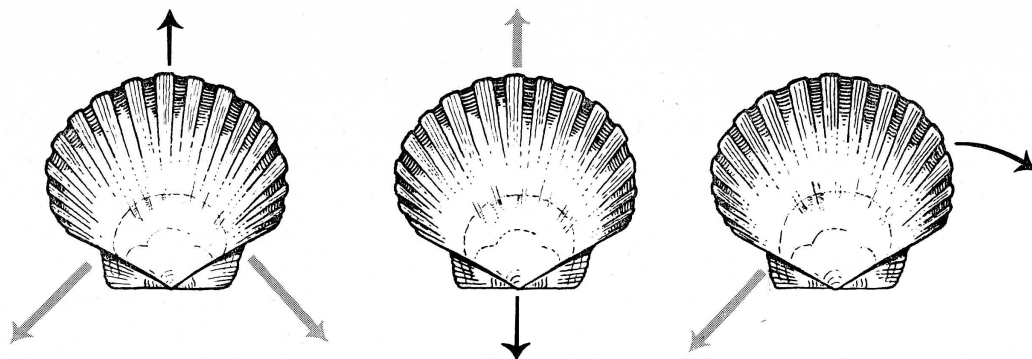
A scallop is easy to pry open, at least compared to the stubborn clam or oyster which yield, in the opinion of many seaside foragers, only to some special magic possessed by the operators of seafood establishments or to being dropped from great heights by seagulls. Once the scallop has been opened the uninitiated observer is again taken unawares. The short, white cylinder listed on American menus as the scal-

lop is actually the adductor muscle alone and occupies only a small portion of the interior of the shell. Underlying the large reproductive gland or gonad, and protruding out from it, is a comma-shaped gill which curves around the adductor muscle, following the arc of the shell. Food is filtered from the tip of the gill toward the mouth, which is located with the other digestive organs between the adductor muscle and the hinge. Every item of the scallop's internal anatomy is eminently edible, and the reproductive gland, a veritable caviar, is the best of all; but since the scallop will not stay closed — like the tight-shelled clam or oyster — it spoils, and so only the white muscle is distributed commercially.

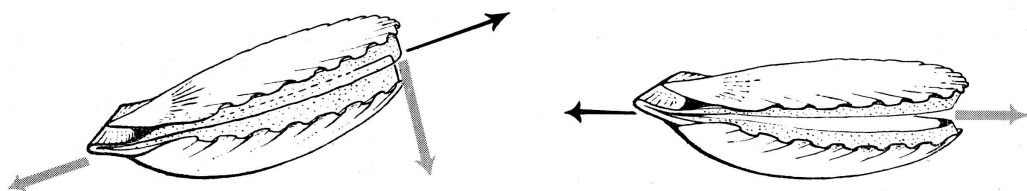
When undisturbed, the scallop drifts along the sandy bottom of the bay or ocean, lying horizontally (and always with the same valve down), rather than embedding itself vertically as do most other bivalves. Its shell remains slightly open to admit the water currents bringing in food and oxygen, a process aided by the beating of the cilia in the gills. Shining like pinpoints of light through this narrow slit between the fluted shells may be seen what many scientists, including some at The Rockefeller University, consider the scallop's most intriguing feature: a double row of brightly shining eyes.

The eyes of *Pecten* are eyes in the truest sense. Other bivalves, as judged by their ability to orient themselves in relation to light, have photosensitive areas; but the eye of the common scallop is far more complex, possessing cornea, lens, and a double-layered retina, the peculiar properties of which will be discussed in more detail. Behind the retina is the

NOTE: Professor Rollin D. Hotchkiss reports that as a young student at Woods Hole, some thirty years ago, he struck upon a brilliant idea for combating the intransigence of the bivalve adductor muscle. When muscles are tired, as is well known, they are flooded with lactic acid. Therefore, he reasoned, one might be able to deceive a mollusc muscle into believing it was tired by exposing it to a dilute solution of this quite harmless substance. He tested this theory first on *Pecten* and to his surprise, far from thinking it was tired, *Pecten*, even at very low concentrations of lactic acid, flapped wildly about in the water in its typical escape maneuvers. Young Dr. Hotchkiss then became convinced that he had struck upon some peculiar and special phenomenon involving scallops and lactic acid. But when he ran a few control experiments, he discovered weak solutions of almost any acid drove *Pecten* into a molluscan frenzy. At this point he abandoned the whole experimental program, and since then Dr. Hotchkiss and the rest of us have scarred ourselves anew each season with oyster and clam knives.



