File-like vein or nervure of cricket's wing, greatly magnified.

The muscular sound-producing "drum" of a male cicada.

Stridulating ridge on hind leg of a male grasshopper.

The "Ears" and Sound-Producing Mechanisms of Insects

Curious Substitutes for Vocal Organs

By Harold Bastin

WHILE it is a fact that insects have no vocal organs, in the strict sense of the term, many species are nevertheless capable of producing loud sounds. Probably the most noisy of all insects are the cicadas, commonly called "locusts." Their resounding hum may be heard each year during the height of summer; but to appreciate fully the sound-producing mechanisms of cicadas one must needs visit the tropics. In Brazil, for example, a very large species gives a sort of scream that is astonishingly loud.

If we examine the under surface of a male cicada we shall find two plates which spring from the metathorax (i. e., the hindmost of the three thoracic segments) and overlap the abdomen to a greater or less extent. Beneath each plate, or operculum, there is a cavity which contains the sound-producing mechanism. The most noticeable organ is a membrane, or drum, to which a muscle is attached. It is to the rapid vibration of this drum that the so-called "song" of the cicada is primarily due, although other membranes within the cavity are probably also agitated, while the whole skeleton of the insect, including the opercula, presumably helps to increase or modify the sound.

Apart from the cicadas most other insects that produce sounds do so by virtue of a "stridulating apparatus." In other words, one part of the body is rubbed against another part, much as the bow is rubbed across the strings of a violin. For example, the chirping of short-horned grasshoppers, or *Locustidae* (the *Acridiidae* of many authors) is produced by rubbing the thigh or femur of the hind leg against the fore wing, or tegmen. On the inner side of each hind femur there is a ridge surmounted by a row of minute tubercles—really modified hairs. These are rubbed against a prominent vein on the tegmen, and a shrill sound is produced. So far as is known, only the smaller kinds of grasshoppers possess this musical apparatus; the larger species of the family are apparently quite silent.

It is scarcely necessary to remind the reader that the crickets and long-horned grasshoppers (including the well-known "katydids") are extremely tuneful insects. In both these families the sound is due to the structure and movement of the tegmina, unassisted by the legs. There is, however, a difference in detail. In crickets (*Gryllidae*) the tegmina of the males are nearly alike, the right one being commonly, though not invariably, uppermost. Each tegmen has a file-like vein, or nervure, on its lower aspect. With the file, the insect rasps a prominent ridge on the upper aspect of the tegmen which lies below. In long-horned grasshoppers (*Phasgonuridae*), however, only the left tegmen (which is invariably uppermost when the insect is at rest) is furnished with a file-like vein. It should be added that in both these families the tegmina are often remarkably modified, doubtless with the object of increasing the sound volume.

With respect to the origin of sound-producing mechanisms among insects most naturalists argue that they are the outcome of long-continued sexual selection. It is believed that the "song" is a kind of courtship accomplishment, calculated to excite amorous propensities in members of the opposite sex. The fact that, with few exceptions, only male insects are gifted with powers of "self-expression" is significant, and accords well with what we know concerning the habits of birds; nor are direct observations lacking to complete the weight of evidence. Harrington, for example, writing of a species of cricket, says: "While the male is

energetically shuffling together its wings, raised almost vertically, the female may be seen standing just behind him, and with her head applied to the base of the wings, and getting the benefit of every note produced."

The fact that many insects are able to produce sounds leads us, not unnaturally, to conclude that they are able also to hear. But in general it has proved very difficult to demonstrate in these creatures any structures that can, with certainty, be regarded as "ears"—that is to say, as specialized auditory organs. For example, among cicadas—a family which admittedly includes the most noisy of all insects—science has completely failed in her efforts to discover any organ of the kind. This has given rise to no little speculation, and more than one ambiguous theory has been advanced. Certain

naturalists, among them Girard, are of opinion that cicadas do not hear in our sense of the word, but "feel rhythmical vibrations." One is inclined to regard this as a distinction without a difference! Again, Swinton claims that one of the membranes connected with the sound-producing mechanism is auditory in function; but if this is so, as Dr. David Sharp remarks, "the male would be deafened by his own noise, while the females, not possessing the organ, should not hear the song."

It is a fact that the sense mechanism of an insect includes vast numbers of minute "nerve endings" which, through microscopic pores in the chitinous exoskeleton, communicate with the centers of perception. The precise functions of these nerve endings, even when their character has received careful investigation, is usually difficult to determine. But we are not without evidence to justify the assumption that while it is often tactile or olfactory it is sometimes auditory. We are free to believe, in fine, that cicadas—and possibly insects of many other kinds—are gifted with a generalized faculty for receiving sound vibrations; and that in this sense they may be said to "hear," notwithstanding the fact that specialized auditory organs are absent.

With certain insects—notably the grasshoppers, crickets, and their allies—the case is quite different. Here we find definite ear-like organs, admirably adapted for the reception and transmission of sound waves. Briefly, there is a tympanum, or "drum," with a complex arrangement of nerve, muscles, and tracheal tubes. These organs are paired, but their external openings are not in the head—as is the case with those of the ears of vertebrate animals. The "ears" of a meadow grasshopper, for example, are to be found in the first abdominal segment, the openings being immediately above the articulations of the hind legs. Similar auditory organs have their place in the fore shins, or tibiae, of crickets, as well as of long-horned or tree-frequenting grasshoppers; while Folsom states that structures, presumably analogous in function, are found on the tibiae of ants, termites, and stone-flies (*Perlidae*); on the femora (thighs) of lice (*Pediculidae*); and on the tarsi (feet) of some beetles (*Coleoptera*).

Many species of flies (*Diptera*) possess organs whose general structure resembles that which has been described above. In the blow-fly, for example, Lowne describes a circular "drum" in connection with air-spaces and nerve-endings—the whole being situated in a cavity beneath the base of the wing; while above this drum, under the scutellum, is a supra-tympanal organ, like that of a long-horned grasshopper.

According to Child, a very beautiful "ear" is found in the second antennal joint of many insects—the organ being most perfectly developed in the males of certain mosquitoes and midges. The joint in question is greatly swollen and cup-shaped; and although in the females of these insects a similar structure is present, it is far less perfectly developed. From this it is natural to assume that the male mosquito relies chiefly upon his sense of hearing when seeking a mate; and, indeed, it has been shown that the minute lateral hairs on the shafts of the insect's antennae vibrate to the note produced by the female's humming flight, and that they do so most strongly when the sound waves strike them at right angles—that is to say, when the tips of the antennae point in the direction from which the sound comes. The male, therefore, must be able to estimate very exactly the whereabouts of the female.

The ears of insects.

1. Young grasshopper with wing rudiments pulled back to show the "ear." 2. In the long-horned grasshoppers the external opening of the ear is in the shin. 3. Male cicada at rest. The plate-like cover, or operculum, of its right sound-producing organ is plainly visible. Swinton claims that one of the membranes beneath the operculum is auditory in function.