THE MANOMETRIC APPARATUS OF FISHES.

NATURE'S MECHANICAL ADAPTATIONS.

BY DR. OTTO THILO.

THE swim bladders of some fishes are furnished with very singular appendages, essentially similar in construction to the manometers or gages which indicate the pressure of steam in boilers. These contrivances are found only in species in which the swim

I have found liquid gages attached to the swim bladders of herrings. A simple gage of this type, which is used in domestic water-heating apparatus, is illus-

upon the diaphragm, which is forced outward, and thus the pressure is transmitted to the liquid which fills the forked tube.

When we study the habits of the herring we find that a pressure gage attached to its swim bladder is a very necessary organ. The walls of the bladder are quite thin and are frequently subjected to very great changes in pressure, for the quantity of air imprisoned in the bladder varies exceedingly. In freshly caught herring the swim bladder is always found nearly empty, and it can be inflated to an astonishing extent

FIG. 1.—DIAGRAM OF KITCHEN BOILER WITH STANDPIPE S.

bladder is filled with air at high pressure which is subject to great and sudden variations when the fish dives or rises to the surface, so that the distended bladder would be in danger of rupture if it were not provided with valves. The proper moment for opening

FIG. 2.—MANOMETER OF HERRING, PARTLY OPENED. (3 TIMES NATURAL SIZE.)

these valves is indicated to the animal by the natural manometers which establish a connection between the front of the swim bladder and the brain, and which, therefore, resemble steam gages in function as well as in form.

FIG. 2A.—SWIM BLADDER OF HERRING.
L. Manometer. G. Diaphragm. L G. Air inlet. V. Valve.

Steam gages are of two general types, of which one employs a standpipe filled with a liquid and the other makes use of the elasticity of thin metal plates. Both types are represented in the manometers of fishes.

FIGS. 3A AND 3B.—FLEXIBLE PLATE MANOMETER OR STEAM GAGE.

H. Lever. P. Plate. S. Steam pipe. In A the plate is horizontal and the pointer indicates a pressure of 0 atmospheres. In B the plate is convex and the pointer indicates a pressure of 10 atmospheres.

trated by Fig. 1. The steam pressure in the boiler is indicated by the height of the column of water in the tube above the water level in the communicating boiler. Gages of this type are used only for low pressures, of one-half atmosphere or less. Now, the swim bladder of the herring and its near relatives terminates, in front, in two narrow tubes arranged like the prongs of a fork (Figs. 2 and 2a). Each tube is about

FIG. 4.—ROTARY LINK.
A. Axis. B. Band.

1/12 inch in diameter just above the junction. Beyond this point it narrows, penetrates by a lateral orifice into the skull, and there expands. The tubes are lined with epithelium and are filled with liquid. Any change in the pressure in the swim bladder is thus communicated to the brain. The cavity of the swim bladder is separated from that of the forked tube by a thin flexible diaphragm at G (Fig. 2a). The existence of this diaphragm is proved by the fact that if the forked end of the bladder is cut off immediately above G, the bladder can be inflated and will remain

FIG. 5.—MANOMETER OF CARP, SHOWING SWIM BLADDERS COLLAPSED AND LIDS OPENED.

F. Aperture in back of skull. R. Spinal cord. D. Lid. S. Link. H. Lever. B. Band. (Manometer natural size, bladders and outline of body greatly reduced.)

inflated for weeks. I have also succeeded in detecting the diaphragm by the examination of sections under the microscope. Now, when the swim bladder is fully inflated the pressure of the inclosed air acts directly

FIG. 6.—MANOMETER OF CARP, SHOWING SWIM BLADDERS DISTENDED AND LIDS CLOSED.

by forcing in air through the air passage L G (Fig. 2a). The rapid evacuation of the distended bladder can be brought about by the fish in the following manner:

The bladder is connected with the anus by a passage furnished with a clack valve, V, which can be opened instantly when the gage indicates an excess of pressure in the swim bladder. The herring dives to great depths, and as a difference of 34 feet in depth corresponds to a difference of one atmosphere in pressure the swim bladder would be in danger of rupture if it were not provided with some such safety appliance.