How the scallop swims. The heavy, grey arrows denote the propelling jets of water, the thin black arrows the direction in which it moves. Above forward swimming movements. Below "escape" movement.



tapetum lucidum, "bright carpet," a mirroring surface such as that found in the eyes of cats and some other night-prowlers. It is the tapetum that gives the eyes their special iridescence. For those who, like Aristotle, are interested in questions of homology and analogy in the parts of living creatures, the eye of the scallop—reached by such a distant evolutionary pathway from our own—offers a provocative example of convergence of form.

The scallop's eyes are remarkable not only for their complexity but for their number. In one specimen of *Pecten irradians*, the blue-eyed scallop which can readily be found in local bays and inlets, Dr. Floyd Ratliff counted 103 eyes almost equally distributed between the upper and lower layers. These eyes are located along the margins of the shells among the thick tentacles which form the fringe of the mantle. They are on short stalks and are scattered irregularly among the tentacles, which overhang them slightly, like long bangs. The optic nerves of each eye connect with the circumpallial nerve that traverses the margin of the mantle, connecting eventually with the scallop's "brain," a pair of ganglia united by a cerebral commissure. These ganglia lie on either side of the gullet, between the adductor muscle and the hinge. The circumpallial nerve carries all the information from the chemoreceptors and touch receptors of the tentacles, and also conducts the efferent im-

pulses coming from the centrally located ganglia.

The eye of *Pecten* is literally blue, unlike the eye of the human being. Blueness in the human eye, though admired by some poets, is a developmental anomaly. In "blue-eyed" persons the stromal cells of the iris fail to develop pigment (as they do in brown- or black-eyed persons) and the reddish backing of the retina shines through as blue by the same sort of optical trickery that makes the red blood of the veins seem blue through white skin, according to Walls. In the blue-eyed scallop, on the other hand—as one can see most vividly through the dissecting microscope in Dr. Ratliff's laboratory—the entire area corresponding to the white of the human eye is a soft powder blue, in the center of which is an iridescent twinkle, the reflection from the tapetum.

New eyes form constantly in the growing *Pecten*, apparently appearing more or less at random as room becomes available for them. Many years ago Dr. Earl Butcher of Hamilton College, working at Woods Hole, studied the stages in eye formation in a species of scallop. An eye begins as a group of pigmented cells forming at the base of a tentacle and growing inward as a bud or cup which develops into a vesicle. The retina differentiates from the wall of the vesicle that is turned away from the light, and the tapetum develops from the other wall. Layers of connective tissue cells differentiate into the retina.

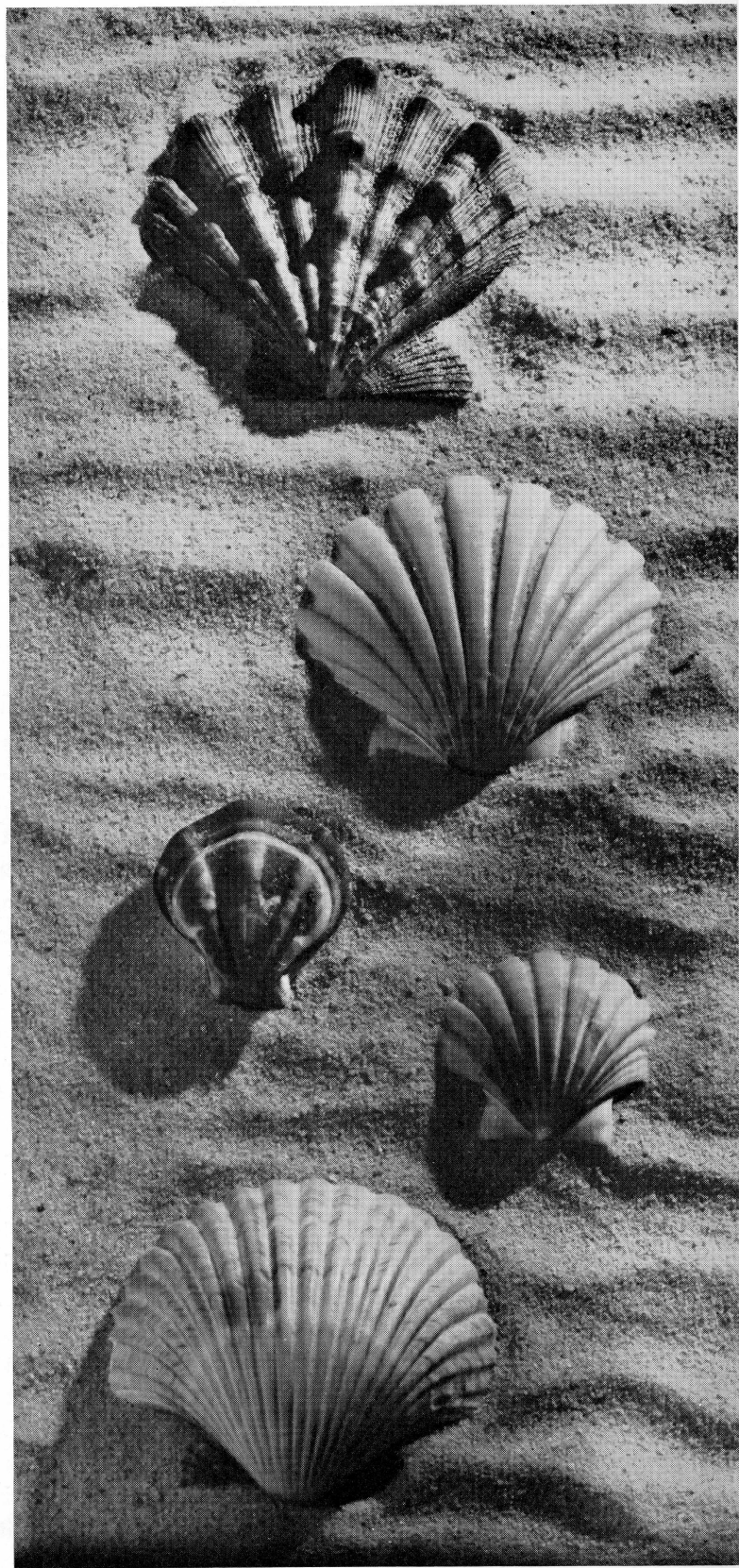
As the eye develops, it is pushed outward on the end of a stalk which turns it toward the light. The epithelium overlying the lens loses its pigmentation to form the cornea, while the cells at the edge of the eye grow darker, eventually becoming the "iris." Nerve cells grow out from the retinal layers reaching toward and finally connecting with the arc of the circumpallial nerve.

Butcher found that the scallop's eye possesses remarkable powers of regeneration. When every single eye was removed from a medium-sized scallop, *Pecten* quite effortlessly grew an entire new complement in about forty days. In a vain attempt to discover the initiating stimulus for eye growth, Dr. Butcher cut the area of the circumpallial nerve supplying some of the tentacles, but found this had no effect on the regeneration of eyes in the area. He also showed that eye buds as well as fully developed eyes could be transplanted to another location—the edge of the gonad proved most convenient—and would differentiate and grow normally, sending out a long, hopeful branch of optic nerve. In other words, both the potential and the inspiration for eye formation lie in the epithelial cells themselves.

Professor H. Keffer Hartline became interested in *Pecten* for different reasons. The scallop has a vigorous "shadow reaction," as Aristotle noted some twenty-five hundred years ago. When a dark body passes over it, *Pecten* closes. Several investigators, including a University trustee, Lord Adrian, and R. Matthews and Ragnar Granit, had shown that many vertebrate eyes respond to a decrease in light intensity by discharging impulses into the optic nerve. Dr. Hartline himself had demonstrated that these "off" responses in the vertebrate eye are transmitted by groups of fibers which do not respond to "on" conditions: either to a light being turned on or to steady illumination. Because of the very complicated cross-connections in the "wiring" of the vertebrate eye, however, it was not possible to determine whether these "off" impulses represented the response, and the only response, of particular receptor cells.

This predicament resulted in the second attraction of *Pecten* for Professor Hartline, its double retina—a feature found nowhere in the vertebrate world.

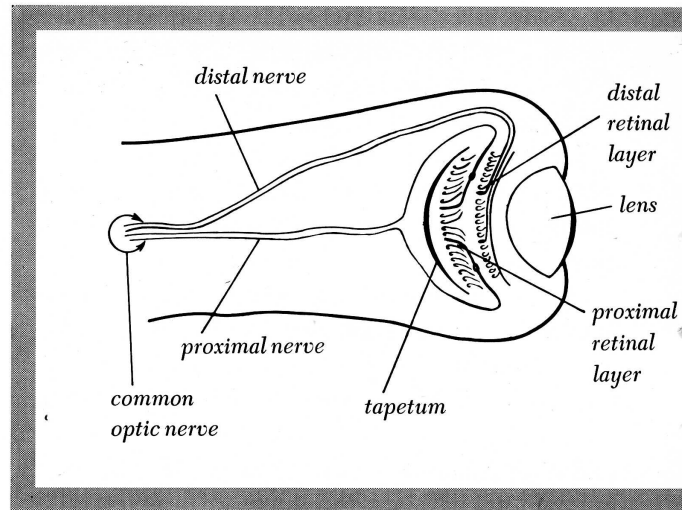
"...they vary greatly in size, color, and form." *Lion's paw*, top, and other species of Pectinidae