Our most reliable steam gages, barometers, and manometers are constructed upon the same principle—that is, they are tubes filled with liquid—and they serve as standards of comparison for the elastic plate

FIG. 7.—MANOMETER OF MUD FISH.
(3 times natural size.) R. Spinal cord. K. Bony envelope of swim bladder. F. Aperture in back of skull. D. Lid. H. Lever.

and dial manometers, like the steam gage shown in Fig. 3A. This consists of a metal box which communicates with the boiler through the pipe S and is closed above by a thin corrugated metal plate P. A lever H presses on the center of this plate and communicates its movement to the pointer on the dial. When the pressure in the boiler increases, the metal plate is forced upward (Fig. 3B) and the pointer indicates the excess of pressure above that of the atmosphere.

The mud fish, the carp, and some other fishes possess manometers constructed on this principle. Fig. 7

shows the peculiar swim bladder of the mud fish, surrounded by a bony envelope, a part of which is removed to show the interior. To the membranous swim bladder within are attached two jointed levers which turn on fulcrums in the vertebræ. The anterior end of each lever is connected by an elastic band with the hinged lid of a little hole in the spine. When the swim bladder is distended, the posterior ends of the levers are forced outward. (See also Figs. 5 and 6.)

Hence, the anterior ends of the levers are carried inward and the lids of the holes in the spine are closed, exerting pressure on the fluid of the spinal cord and brain, and thus indicating the pressure in the swim bladder. Conversely, the evacuation and contraction of the bladder turn the levers in the opposite direction, raise the lids, and relieve the pressure on the brain. That this pressure may be great is indicated by the existence of a sort of safety valve in the skull. In the back of the skull are two large apertures (F, Figs. 5 and 7) closed by a thin membrane which yields when great pressure is suddenly applied to the brain by the closure of the small openings in the spine.

In the carp (Figs. 5 and 6) a rotary guide link of bone (Fig. 4) is interposed between the lever and the lid. This guide is not found in fishes like the mud fish, shad, and electric eel, in which the swim bladder

is firmly attached to the ribs and covered by a stout cartilaginous or bony envelope. The swim bladder of the carp is less rigidly attached, and consequently the levers are subject to displacements at right angles to their plane, which would impair the accuracy of the manometer. This source of error is removed by the interposition of the guide link, which has a remarkably long axis of rotation. Hence, its plane of rotation is little affected by lateral deviations of the lever, and these have no appreciable effect on the movements of the lid. The axes of the lid and the lever are nearly as long as the axis of the guide link.

In the mud fish (Fig. 7), on the contrary, the lever has no axis, but turns about a point pressed against the spine. The long axis and the guide link are not needed because the posterior end of the lever moves in a slit in the bony envelope of the swim bladder, and the whole lever is closely surrounded by masses of bone, so that it cannot deviate from its normal plane of rotation. Between these two extreme forms, represented by the carp and the mud fish, a great variety of intermediate forms is found. The pressure or absence of the guide and the peculiarities of the levers are dependent upon the construction of the swim bladder, which may consist only of a tough membrane or may be partly or entirely surrounded by bone. Swim bladders of all three of these types are found in the

single family which includes the shad. The whole manometric apparatus is so small that a magnifying glass must be used in dissecting it and studying its movements, which are easily understood when they are compared with those of steam gages.

It is evident that this comparison did not occur to my predecessors in this field and that they did not thoroughly investigate the motions of the little bones. These bones were first described in 1820 by Emil Weber, who likened them to the small bones in the ear and gave them the same names—hammer, anvil, and stirrup. Hence, he assumed that the swim bladders of the carp and some other fishes served, in a measure, as organs of hearing. This view was not generally adopted. Gegenbaur, and also Bridge and Haddon, after minute study of the subject, asserted that the so-called Weber's bones had nothing to do with hearing, and that they were, for the time being, inexplicable. They have since been regarded as one of the unsolved riddles of science.

If the posterior swim bladder of a carp is squeezed by the hand, thus increasing the pressure in the anterior bladder, the movement of the levers and the closure of the little lids can be observed with the aid of a lens, and when the skull is opened the fluid contents of the brain can be seen to move in response to pressure applied to the swim bladder.—Umschau.