More recent experiments by Dr. Michael Land of University College, London, have disclosed another extraordinary phenomenon involving the double retina. In the eye of man and of the camera, the lens forms an image on the light-sensitive area behind it — either the retina or the photographic emulsion. Dr. Land has shown that in the eye of *Pecten*, however, the lens does not form an image on either retina. Rather, according to his calculation, the image is reflected from the argentea, the bright mirrorlike coating of the tapetum, back to the distal retina. The distal retina is an almost perfect hemisphere, and the concave tapetum lying behind it forms a second and concentric hemisphere, so the image can be reflected from the mirror surface over the entire area of the distal retina. These two retinal layers are anatomically separate. Both are inverted, like the retina of the vertebrate eye, with the rows of receptor cells pointing toward the back of the eye so that the light must pass first through the transparent layers of nerve fibers to reach the light-receiving points. In *Pecten* the cells in the proximal layer, nearest to the back of the eye, are long and rodlike; those in the distal end are short and rounded. The proximal and distal branches of the optic nerve remain separate for one or two millimeters before fusing to form the common optic nerve. This unique feature makes it possible to record separately the activity of the distal or of the proximal fibers. For experimental purposes Dr. Hartline placed a bright blue eye of *Pecten irradians* in a moist chamber filled with sea water. The eye was illuminated through the glass front of the chamber, and short nerve twigs were brought out and suspended on fine wick electrodes connected to an oscillograph.

In these experiments Dr. Hartline found what he had hoped for. There was a marked difference between the responses from the two retinal layers. The response from the proximal cells resulted from the onset and continuation of illumination, and fibers from these cells never showed the “off” response. These effects are similar to those seen in the optic nerve fibers of *Limulus*, the faithful and archaic collaborator in so many investigations originating in Dr. Hartline’s laboratory.

In contrast to the proximal cell responses, the nerve fibers from the distal cells showed no activity whatsoever when light shone on the bright blue eye.



The eye of Pecten (after Dakin)

Distal cell responses were elicited only when the light was turned off or suddenly reduced in intensity. These pure “off” responses are practically indistinguishable from those seen in the “off” fibers of the vertebrate eye and led Dr. Hartline to the question of whether, contrary to the usual opinion, there exist in the vertebrate eye, as well as in *Pecten*, special sensory cells that respond only to the cessation of the light stimulus.

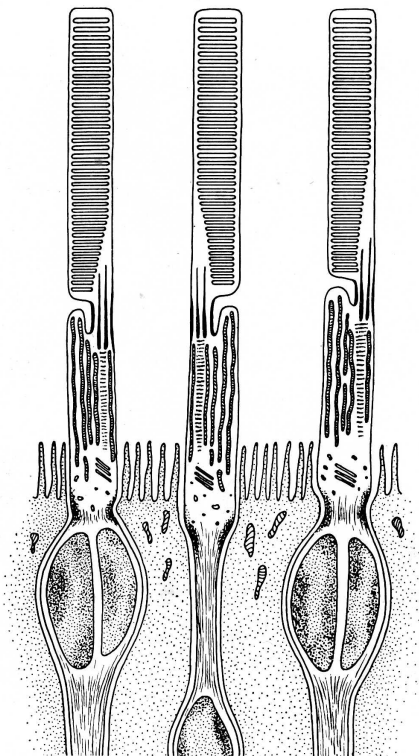
Pecten has also been studied by Dr. Floyd Ratliff, who at this writing is keeping three dozen scallops in an aquarium of Instant Ocean along with a remarkably large barnacle and a tube worm. In his investigation he placed an electrode on the posterior pole of the eye and inserted another near the lens in order to study the change in electrical potential across the eye in response to light. This is the field in which Baron Edgar Douglas Adrian of Cambridge had been one of the great pioneers some thirty-five years ago. Dr. Ratliff was able to demonstrate a retinal action potential of approximately one millivolt when the eye was fully dark-adapted. He also found that recovery of maximum sensitivity of the eye following exposure to light takes about 40 minutes, approximately the same time as it takes the human eye to become completely adapted to the dark.

More recently, Dr. William H. Miller, formerly at the University and now at Yale, has made electron microscope studies of the “off” cells of the eyes of *Pecten*, comparing them to the photoreceptors of the

vertebrate eye. In the vertebrate, the receptor areas of the rods and cones resemble tall stacks of coins. The coinlike appearance is presumed to indicate that this area is composed of separate layers or lamellae. Connecting each cylinder with the nucleus and axon of the elongated cells is a stalk that has the typical internal structure of a cilium, a ring of nine fibrils or pairs of fibrils usually circling two central fibrils. This same general internal structure is found in the cilia and flagella of protozoa, in the hairlike processes that line the vertebrate respiratory tract and the gills of molluscs, and in the whiplike tail that propels the human sperm.