UNUSUAL AGENTS OF POLLINATION. SOME CURIOUS DEVICES OF NATURE.

BY G. CLARKE NUTTALL, B.SC.

THE cross-fertilization of flowers is commonly said to be brought about either by the wind, as in the pines and the hazels, or by insects, as in lilies, jessamine, and orchids. And among insects, the bees, the moths, and the various kinds of flies are those which gain all the credit, in the popular mind, of being beneficial flower visitors. Though this assumption is justified to a great extent, inasmuch as these two agents account for the large majority of cross-fertilizations effected in the flower world, yet there is an important minority of plants which depend on outside agents other than these to give that magic touch which alone can call posterity into being, and the consideration of these rarer agents of pollination is one which brings forward various points of interest in the interaction between the plant and animal worlds.

For instance, the fact that certain plants rely for the fertilization of their flowers upon bats has only been recognized within the last few years, and our knowledge upon this point is certainly not yet fully exploited. In the Royal Botanic Gardens at Trinidad the work of bats in this respect has, however, come under direct observation. A certain tree known as *Bauhinia megalandra*, which grows to the height of about thirty feet, produces in January each year long, white flowers which first appear in the later part of the afternoon and gleam out in their full glory in the dusk. About half-past five, when the dusk begins to deepen into darkness, the bats come out of their day hiding-places and fly swiftly hither and thither. The white gleaming *Bauhinia* tree specially attracts them, and they quickly pounce on the flowers one after another to the great injury of their beauty. For a bat, when it settles on a flower, secures itself by seizing on the white petals whose delicate fabric cannot withstand the rough onslaught, so fragment after fragment flutters to the ground as the bat struggles for foothold. The stamens, too, show traces of rough usage, and are sometimes torn right away and follow the petal fragments, but the stigmas in the center of the flower remain for the most part unharmed. One would naturally imagine that the bats found nectar in these flowers as their visits are so eager, but a close examination shows that the flowers contain in themselves no honey or anything else of that nature of value to the bats, but doubtless they harbor many small insects, and so the bats are attracted, for they find a generous meal in the depths of the flower with very little expenditure of energy.

A Wallaba tree (*Eperua flacata*) growing in the same gardens is also visited largely by what were first taken in the dusk to be big moths, but a more minute inspection showed that these "moths" were really little bats of a variety that has the same kind of brush-like tongue that a humming bird has, and whose name, *Glossonycteris geoffroyi* gray, does not accord with their size. These little bats flit about and act precisely after the manner of moths. In both the Wallaba and the *Bauhinia* it is evident, from subsequent events, that the bats are the direct agents that bring about the cross-fertilization of the flowers, and the transference of pollen is wholly effected during their visits.

Another plant that appears to be fertilized by bats is a Java creeper—by name *Freycinia*—which climbs

to the very top of trees and produces pale rose-colored flowers, some male and some female, among long, dark green leaves. Now a certain well-known bat, the Kalaya, or Flying Fox, particularly affects this creeper, for it tears out the three inner petal structures and devours the succulent tissue with avidity. But this wanton destruction by the bat is amply made up to the flower by the fact that, as it eats the petals of the male flower, its head becomes covered with pollen from the stamens; and while it munches those of the female its head perforce rubs some of its golden burden on to the stigma and so cross-fertilization is insured, and, though the flower loses its petals, it gains posterity.

We know, at present, of no cases of pollination by bats in the flora of Europe.

Birds, too, must be classed among the rarer but undoubted agents of pollination. In Europe, perhaps, again, no authentic cases of regular pollination by birds are known, but in many other parts of the world—the Tropics, South Africa, Philippine Islands, New Zealand, Madagascar, etc., birds play a definite and prominent part in this work. Fritz Muller, whose researches into the pollination of plants are classical, says: "Humming birds, which constitute one of the most important groups of pollinators, are on the wing in Brazil throughout the year. Their activity in visiting flowers is far greater than would appear from accounts known to me. I could almost believe that the list of flowers not visited by them would be considerably smaller than a list of those that are visited" (i. e., of Brazilian flowers). One reason why they have not received all the credit due to them as pollinators is because some of their species are so remarkably like a certain hawk moth—known as the humming bird hawk moth—that frequently they have not been distinguished apart by naturalists. Bates, in "The Naturalist on the River Amazon," tells how he was completely deceived on various occasions, and once actually shot a humming bird hawk moth for the bird itself.