Stalks with this same ciliary structure are also found at what are believed, by analogy, to be the bases of the receptor ends of the distal retinal cells of *Pecten*. The receptors themselves are not composed of coinlike stacks, however; but, judging by the electron micrographs, the individual cilia splay out into broad leaves which fold over upon one another like the leaves of a cabbage.

Schematic drawing of retinal receptors (rods) in the vertebrate eye showing "stacks of coins" and connecting cilia



Graduate Fellow Jack W. Bradbury has been interested in the question of the sensory function of cilia and has made some studies on the ciliary bases of the photoreceptors of starfish — small reddish spots located at each point of the star. From his survey of the literature, he reports that many — perhaps half — of the sensory organs of both vertebrates and invertebrates seem to be derived from cilia, including the chemoreceptors of insects, the touch receptors on the suckers of octopi, the mechanoreceptors of the human ear, and the olfactory receptors in the human nose.

Thus the eyes of man and *Pecten* appear to share with one another and with many other creatures a common though far-distant ancestry, perhaps linked through some long-absent phytoflagellate. Both also, as Dr. Miller points out, have solved the problem of photoreception by presenting a series of membranes — in one case, the "coins"; in the other, the "cabbage leaves" — to the incoming light waves.

No one ventures to answer the question of why — by what evolutionary byway — the scallop acquired any eye at all, much less one so marvelous. The feeding habits of the scallop, like those of most of its relations, involve only the sifting of whatever riches are brought to it by the tides and currents of its world. Its chief enemy is the starfish, which locks the scallop in a firm embrace, pulls apart the valves by the suction exerted by its tube feet, and extrudes its stomach around the soft parts of the mollusc. If juice extracted from the starfish is released into the waters surrounding *Pecten*, it reacts immediately with its characteristic leap of alarm, in response to stimulation of the chemosensory receptors in its tentacles. But a model of a starfish dangled before its 100 shining eyes is greeted only with molluscan sangfroid. In other words, its eyes seem to serve neither in the quest for food nor for escape from predators.

At a loss for a logical interpretation, one can only recall the centuries through which its lovely, fluted shell has been a source of aesthetic delight to the eyes of man; and so one is led to hope, in foolish human fashion, that some of the objects that pass before the eyes of *Pecten* as it floats along the bottom of the sea bring to it also some scalloplike equivalent of pleasure.

"The Bright-eyed Scallop" was written by Helena Curtis



Electron micrograph showing cross-section of receptor end of distal retinal cell in Pecten

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One of many scallop designs on façade of Founder's Hall

THE ROCKEFELLER UNIVERSITY

NEWS & NOTES

Honors and Awards

PROFESSOR GEORGE E. UHLENBECK has been elected a foreign member of the Accademia Nazionale dei Lincei, the Accademia announced in July. The forerunner of the present-day Accademia, the Accademia dei Lincei, existed during the first quarter of the seventeenth century. The proceedings of the society were written down as *Gesta Lynceorum*, and have the distinction of being by far the earliest (1609) recorded publication of scientific endeavors by any society.

Henry G. Kunkel, Professor in the University, was awarded the first annual Allergy Foundation award for his research in allergy. The award, made on the second of July, carries a \$1000 honorarium.

In August it was announced that Dr. Martin Levey, Guest Investigator, had won the \$1000 Dexter Award of the American Chemical Society's Division of History of Chemistry, sponsored by the Dexter Chemical Corporation. An internationally known historian of chemistry, Dr. Levey has written eleven books and seventy-five articles on ancient science based on medieval Latin, Arabic, Persian, and Hebrew sources.

The Franklin Institute in Philadelphia has also announced the award of the Elliott Cresson Medal to Dr. Donald D. Van Slyke, Member Emeritus of the University. Dr. Van Slyke will receive the award at the Annual Medal Day ceremonies on October 20.