The tropical Abutilons are flowers that are almost entirely fertilized through the agency of humming birds. Fritz Muller, writing from Brazil, says: "A large and beautiful humming bird, the black breast of which shines like a glowing coal whenever the bird is in any way excited, has, with his inconspicuous wife, made himself almost completely master of the Abutilons in my garden, and drives away all other species. All flowers that are not under cover are pollinated by him."

The climber *Marcgravia* (a Nicaraguan plant) carries aloft pendulous flowers which hang in circles, a dozen or more together, from one stalk. Below the flowers sway numerous nectaries of pitcher form which hold large quantities of nectar. This attracts many insects, and they in their turn are sought by humming birds, who, in picking them out of the pitchers, rub their backs upon the drooping stamens and transfer the pollen from one flower to another.

In North America not only are many native flowers pollinated by humming birds, but also various species of European plants, which, in their own country, have their pollination performed by insects with long probosces; such plants, for instance, as the evening primrose, the red clover, and the figwort being visited and pollinated by these birds.

The banana is another plant that has this service frequently performed for it by birds. Indeed, its pollen is particularly adapted for this method of transmission, as the grains are bound together in numbers by threads, and in Natal, birds of the *Cinnyridæ* species may often be seen in the banana groves carrying it about on their beaks. On the other hand, the bananas of Mauritius do not appear to be frequented by birds at all, and there the transference of the pollen is made by insects.

Though small birds, such as humming birds and honey-suckers, form the large majority of bird pollinators, yet in some cases much larger birds fulfill this office. For instance, the large flowers of *Carolinæa* are far too big for little birds to negotiate, so they look to woodpeckers to be their pollen carriers, and these birds, no doubt, search both for honey and for insects in the recesses of the flowers.

In one curious case succulent petals are the bait held out to birds, just as they are to bats in the *Bauhinia*. The flower of a certain Brazilian tree known as *Feijoa*—a myrtle—is deep red and particularly striking. As it matures, the red petals, which are then fleshy and sweet, roll up and disclose a shining white inner surface so that they form four little white rolls, which have been compared to omelettes. Anyway they are a *bonne bouche* to various birds who search them out and rapidly devour them, and during the meal successfully cover themselves with pollen. This pollen they carry away, and while feeding on the next similar flower rub some of it off on the waiting stigma, and meanwhile are again sprinkled with a fresh supply. But with birds, as with bats, there yet remains much to be added to our knowledge of them as pollinators.

One of the most curious and certainly one of the rarest pollinators as a class are slugs and snails, yet they, too, must be classed among the direct agents of pollination. The plants that come under their influence—malacophilous plants—have usually small flowers set closely together, such as we find in the family of the Compositæ, or in the Aroids where male and female flowers are massed within a sheathing spathe, and snails as they wend their slimy way across them drag the pollen grains along and distribute them. A certain Italian, Delphino, was the first to call attention, a number of years ago, to this possibility, for he observed that in various plants under his observation, such as *Rohdea japonica*, *Alocasia odorata*, *Anthuriums*, and others, only those which were touched by snails set seed, the others did not. Unlike birds and bats, snails and slugs act as pollinators in this country. For instance, the ox-eyed daisy is frequently visited by a small snail in wet weather when flying insects are not in evidence. The snail feeds upon the white ray petals, and as it crawls around it very effectually performs the insect's work of pollination. The same thing has been observed in the golden saxifrage, and also in the common duckweed. Hence, even if we consider that snails are "only the occasional and not the exclusive agents of pollination," these facts prove, as Ludwig observes, "that plants which lack the customary agents of pollination when continuous rains occur during the flowering season, and would otherwise produce no fruit, may find in slugs effective substitutes for insects which are only active in dry weather."—Knowledge and Scientific News.