Ekistics Meeting

FROM JULY 12 to July 19 Professor Theodosius Dobzhansky was on board the *Semiramis*, visiting some of the Greek Islands and attending the Third Delos Symposium sponsored by the Athens Technological Institute — Athens Center of Ekistics. The Symposium brought together a group of men and women of different professional, cultural, and national backgrounds to consider the continuing and accelerating crisis of world urbanization. Dr. Dobzhansky's contribution was "On Possible Evolutionary Conse-

quences of Different Settlement Patterns," in which he said "we must see to it that both the genetic and the cultural evolutions of the human species be directed towards the ends which we, humans, consider good and desirable. Apart from the maintenance of physiological health, this means development of those human qualities which led Aristotle to characterize man as the 'politikon zoon.'" Ekistics, the study of human settlements, is of interest to people in many different fields, and among the participants were such figures as historian Arnold J. Toynbee, architect Richard Llewelyn-Davies, and biologist C. H. Waddington from Great Britain; American designer and engineer R. Buckminster Fuller; and anthropologist Margaret Mead. The *Semiramis* stopped at Skiathos, Thassos, Samos, Rhodos, Santorini, and Myconos, and the closing session of the Symposium was held in the ancient theater of Delos.

Journal Tercentenary

THE SCIENTIFIC learned journal and indeed scientific journalism began with a modest sixteen-page pamphlet in 1665: no. 1 of the *Philosophical Transactions* of the Royal Society, with the lead article on "improvement of Optick Glasses." This summer, 300 years later, the theme of no. 1086 (vol. 257) is optics still, but of the electron variety: "The Geometrical Aberrations of General Electron Optical Systems."

Apprehensive of a dearth of manuscripts, the Council of the Royal Society directed the editor, Henry Oldenburg, to print "on the first Monday of every month, if he have sufficient matter for it." But it was the plague, "the great Mortality in London," that suspended publication for three months the first year and forced a change of printers from London to Oxford. Also started in 1665 was the *Journal des Sçavans* in France, but it was primarily a book-reviewing journal stimulated by the new art of printing — production increased from 65,000 volumes in the period 1450-1550, to over 225,000 by 1665.

"The *Philosophical Transactions* were Oldenburg's own invention," *The Times Literary Supplement* wrote recently, "as he reminded the Fellows of the Royal Society, they represented 'onely the Gleanings of my *private* diversions in broken hours'.... Important papers for communication to the society were written in the form of letters to some Fellow, very

"that the Curious and Learned may be invited and encouraged to search, try, and find out new things, impart their knowledge to one another, and contribute what they can to the Grand Design"

often Oldenburg... Undoubtedly the most famous example is Newton's paper on light and colors."

The idealism of Oldenburg, often a ruthless editor demanding direct and simple style, is shown in his preface to a later number. He writes, "I hope, our Ingenious Correspondents have examin'd all circumstances of their communicated Relations, with all the care and diligence necessary to be used in Collections; not only taking up old Fame, or flying Reports, upon too easie Truth; ..."

Communication by letter encouraged an economy of exposition more direct than was usual in books, and this simpler style influenced journals devoted to science. It finds skilled expression in our own distinguished *Journal of Experimental Medicine*, founded by William H. Welch, first President of the Board of Scientific Directors; as also in *The Journal of General Physiology*, founded by Jacques Loeb; in *The Journal of Cell Biology*, which has just completed its first decade, and in the *Journal of Lipid Research* and the *Biophysical Journal*.

...from the bookshelf

MACH BANDS: *Quantitative studies on neural networks in the retina*, by Associate Professor Floyd Ratliff. San Francisco: Holden-Day, Inc., August 1965.

Dr. Ratliff's book is the first devoted to a detailed consideration of these visual phenomena, and it appears, appropriately, on the one-hundredth anniversary of their discovery by Ernst Mach. "Mach's application of mathematical modes of thought to the study of the nervous system was so far ahead of the times that his papers attracted little attention when they first appeared," Dr. Ratliff states in his preface; "... only within the last quarter-century or so have the techniques of electrophysiology finally become sufficiently advanced to provide a sound empirical foundation for such studies. The interplay of the fundamental neural processes of excitation and inhibition, about which Mach could only speculate, can now be observed directly and with relative ease in practically

PHILOSOPHICAL
TRANSACTIONS:
GIVING SOME
ACCOMPT
OF THE PRESENT
Undertakings, Studies, and Labours
OF THE
INGENIOUS
IN MANY
CONSIDERABLE PARTS
OF THE
WORLD.

Vol I.

For Anno 1665, and 1666.

In the SAVOY,
Printed by T. N. for John Martyn at the Bell, a little without Temple-Bar, and James Allestry in Duck-Lane,
Printers to the Royal Society.

all parts of the nervous system." Dr. Ratliff uses as examples not only specimens from the laboratory but an American Indian pictogram, Banquo's ghost, and "heat waves" rising from pavement.

Summer Biology

DURING JULY and August twenty-one graduate fellows at Rockefeller again taught a summer biology course for high school students from the New York City area. Eighteen students, most of them entering their senior year, attended the course, which covered topics in chemistry, biochemistry, genetics, microbiology, development, physiology, neurophysiology, and behavior. Lectures were given in the morning, and laboratory work took up afternoons and some evenings. During the two weeks devoted to chemistry and biochemistry, students learned basic techniques such as paper chromatography, spectrophotometry, and qualitative analysis. One genetics problem was the identification of the "lac" region of *E.*

coli; during the week devoted to microbiology there was a very early morning field trip to Pelham Bay Park "to go out with the tide;" two topics in the development unit were seed germination and the development of *Xenopus laevis*; and for neurophysiology and behavior, salamander nerve regeneration and cockroach behavior were examined. Graduate fellows Lyndell L. Millecchia and Barry W. Peterson were co-chairmen of the committee that organized the course and chose the limited number of students from the many applicants.

Alumni

ROGER E. THIES, Ph.D. 1961, has been appointed Lecturer in Physiology in the Medical School at Makerere University College, Uganda, East Africa.

ELENA OTTOLENGHI NIGHTINGALE, Ph.D. 1961, recently Instructor in the New York University College of Medicine, has been appointed Assistant Professor in the Department of Microbiology of the Cornell University Medical College.

PETER J. GOMATOS, Ph.D. 1963, has just returned from the Institute of Virology in Glasgow, Scotland to his position as Associate Member and Chief of the Division of Virology at Sloan-Kettering Institute. Dr. Gomatos is also Associate Professor at Cornell University Medical College.

C. PETER WOLK, Ph.D. 1964, has left his position as Post Doctoral Research Fellow in Biology at California Institute of Technology to become Assistant Professor of Botany and Plant Pathology in the Michigan State University, at East Lansing, where he will be associated with the Atomic Energy Commission Research Laboratory.



■ President Detlev Bronk has been re-appointed a Member of the Board of Directors of the New York State Science and Technology Foundation for a term of seven years and designated Vice Chairman of the Board.

■ Members of The Rockefeller University who attended the Second International Conference on Pro-

tozoology held in London this summer included Professor William Trager who, in addition to presenting an invited paper on the cultivation of intracellular protozoa, presided at the session on morphogenesis and was elected an honorary member of the Society of Protozoologists. Dr. Maria A. Rudzinska also presented an invited paper, "Feeding in *Tokophrya infusum*;" an electron microscope study," at the plenary session on cytology, and Larry P. Simpson spoke on "The kinetoplast and transformation in *Leishmania*" at Dr. Trager's session.

■ The Wilhelmine E. Key Lecture, delivered by Rollin D. Hotchkiss to the American Institute of Biological Sciences in August, was the subject of widespread editorial comment. Dr. Hotchkiss, speaking at the University of Illinois, stated: "We have all the raw materials now to begin to contemplate making genetic changes in humans." Dr. Hotchkiss, urging his colleagues to "go rather slow," likened the situation to the sudden thrusting of the atomic bomb upon a world not ready for it, unaware of the potential dangers. Among those in public agreement with Professor Hotchkiss is Philip H. Abelson, editor of *Science*. In a July editorial, Dr. Abelson commented on a paper in a similar vein which Professor Hotchkiss had contributed to the symposium on *The Control of Human Heredity and Evolution*. Dr. Abelson stated: "I agree. Geneticists will create new knowledge and will have high ideals for its proper application. In practice, power to apply that knowledge, as was the case in atomic energy, will come to rest in other hands."

■ Dr. Francisco J. Ayala, Research Associate with Professor Th. Dobzhansky, participated in the Fordham Interscience Conference of 1965 held at Sterling Forest from June 21 through June 25. The theme of the Conference was "Twentieth Century Images of Man," and the purpose of the meeting was to bring together a limited number of scholars from various fields for intensive discussion. Father Ayala's contribution was "Biological Evolution in Man." Among the thirteen other participants were philosophers Ernest Nagel of Columbia and Paul Weiss from Yale; physicist Jesse L. Greenstein, California Institute of Technology; psychologist C. H. Graham of Columbia; and biologist Bentley Glass, the newly appointed academic vice president at Stony Brook.

J. J. THOMSON

ON EDUCATION AND RESEARCH

ON AUGUST 30th many scientists throughout the world recalled that it was the twenty-fifth anniversary of the death of an immortal pioneer of modern science: J. J. Thomson. During fifty-six years the discoverer of the electron had been Cavendish Professor of Physics and Master of Trinity College in Cambridge University, and President of The Royal Society.

In a recent book, Sir George Thomson reveals some of his father's basic motives and convictions on education, research, and science:

"J. J. believed that some teaching was a positive advantage to a man's research:

There is no better way of getting a good grasp of your subject, or one more likely to start more ideas for research, than teaching it or lecturing about it, especially if your hearers know very little about it, and it is all to the good if they are rather stupid. You have then to keep looking at your subject from different angles until you find the one which gives the simplest outline, and this may give you new views about it and lead to further investigations. I believe, too, that new ideas come more freely if the mind does not dwell too long on one subject without interruption, but when the thread of one's thoughts is broken from time to time. It is, I think, a general experience that new ideas about a subject generally come when one is not thinking about it at the time, though one must have thought about it a good deal before. It is remarkable that when ideas come in this way they carry conviction with them, and depose without a struggle ideas which previously had seemed not unsatisfactory. The psychology of the incidence of ideas must be a very interesting subject....

"He believed strongly in the educational value of research:

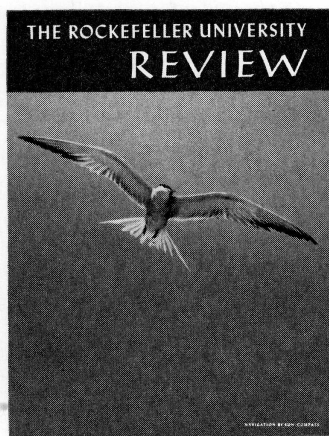
In my opinion research has great educational value and can be made a good test of a man's mental power. I have often observed very striking mental development in students after they have spent a year or two on research: they gain independence of thought, maturity of judgment, increased critical power and self-reliance, in fact

they are carried from mental adolescence to manhood. It is essential, however, that when using the dissertation as a test of mental power, other things should be taken into account besides the scientific importance of the results it contains. This may be due to his teacher having unexpectedly interesting results, and to having helped him out of his difficulties almost as soon as he got into them. In such a case the dissertation may not prove more than that the candidate is industrious and a careful experimenter; it does not prove that he is capable of making discoveries without guidance. I think when once the research has been started, the student should be encouraged to try to overcome his difficulties by his own efforts, and that the assistance given by the teacher should not be more than is necessary to keep him from being disheartened by failure, and to prevent the work getting on lines which cannot lead to success....

"I once asked him if he thought that the ultimate object of physicists would ever be reached, namely to find one all-embracing theory which would explain everything except for the inevitable difficulty of working out its application to complicated cases:

A great discovery is not a terminus, but an avenue leading to regions hitherto unknown. We climb to the top of the peak, and find that it reveals to us another higher than any we have yet seen and so it goes on. The additions to our knowledge of physics made in a generation do not get smaller or less fundamental or less revolutionary as one generation succeeds another. The sum of our knowledge is not like what mathematicians call a convergent series, where each new addition is less important than the one which went before, and where the study of a few terms may give the general properties of the whole. Physics corresponds rather to the other type of series called divergent, where the terms which are added one after another do not get smaller and smaller, and where the conclusions we draw from the few terms we know cannot be trusted to be those we should draw if further knowledge were at our disposal."

J. J. Thomson and the Cavendish Laboratory in his Day, by George Paget Thomson. New York: Doubleday & Company, Inc., 1965.



THE COVER shows the common tern, which “has the ability to select a particular compass direction [using the sun] and, presumably, to fly in that direction if free to do so” — a form of navigation less sophisticated than the goal-directed orientation of homing pigeons and Manx shearwaters, or the remarkable feats of the “North Star Mallards” mentioned on page eight. Photograph by Walter Dawn.

ACKNOWLEDGMENTS: Page 1 “Celestial Navigation” from *Bird Migration* by Donald R. Griffin, copyright © 1964 by Educational Services Incorporated. Reprinted with the kind permission of Doubleday & Company, Inc., Heinemann Ltd., and the author. Photograph by Gordon S. Smith from National Audubon Society. Page 5 photograph by Joe Van Wormer from National Audubon Society. Page 11 photographs, Dr. Griffin courtesy of Harvard University News Office, Dr. Rota by The Rockefeller University Illustration Service. Page 13 photograph by The Rockefeller University Illustration Service. Page 14 photograph courtesy of Roman Vishniac. Page 16 drawing courtesy of The “Shell” Transport and Trading Company, Limited, London, adapted from *The Scallop* (ed. Ian Cox), 1957, page 29. Page 17 photograph by The Rockefeller University Illustration Service; shells courtesy of Floyd Ratliff. Page 18 drawing from fig. 1, H. K. Hartline, *J. Cell. Comp. Physiol.*, 11:466, courtesy of The Wistar Institute Press. Page 19 drawing courtesy of Academic Press, adapted from *The Structure of the Eye* (ed. George K. Smelser), 1961, page 7. Page 20 electron micrograph courtesy of William H. Miller. Photograph of Founder’s Hall by Heka. Page 23 photographs by The Rockefeller University Illustration Service.